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Whitebark Pine Communities in the Olympic Mountains: Microclimates, Physical and Competitive Environments, and Effects of White Pine Blister Rust

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Cover photo: A large, dead whitebark pine, killed by white pine blister rust, is surrounded by younger whitebark pine and shore pines, and a young and vigorous subalpine fir tree is growing in front of it. This is a typical scene on south-erly exposures in the study area. Most of the older and larger whitebark pines succumbed to white pine blister rust long ago, and their progeny generally succumb to the disease before reaching large sizes. Shade-tolerant subalpine fir trees, unencumbered by serious disease, are gradually increasing at the expense of whitebark pine. Photo by David H. Peter.

Abstract

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We examined the relation of an Olympic Mountain (Washington, U.S.A.) whitebark pine (*Pinus albicaulis*) population to its physical and biological environments. We analyzed temperature, light, soil moisture, foliar nutrients, tree size and age, white pine blister rust (*Cronartium ribicola*), plant species canopy cover, slope stability, and snow cover data to assess the dynamic nature of the whitebark pine population and plant communities since the end of the Little Ice Age around 1850 Common Era. We found that high summer temperatures, drought, and slope stability were important in controlling tree growth on south-facing slopes. Soil temperatures low enough to limit tree root growth existed only in microsites; and the tree line, as defined by cold, root growth-limiting soil temperature, was mostly higher in elevation than our study area, even though much of the area was dominated by tundra. We found evidence that there had been an increase in the elevation of vegetation zones following the Little Ice Age when the tree line likely fell within the study zone. Whitebark pine suffered high mortality as a result of white pine blister rust. Shade-tolerant subalpine fir (*Abies lasiocarpa*) is increasing in density, and the combination of its competition with whitebark pine and blister rust mortality places the long-term survival of the whitebark pine in question. Although there was little evidence of past fire, the current trend is toward increasing fuels and greater wildfire risk.

KEYWORDS:

Alpine
Alpine tundra
Climate change
Cronartium ribicola
Lapse rates
Little Ice Age
Olympic Mountains
Pinus albicaulis
Soil temperature
Solifluction
Subalpine
Tree line

Summary

We studied Olympic Mountain whitebark pine (*Pinus albicaulis*) communities in Washington State, U.S.A., relative to temperature, moisture, soil instability, climate change, and white pine blister rust (*Cronartium ribicola*). We compiled a 3-year air, soil surface, and 20-cm-deep soil temperature record over a dissected west-facing ridge from 1420- to 1893-m elevation. Plot mean annual air temperatures ranged from 1.1 to 4.1 °C, and frost-free intervals ranged from 48 to 132 days. Air temperature lapse rates (i.e., the relationship between air temperature and elevation) varied by canopy cover, season, and time of day, but overall, temperature decreased 4.94 °C per kilometer of elevation gain. We recorded plant community information, including tree growth, age, and species canopy cover, and we documented the effects of white pine blister rust on whitebark pine.

Plant species richness was highest on warm, dry, southwest-facing slopes. It correlated negatively with overstory canopy closure and positively with soil drought, temperature, and the standard deviation of ground-level light that indicated a mix of canopy gaps and shade. Subalpine fir (*Abies lasiocarpa*) grew densely on cool aspects where its shade maintained cold soil and low species diversity. Subalpine fir dominated all aspects and elevations except mid-elevation, southwest-facing slopes where whitebark pine dominated, and lower, southwestern aspects where Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), whitebark pine, and shore (beach) pine (*Pinus contorta* var. *contorta*) codominated. Subalpine fir was more vigorous on cool aspects but had more seedlings than any other species on all aspects. Because of its greater shade tolerance, it may eventually dominate all but the driest microsites.

The soil-temperature-dependent tree line was mostly above our study area, but decreasing tree age with elevation and species with alpine affinities in lower elevation canopy gaps suggested the tree line was lower near the end of the Little Ice Age (around 1850 Common Era). We found little evidence of fire, even at the lowest elevations, so trees were not reinvading former habitat but rather appeared to be invading formerly unsuitable habitats. Douglas-fir trees had many large, lower limbs, indicating that they grew free of inter-tree competition. Low limbs could have carried ground fire into the crown, also suggesting that fire has been absent.

The lowest air temperatures occurred from December through February, with February as the coldest month, but they were broadly distributed over the sample area, suggesting they would not differentially affect our plant communities. Low summer soil temperatures limited forest growth in some areas, but large, open areas, including much whitebark pine habitat, appeared to be due to other limitations, including soil instability, damaging high soil surface temperatures, and soil drought. Our soil moisture data revealed areas of relative drought with few trees and therefore support this argument circumstantially.

Solifluction (i.e., gradual downhill movement of surface soils as a result of freezing and thawing), which was more common on south- and west-facing slopes than on north-facing slopes, limited tree establishment. About 15 to 20 percent of the study area had unstable soils, locally lowering the tree line on south- and west-facing slopes relative to north-facing slopes. Unstable soils appeared to be related to slow, early-winter snow accumulation resulting in freezing and thawing soils. Where snow accumulated faster, soil temperatures hovered near 0 °C.

White pine blister rust was the most important agent of whitebark pine mortality. Although macrotopography controlled the presence of whitebark pine habitat on steep, south-to-west-facing slopes, within that constraint, stand structure controlled near-ground air temperatures, soil surface temperatures, soil temperatures, and subcanopy light, which all correlated positively with the frequency and severity of white pine blister rust infection. White pine blister rust infection frequency was greater where warm nights extended into October, but the warmth of summer was probably more important for fungal growth inside the trees. Thus, lower elevation whitebark pines had the most severe infections as this was where warm summer and fall conditions co-occurred. Alternate host species for white pine blister rust were present on 94 percent of whitebark pine plots. We concluded that the continued presence of whitebark pine in our study area and perhaps more widely on the Olympic Peninsula is in jeopardy because of the combined effects of white pine blister rust and subalpine fir encroachment on whitebark pine habitat. Even in the absence of the disease, the encroachment of subalpine fir would continue, so managing this process will be key to maintaining whitebark pine and its associated diversity in this area.

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Introduction

Much concern has been expressed in recent decades over the fate of whitebark pine (*Pinus albicaulis*) populations due to several factors, including its susceptibility to white pine blister rust, mountain pine beetle infestation, wildfire, and community succession toward late-seral species dominance. These factors play out differently across the range of whitebark pine, with some more important in some areas and with multiple factors combining in others. Whitebark pine is considered endangered in Canada and threatened in the United States. While many studies of whitebark pine have been conducted in the Rocky and the Sierra Nevada Mountains, fewer studies have focused on the maritime populations of the Pacific Northwest.

The object of this study is a small population of whitebark pine scattered throughout higher elevations of the northeastern Olympic Peninsula in Washington State, U.S.A. In this unique maritime rain shadow, whitebark pine has a distinct affinity for the warmest and driest sites within this cold, high-mountain environment. Elsewhere, more extensive whitebark pine populations are found in the Rocky Mountains, from Wyoming, U.S.A., to British Columbia, Canada, and in the rain shadows of the Sierra Nevada, Cascade, and British Columbia Coast Mountains. Whitebark pine is generally considered to be a climax species on cold, dry, windy sites, but it is seral to more shade-tolerant species, such as subalpine fir (*Abies lasiocarpa*), elsewhere (Arno and Weaver 1990).

Physical Environment

Whitebark pine is found in greatest abundance near the alpine tree line where it may be the first and sometimes only arborescent colonizer (Arno and Hoff 1990). In such tree line habitats, plants are energy-limited by summer temperatures or insufficient soil warming that results from short, cool seasons and lingering snowbanks (Albright and Peterson 2013, Graumlich and Brubaker 1986, Körner and Paulsen 2004, Peterson et al. 2002). Subalpine and alpine environments subject plants to harsh environmental conditions, including deep, long-lasting snow, short growing seasons, high winds and associated desiccation, freezing and thawing, low temperatures, poor soil nutrition, and excessively wet or dry soils. These harsh conditions strongly influence plant growth and reproduction (e.g., Billings 1974, Bliss 1956, Canaday and Fonda 1974, Holway and Ward 1965, Johnson and Billings 1962, Kuramoto and Bliss 1970, Loneragan and del Moral 1984). Radiation loads can be high in these high-mountain environments, which also tend to have extremely coarse soils with low water-holding capacity. As whitebark pines become established in these harsh habitats, their growing canopies can ameliorate the radiation load, soil temperature extremes, and wind, such that more sensitive species, including the more shade-tolerant subalpine fir, are able to become established (Callaway 1998, Pyatt et al. 2016, Resler et al. 2014).

Biological Relationships

Whitebark pines provide food and hiding and thermal cover for many birds, mammals, and insects; and in some landscapes, they are the principal provider of these services, making it a keystone species. One of their most important contributions are their large, nutritious seeds. Cones from the whitebark pine do not open when mature, and so they do not self-disperse (Lanner 1982). Instead, they have evolved to depend on the Clark's nutcracker (*Nucifraga columbiana*) for this service (Hutchins and Lanner 1982, Tomback

1982). Although Clark's nutcrackers can forage on seeds from other conifers, they prefer the large, whitebark pine seeds to the near exclusion of all others from August to November (Hutchins and Lanner 1982, Tomback 1982). In Wyoming, individual Clark's nutcrackers were observed to harvest 129,000 seeds—76 percent of which they cached in the soil (Hutchins and Lanner 1982). Some of these seeds were later recached up to 3.2 km away (Hutchins and Lanner 1982). Should they need the seeds over the course of the following year, they can find their way back to each of their caches. However, this need is rarely realized, as they usually cache several times their caloric need, so many seeds are left to germinate and grow into new trees (Tomback 1982). Because Clark's nutcrackers carry seeds at such distances and cache seeds at a depth in the soil that is ideal for germination and establishment, they are effective dispersers for whitebark pine (Tomback 1982). In fact, the Clark's nutcracker is the only effective disperser and establisher, as all other species that forage on whitebark pine seeds consume them as they are harvested, or in the case of Douglas squirrels (*Tamiasciurus douglasii*), cache them in ways not conducive for germination.

Douglas squirrels also harvest and cache large numbers of whitebark pinecones for later seed extraction (Hutchins and Lanner 1982). They effectively compete for seeds with Clark's nutcrackers in forest settings but do not venture into more open settings where Clark's nutcrackers have the whitebark pine seed crop almost to themselves (Hutchins and Lanner 1982). Douglas squirrels cache whitebark pinecones in large middens for later use. These middens feed not only squirrels but are actively sought out by black bears (*Ursus americanus*), which occur in the Olympic Mountains, and grizzly bears (*Ursus arctos horribilis*), which do not occur in the Olympic Mountains but are important consumers of seed caches elsewhere (Hutchins and Lanner 1982, Mattson and Reinhart 1997). Other species observed consuming smaller amounts of seed include chipmunks (*Tamias* spp.), ground squirrels (*Marmotini* spp.), Steller's jays (*Cyanocitta stelleri*), ravens (*Corvus corax*), mountain chickadees (*Poecile gambeli*), and red-breasted nuthatches (*Sitta canadensis*), but none of these species are effective dispersal agents (Hutchins and Lanner 1982).

Disease

Whitebark pine populations are currently challenged in several ways. They suffer heavy mortality from white pine blister rust, a disease caused by the exotic, invasive fungus, *Cronartium ribicola*, that has spread throughout the range of the species (Campbell and Antos 2000, Kendall and Keane 2001, Zeglen 2002). In much of its range, whitebark pine suffers heavy mortality from attacks of mountain pine beetles (*Dendroctonus ponderosae*) (Logan and Powell 2001, Meddens et al. 2012), and it is subject to successional loss of habitat from the more shade-tolerant subalpine fir (Arno 1986, Keane and Arno 1993). Mountain pine beetle attacks and succession to subalpine fir may both be related to a history of fire suppression and a warming climate (Hamann and Wang 2006, Lanner 1996, Logan and Powell 2001, Schwandt 2006). These combined influences have resulted in a general range-wide decline of whitebark pine. Studies of whitebark pine increased as the magnitude of its decline became evident; however, studies of west coast whitebark pine communities have lagged those of interior populations (Carlson et al. 2017, Larson and Kipfmueller 2012).

Because of its keystone value to many wildlife species and its important hydrologic and scenic values, there has been widespread concern over the decline of whitebark pine in the

face of white pine blister rust, bark beetles, and successional loss of habitat. The question has been raised: Could whitebark pinecone production fall to a point where Clark's nutcrackers cease to be interested in this food source and thus stop dispersing seeds (McKinney et al. 2009), resulting in extirpation of the tree? If so, where is that threshold?

Although large epidemics of mountain pine beetle have repeatedly moved up into whitebark pine communities in the Rocky Mountains from extensive lodgepole pine (*Pinus contorta* var. *latifolia*) stands below them, this does not appear to have happened in the Olympic Mountains, perhaps because of the relatively small populations of both whitebark pine and the shore pine variety of lodgepole pine (*Pinus contorta* var. *contorta*). Rochefort (2008) also suggested that the low incidence of mountain pine beetle mortality at Mount Rainier and in North Cascades National Park was due to small populations of these pines. However, white pine blister rust has severely affected the Olympic Mountain whitebark pine population. In 1943, 92 percent of trees were infected (Bedwell and Childs 1943), and infection rates are still high. Shoal and Aubry (2004) found that 21 percent of whitebark pine clumps were infected with blister rust on the Olympic National Forest, and 25 percent of the stems were dead. There is a concern that this small population could shrink to levels that would no longer attract their principal dispersal agent, the Clark's nutcracker, condemning the population to extirpation. Also, continued shrinkage of the population may have negative consequences for this population's genetic diversity.

Climate

Because the climate is not stable in time, vegetation is not stable in space. As recent as the late 1800s, the world's climate was cooler in a period known as the Little Ice Age, which lasted about 600 years. Although not monolithic, it was a time of generally cold and unfavorable climate in the northern hemisphere (D'Arrigo et al. 2005, Henderson et al. 1989, Luckman and Wilson 2005). Since the Little Ice Age ended around 1850 to 1890, the mean annual temperature in western Washington has risen between 0.5 and 1 °C (Abatzoglou et al. 2014, Graumlich and Brubaker 1986, Mote 2003).

Because alpine and subalpine species are physiologically limited by low temperatures and snowpack (Gavin and Brubaker 1999, Hansen-Bristow et al. 1988, Körner and Paulsen 2004), they are particularly sensitive to climate change (Pauli et al. 2003), which causes changes in the distribution of individual species and plant species assemblages (Mitchell et al. 1990, Zolbrod and Peterson 1999). As detectable climate change has already occurred since the end of the Little Ice Age, it is reasonable to expect that vegetation is currently in a state of flux and that some change has already occurred. In fact, since around 1920 and possibly before, subalpine fir and mountain hemlock (*Tsuga mertensiana*) have been invading Pacific Northwest subalpine meadows that were formerly kept free of trees by long-lasting snowbanks (Brink 1959, Fonda and Bliss 1969, Franklin et al. 1971, Miller and Halpern 1998, Rochefort and Peterson 1996, Rochefort et al. 1994, Woodward et al. 1995). The Pacific Northwest climate is expected to continue warming in both summer and winter, resulting in less snowpack and summer precipitation (Miles et al. 2010). By the 2080s, the mean annual temperature is expected to increase by 3 °C (Mote and Salathe 2010), which begs the question of how this will affect whitebark pine communities.

Fire

The relation of whitebark pine to wildfire further complicates its changing footprint on the landscape, especially because the occurrence of wildfire is closely tied to climate change. Also, people have attempted to suppress wildfires on the Olympic Peninsula for about a century and continue to do so except in some protected areas (e.g., wilderness). Whitebark pine tends to fare better than its more shade-tolerant competitors; much of its habitat is more open and fuel-poor because Clark's nutcrackers prefer to cache seeds in open areas, such as recent burns (Arno 2001, Tomback 2001), and because its early growth is more rapid than that of most of its competitors. However, whitebark pine is quite vulnerable to wildfire mortality when growing in areas with sufficient fuels. It has thin bark, and heat can easily damage the cambial layer in stems and branches. Wildfire and climate change also directly or indirectly influence the outcomes associated with blister rust, bark beetle infestations, and subalpine fir succession. Thus, it is important to consider each of the factors causing whitebark pine decline in context with the others. Although fires initiate successions at a single point in time, the trajectory of the succession will be determined by the nature of the fire and the climate. Thus, the fire history of an area is key to understanding the existing community and assessing future potential. Although the present study is not a fire history, we made relevant observations, which combined with published fire histories (Henderson et al. 1989, Pickford et al. 1980, Wendel and Zabowski 2010, Wetzal and Fonda 2000) provided a way for us to evaluate our results in this context.

Focus, Goals, and Scope

Our goal for this project was to examine the successional trajectory of Olympic Mountain whitebark pine communities, as well as the causal mechanisms forcing community succession, and to use our acquired understanding to speculate on the future form that the vegetation of our study area might assume. We begin by describing the current physical environment of the area, with special attention to the current and past climate. We measured air, soil surface, and 20-cm-deep soil (hereafter, soil) temperatures to provide a relative index for differentiating growing conditions among the study plots, such as the duration of the winter snowpack and potential limitations of root growth. This description provides the basis for comparisons with whitebark pine habitats elsewhere and in times past and will provide a baseline for future comparisons with our time. We then describe the autecology of 20 of the most common vascular plant species in our study area, primarily in terms of temperature and soil moisture. We used this to interpret the community ecology within our study area, which we augmented with a description of stand and age structures of the tree component. This led to consideration of the dynamic nature of the community; and perhaps foremost were the effects of white pine blister rust on two prominent species, whitebark pine and western white pine (*Pinus monticola*). Finally, we considered the importance of fire in our study area. These combined descriptions allowed us to evaluate the current condition of the vegetation and of the whitebark pine population and to speculate on how they have changed since the Little Ice Age as well as suggest management methodologies to sustain the population in the future. This is a detailed study of the dynamics of an isolated Olympic Mountain population of whitebark pines and the communities in which they grow. However, we believe that our detailed and integrated descriptions of both the environment and the communities provide useful context for the study of whitebark pine and other subalpine plant communities wherever they are found and suggest fruitful lines for future research.

Methods

Study Area

The study area is in the Buckhorn Wilderness, Olympic National Forest, on the Olympic Peninsula in Washington State (fig. 1). Most of the Olympic National Forest population of whitebark pine is in the Dungeness River watershed. The topography is steep and mountainous, ranging in elevation from about 1000 m in the Dungeness River valley bottom to 2130 m at the summit of Buckhorn Mountain, a distance of 2.7 km. In this area, whitebark pine is found from about 1500-m elevation to nearly the summit of Buckhorn Mountain, from Buckhorn Pass in the north to Constance Pass in the south, and around Goat Lake west of the Dungeness River. In the Olympic National Park, whitebark pine is found in Royal Basin, Grand Valley, and in the headwaters of the Lillian River in the Elwha River watershed. This paper focuses only on the portion of the population in the Dungeness River headwaters in the vicinity of Marmot Pass (fig. 1).

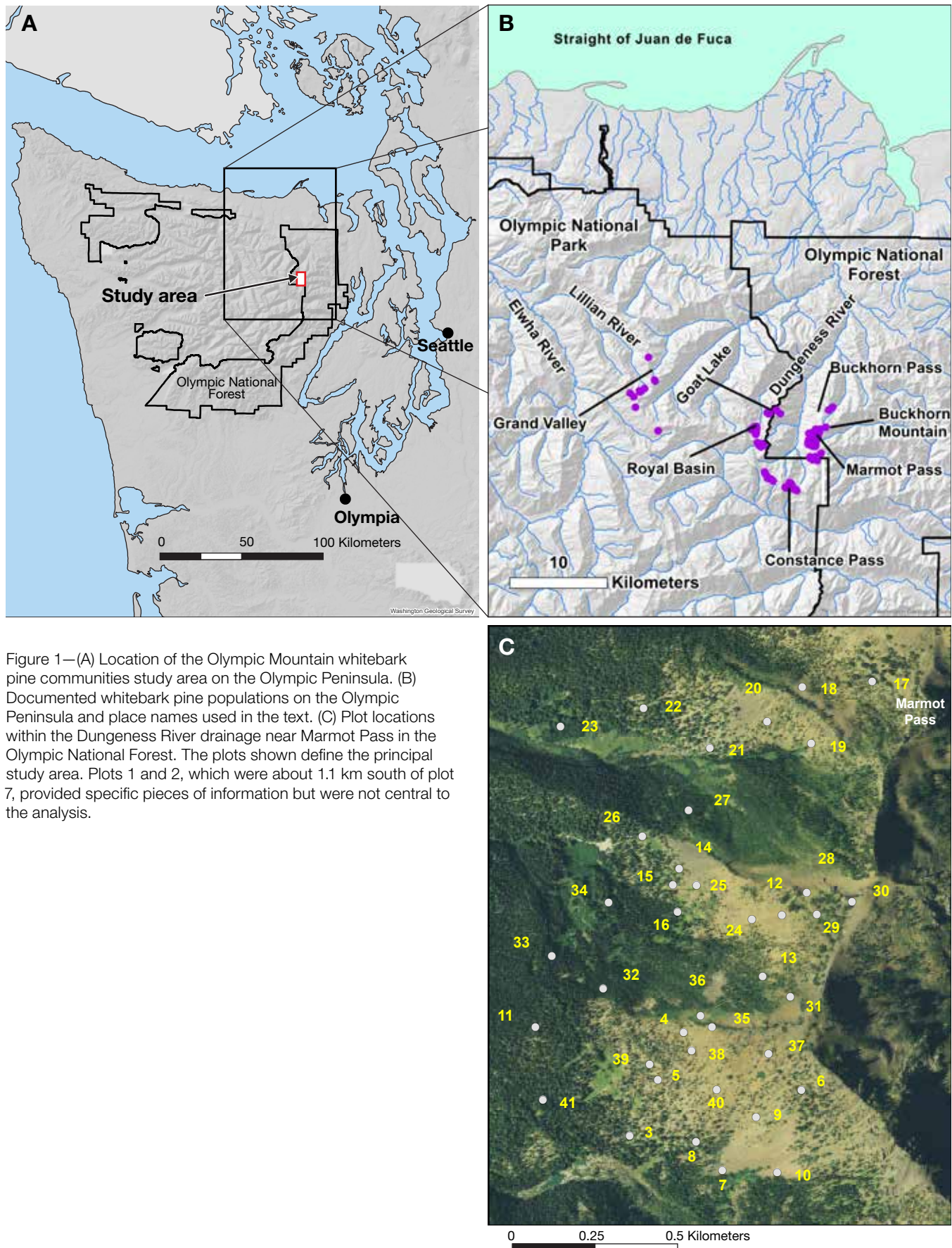
The sampling area was about 1 by 1.5 km, or 150 ha, in size (fig. 1). We also sampled two points (plots 1 and 2) about 1.1 km south of the main study area. The sampling area is entirely on the west side of a major north-south trending mountain axis and extends from the ridgeline to nearly the valley bottom. Because of erosional dissection, it includes northwest-, west-, and southwest-facing slopes but no east-facing slopes. In the general area, there is little whitebark pine on east-facing slopes, and elsewhere it is mainly on west- and south-facing middle to upper slopes and ridgetops.

The bedrock in the higher, eastern parts of the study area is predominantly Eocene marine basalt of the Crescent Formation, which consists of massive and pillow basalts as well as breccia. Lower, more western parts of the study area are in the Blue Mountain unit, which consists of volcanic rich sandstone and argillite (Tabor and Cady 1978). Within the study area, brittle, black-colored argillite predominates. The soils tend to be coarse but of variable depth. The three main soil associations present are (1) rubble land-rock outcrop-Dystrocryepts association, 60 to 100 percent slopes; (2) rock outcrop-Haplocryands association, 10 to 40 percent north-facing slopes; and (3) rock outcrop-Haplocryands-rubble land association, cirque headwalls, 60 to 100 percent slopes (USDA NRCS 2020b).

The Olympic Peninsula has a generally maritime climate with relatively mild, wet winters and cool, dry summers. Prevailing winds are from the southwest, and our study area is in the northeast part of the peninsula in a local rain shadow. The orientation of the mountains produces variations on the maritime theme. The wettest location in the continental United States and the location on the west coast with the lowest annual precipitation outside of southern California are within 65 km of each other on the Olympic Peninsula (Kuramoto and Bliss 1970).

According to the Parameter-elevation Relationships on Independent Slopes Model (PRISM) (PRISM Climate Group 2020), the mean annual temperature ranges from 2 to 4.5 °C in our study area, and the mean annual precipitation varies from 1810 to 2404 mm (decreasing from south to north). This is less than half the precipitation that falls a little over 50 km to the southwest on the first ranges of the Olympic Mountains that lie between our study area and the ocean, and those mountains are only around 1200 m in height.

The measured mean annual precipitation for the Waterhole SNOTEL (USDA NRCS 2020a) weather station, 26 km northwest of our study area, was 1790 mm (fig. 2). SNOTEL, or the Snowpack Telemetry Network, is a system of automated data collection sites in



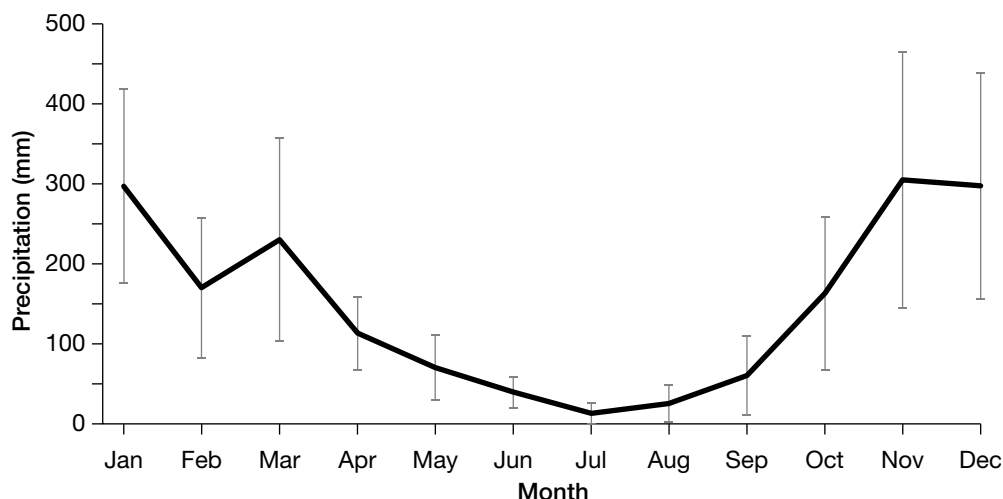


Figure 2—Mean monthly precipitation at the Waterhole SNOTEL weather station site used in the Olympic Mountain whitebark pine communities study for the period of water years October 1999 through September 2020. The error bars are standard deviations.

remote, high-elevation mountain watersheds in the Western United States that the U.S. Department of Agriculture, Natural Resources Conservation Service (USDA NRCS) maintains. Most of the precipitation at the Waterhole SNOTEL weather station falls as snow from mid-November through mid-April, but rain can and does fall in every month of the year. At the Waterhole SNOTEL weather station, 67 percent of the mean annual precipitation from 1981 through 2010 fell during the mid-November through mid-April period.

Plot Establishment

The purpose of the study was to describe vegetation composition, structure, environment, and dynamics of Olympic Mountain whitebark pine communities and to assess the effect of white pine blister rust on whitebark pines and their associated plant communities. In 2007, four vegetation plots were established, and we collected plant community data on a reconnaissance trip to the study area. The purpose of these plots was to provide data for planning purposes. In the end, we incorporated only two of these plots (plots 3 and 4) into our general sample described below.

In ArcMap version 10.5.1 (ESRI 2017), a polygon was drawn to encompass a portion of an area with a known whitebark pine population, and random points were generated within this polygon to demarcate potential plot locations. More points were generated than could be sampled so that we would have flexibility in selecting safe work locations in the field that were accessible on foot, as there were no roads and few trails in this wilderness area. The coordinates for these points were entered into a hand-held Global Positioning System (GPS) device, which was carried in the field where we selected 37 of them for plot locations.

We hiked routes on and off trails, sampling each point that we could reasonably access by using the GPS device to locate the points. A concerted effort was made to cover the entire area of the sample polygon. In one case, a point, which fell on a cliff face, was moved to the closest safe location. In all other cases, we selected the point indicated by the GPS device as the plot center. Each plot center was referenced to surrounding trees or rocks by using distance, azimuth, and photographs for future relocation. Permanent markings are not allowed in U.S. Department of Agriculture (USDA), Forest Service Wilderness Areas.

Thus, forty-one 500- or 1000-m² circular plots were installed between 2007 and 2010 using methods such as the intensive plot methods of the Forest Service Ecology Program (Henderson et al. 1989). Plots 1 through 4 were located and sampled in 2007. Plot 2 documented a single, large krummholz (i.e., stunted, twisted growth form of trees near the alpine tree line) pine tree and was not subsequently remeasured. Plot 1 was in the same area as plot 2 and was not in the main study area. Plots 1 through 3 were 500-m² plots, but plot 4 was 1000 m² in size. After sampling plot 4, we settled on 500 m² as the standard size for all remaining plots. Plots 5 through 16 were located and sampled in 2008. Plots 17 through 41 were located and sampled in 2010. Sampling included percentage of vegetation canopy cover, tree measurements, dead and down wood measurements, and litter depth data (see “Vegetation and Biological Relations” below).

Percentage of canopy cover was based on the vertical projection of the plant onto the ground. A solid (excluding sunflecks) polygon was drawn around the plant’s foliar canopy within the plot. For a given species, crown overlap was ignored, so a single polygon might encompass more than one overlapping individual. Percentage of canopy cover was estimated to the nearest one percent unless the species cover was less than one percent. In that case, estimations were made to fractions of a percent by multiplying the number of individuals seen by the average coverage of an individual. However, the smallest number recorded was set at 0.01 percent.

In subsequent years, we also collected temperature, soil moisture, and other physical site data (see “Physical Environment” below). In 2016, we obtained high-precision GPS measurements for each plot center by using a JAVAD GNSS¹ GPS instrument, which recorded data for the duration we were on the plot (generally at least 30 minutes). Our taxonomic treatment of plant species follows the USDA PLANTS Database (USDA NRCS, n.d.) unless otherwise noted. Appendix 1 is a complete list of the plant species found on our plots (as well as plant species that appear in this report for other reasons) with scientific names, authorities, common names, as well as the USDA PLANTS Database symbols (USDA NRCS, n.d.). Our plant association classification for forested vegetation follows Henderson et al. (1989).

Plant Associations and Communities

Plant associations originated with the idea of plants as environmental indicators and the recognition that different sites support different plant communities with different resource values (Henderson et al. 1989). Plant associations, as used here, are units of potential vegetation that would have similar composition in the climax plant community, assuming that there is sufficient environmental stability for this to occur. Thus, within the area of an association, differences in vegetation are attributable to historical events or chance dissemination rather than inherent differences in environments (Daubenmire 1952). This implies a similar environment for all vegetation that is given the same plant association name. Associations are named after late-seral dominant or indicator species. A binomial naming system is typically used for forest plant associations. The first species in the plant association is often a dominant or codominant climax tree species typical of a larger climate zone. This is followed by one or more dominant shrubs or herbs from the climax community.

¹ The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Plant associations are theoretical entities in that environmental changes, including climate change, ensure that the potential is never fully realized. Thus, they are identified based on the most advanced successional vegetation that can be found. We employed an indicator species approach whereby species with exceptional environmental indicator value or that are known to express dominance in late-seral stages are used to identify the seral community's affinity to a plant association. Areas with similar seral vegetation may or may not have the same climax community potential, but this can be assumed when found on similar landforms and soils and in similar microclimates. The utility of plant associations is that they define areas with similar environments in which the vegetation responds in similar ways to environmental perturbations, and the successional vectors then point toward a common endpoint. As a formal classification of plant associations has not been done for the entire study area, we used the forested plant association classification in Henderson et al. (1989) and classified the remaining plots into broadly similar plant community groupings based on their dominant species. We refer to these as community types as their seral status is currently not known.

Overall Statistical Analysis

We used SAS version 9.4 (SAS Institute Inc. 2016) to conduct statistical analyses (unless otherwise stated), and we set the significance level at $\alpha = 0.05$, although we occasionally refer to marginal significance of $0.05 < \alpha \leq 0.1$. We evaluated normality of datasets with scatterplots of residuals versus estimated values. Where normal distribution of data was indicated, we used parametric analysis techniques; otherwise, we used nonparametric methods. We used the GLM (generalized linear model) procedure (PROC GLM) for parametric analysis of variance (ANOVA) and Tukey tests; the TTEST procedure (PROC TTEST) for t-tests of two means; the NPARIWAY procedure (PROC NPARIWAY) for nonparametric Wilcoxon analysis of variance; the REG procedure (PROC REG) for simple, multiple, and stepwise linear regression analysis; and the CORR procedure (PROC CORR) for Pearson product-moment and Spearman correlation analyses. Ordination analysis was conducted with PC-ORD version 5.31 (McCune and Mefford 2006). The statistical analyses that pertain to each kind of data are included under "Physical Environment" and "Vegetation and Biological Relationships" below.

Physical Environment

Temperature

We collected temperature data on most of the plots from September 2011 through July 2016 to help characterize the plot environment. The need to follow wilderness work protocols on federally managed lands as well as the remoteness and limited seasonal access to the study area constrained the methods (e.g., instrument sheltering, measurement precision). Comparability to existing long-term temperature records was limited because the sampling protocols differed from typical meteorological approaches.

To monitor soil and air temperatures, we installed iButton sensors (model number DS1921G; 0.1 °C precision; iButtonLink, LLC) on 33 plots in 2011 and on an additional 3 plots in 2012.

These sensors had the capacity to store data for 1 year. For protection, each sensor was placed in a white, 3/4-inch (1.9 cm), threaded, polyvinyl chloride (PVC) plastic pipe endcap and was held inside with a threaded PVC plug. On each plot, we buried one sensor 20 cm

deep in the soil. We tethered it with a plastic zip tie to another sensor that we placed on the soil surface. The white color of the soil surface sensor's enclosure likely resulted in conservative estimates of maximum soil surface temperatures under direct solar exposure. We placed two more sensors on the north side of a tree trunk—one at 1.5-m height and one at 3-m height—on plots that had trees of the necessary size. We drilled a hole in the PVC plug, nailed it to the tree bole at the required height, and screwed the endcap with the sensor onto the plug. We removed all materials at the end of the study.

Each summer from 2012 through 2014, we collected the sensors for later downloading and replaced them with new ones. In 2014, we replaced the old sensors on 23 of the plots with larger capacity sensors (model number DS1922L-F5; ± 0.5 °C precision; iButtonLink, LLC), which could store data for 3 years. We collected the sensors from the other plots but did not replace them. We left the larger capacity sensors to record for 2 years and then collected them in July 2016 without replacement, thus terminating the temperature measurements.

The failure rate for the sensors left for 1 year was 26 percent; those left for 2 years had an 83 percent failure rate. There were two kinds of failure. Some sensors stopped recording data prematurely but retained already recorded data. In these cases, we often only lost 1 or 2 months of data. However, some also failed entirely and yielded no data. Sensors recording soil temperatures, particularly those on the soil surface, had the highest rates of failure. We also had several instances in which apparently curious people who discovered our installations removed the sensors from where we had placed them. Thus, some data gaps exist.

Because of sensor failures, especially in the final year of recording, we used only the first 3 years of data from each plot to describe the climate over the study area (September 2011 through August 2014). The data was relatively complete for air temperature at 29 plots, for soil surface temperatures at 19 plots, and for 20-cm-deep soil temperatures at 22 plots. In this report, the term “year” refers to a sample year unless otherwise noted. The sample year begins in September.

Each sensor recorded data at slightly more than 4-hour intervals; however, the recording time was not the same among sensors. Because the recording interval was slightly more than 4 hours, the recording interval advanced a small amount each day. To standardize these data, each day was divided into quarters (quarter-days) starting at midnight (0000 [midnight] to 0600, 0600 to 1200, 1200 to 1800, 1800 to 2400 [also midnight]), and each recorded temperature was assigned to the quarter-day in which it fell. For all calculations involving subdivisions of days, we used averages of the data assigned to these intervals rather than actual times. Depending on where data recordings fell in the 6-hour interval, there were either one or two recordings for each quarter-day from a single sensor. We averaged multiple readings within each quarter-day, so the resulting dataset consisted of a single mean temperature for each quarter-day per sensor. We used this dataset for all further statistical operations involving subdivisions of days.

Air temperatures were mainly derived from the sensors placed at 3-m heights, which generally produced slightly lower temperatures throughout the year than the 1.5-m-high sensors. The 1.5-m-high sensors had three functions: (1) as a backup in case the 3-m-high sensors failed, (2) as a reference to mitigate against sun fleck heating of the 3-m-high sensors, and (3) as an indicator of when the snow depth surpassed 1.5 m or melted back below 1.5 m. For a given quarter-day, when there was a difference between the two heights, we selected

the lower temperature of the two to represent air temperature. Although snow depths in the study area were greater than 1.5 m, most of the 1.5-m-high sensors remained above the snow in winter (as indicated by continuous daily fluctuations) because of tree wells that developed in the snow around the trees.

In addition to our study site measurements, we used temperature data collected by the Forest Service Ecology Program (plot 1652) at Mount Townsend, 9 km northwest of our study site. The Mount Townsend dataset included soil and air temperatures collected from August 25, 1994 through August 25, 1996 and August 13, 1997 through August 13, 1999. This site is at 1649-m elevation, with an aspect of 66° and a slope steepness of 59 percent. Temperatures were collected at 3-, 10-, 20-, 50-, and 100-cm depths in the soil as well as air temperature.

Mount Townsend temperatures were recorded with thermocouples and logged eight times a day with a Unidata logger (Unidata Pty Ltd.). Air temperature thermocouples were placed in Unidata white, aerated metal enclosures and attached to the north side of a tree bole. The entire forest stand was densely shaded by subalpine fir trees, such that sun flecks were small. The plant association was subalpine fir/Cascade azalea (*Rhododendron albiflorum*) and was like several plots at our study site. We used these data for descriptive purposes and as insight into deeper soil temperatures than we were able to record. We present mean monthly air and soil temperatures from the Mount Townsend site over the period of record.

We also used mean annual air temperature data from four SNOTEL weather stations in the Olympic Mountains. SNOTEL weather stations are in open areas and use standard meteorological methodologies to collect temperature and other data. They are designed to automatically collect and send data to receiving stations for up to a year at a time unattended. They are operated by the USDA NRCS National Water and Climate Center (USDA NRCS 2020a). Two of the SNOTEL stations are at lower elevations than our plots, but two (Waterhole and Buckinghorse) fall within the elevations encompassed by our plots. We calculated these mean annual air temperatures from data extracted for the same 3 years over which our data were recorded. Note, however, that we calculated mean annual air temperatures for our study area from multiple plots across a large area and range of elevations. In addition to air temperature, the Buckinghorse SNOTEL weather station also reports soil temperature measurements from several depths, including 20- and 50-cm depths, which we also used.

The Waterhole SNOTEL weather station location is most like our study area in terms of vegetation. It is located between Hurricane Ridge and Obstruction Point in Olympic National Park on a broad, rolling ridgetop with a gentle northeastern aspect at 1527-m elevation. The Dungeness SNOTEL weather station is on a generally west-facing, lower slope at 1222-m elevation, while the Mount Crag SNOTEL weather station is located on an upper slope bench with a northern aspect at 1207-m elevation. The Buckinghorse SNOTEL weather station is in an upper slope position on a generally western aspect at 1484-m elevation, 26 km to the west-southwest of our study area. This is several prominent ridgelines toward the ocean, meaning that the Buckinghorse SNOTEL weather station site is more maritime in nature than ours, with about one-third more annual precipitation. For additional context, we present mean, maximum, and minimum annual temperatures from these four SNOTEL weather stations over the same 3 years from which our data were recorded.

Light Measurement (Photosynthetically Active Radiation)

During our sampling visits in summers of 2011 and 2012, we measured photosynthetically active radiation (PAR) at 1.3-m height and at the surface (hereafter, ground level) on each plot with a Decagon AccuPAR ceptometer in terms of percentage of full sun PAR. Measurements were taken on each plot about 6 m from the plot center at azimuths of 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°. A fully open-canopy reference measurement was taken in a nearby open area immediately before each plot measurement. For each pair of measurements, PAR was expressed as the ratio of the plot reading to the open-canopy reference reading (i.e., proportion of full sun). Each 1.3-m-high measurement included four subsample measurements: one each facing 0°, 90°, 180°, and 270° azimuth. For these four measurements, the sensor bar was leveled horizontally before taking a reading. Care was taken for each subsample measurement to ensure that the observer did not cast shade on the sensor. We report the mean of these four measurements. The ground-level measurements were taken by slipping the sensor bar under the vegetation along the contour of the slope. We took two measurements (end to end) at each of two points, 50 cm apart, one above the other on the slope. We report the mean of these four measurements.

Solar Radiation

We obtained online data for the number of clear days from the Office of the Washington State Climatologist (2020) for the period of 1971 through 2000. The monthly cloud cover data was measured at the Naval Air Station Whidbey Island, Washington, which lies in the Olympic Mountains rain shadow at an elevation of 14 m, about 60 km northwest of the study area. Cloud cover was automatically measured in oktas (eighths) by using a ceilometer, which is accurate to 3658-m elevation. This was the closest weather station that reported these data.

We used mean monthly solar radiation data collected at the Waterhole SNOTEL weather station in the Olympic Mountains, the closest site at which these data were collected. A LI-COR device was used to collect solar radiation measured in watt hours per square meter. From these data, we calculated the mean monthly solar radiation as an average of hourly values for the water years (October 1 through September 30) beginning in fall of 2011 and extending through fall of 2014.

We also used ArcMap version 10.5.1 (ESRI 2017) to calculate the mean monthly potential direct and diffuse solar radiation as well as the duration of direct solar radiation for each plot at our study site by month and for the entire year. We input x and y coordinates from high-precision GPS measurements on our plots and used a 5-m digital elevation model for the z (elevation) coordinate. We used default values for sky size (200 cells per side), the number of calculated horizon angles (32), and a value of 0.6 (ratio of terrestrial to extraterrestrial solar radiation) for transmissivity, indicating a clear sky. ArcMap (ESRI 2017) incorporates topographic horizons and seasonal changes in the angle of the sun into the calculation.

Summer Soil Moisture

We sampled soil moisture at eight locations on each plot with a Hydrosense sensor (Campbell Scientific) in 2011 (September 13 to 16), 2012 (August 6 to 10), 2013 (July 31 to August 4), 2014 (July 28 to 31), and 2016 (July 25 to 28). This sensor uses standard laboratory calibrations to provide the percentage of volumetric water content, ranging from air-dry to saturation, integrated over the 12-cm length of the probe. Such shallow soil moisture measurements

do not reflect the totality of the rooting zone; but we assume they are important for plant establishment and shallower rooted herbaceous species and are especially important to nutrient cycling. In our cold subalpine and alpine soils, these measurements nevertheless reflect an important portion of the rooting zone, and we assume they also reflect, at least comparatively, somewhat deeper conditions among plots that develop at somewhat later dates. The measurements were taken about 6 m from the plot center at azimuths of 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°. At each of these azimuth-based locations, a center point was established, and five measurements were taken along the outer line of a circle 30 cm from the center point. We averaged these five soil moisture readings to provide a single value for the point. We further averaged the eight location means to provide a single mean and standard deviation for the plot. Finally, we averaged the annual measurements over the 5 years of data collection for an overall mean and standard deviation for each plot. We also averaged the individual plot standard deviations over the 5 years for an index of in-plot variation.

Solifluction

We made field notes of solifluction (i.e., processes related to freeze-thaw activity causing soil and rock to gradually move down slope) features on our plots, such as loose, unvegetated, actively moving rock stripes separated by stable, vegetated strips or elongated, teardrop-shaped islands of tundra vegetation. The teardrop-shaped islands were largest uphill and narrowest downhill and 30 to 50 cm at their widest points.

Solifluction is caused by alternate freezing and thawing of the soil, so autumn and early winter temperature data taken before the snowpack becomes deep enough to insulate the soil from freezing air temperatures are relevant. Thus, we graphically analyzed soil temperature fluctuation from October through January with our 20-cm-deep soil temperature data on the 14 plots showing visible signs of solifluction. We summarized our findings by calculating the percentage of the time between October 1 and January 31 that temperatures were below 0 °C and noting the lowest temperatures attained.

Soil Texture, Coarse Fragments, and Bedrock

We acquired coarse fragment content and soil texture data in the field for 37 plots. The surficial soil texture (top 5 cm) was measured 10 m from plot center at each cardinal direction. We used ribbon and feeling tests to place the soil in one of the standard soil triangle classes (USDA NRCS 1999). Surficial coarse fragment content was visually estimated for the top 20 cm of soil by digging and examining a shallow pit in the ground. Although we were restricted by wilderness regulations from digging deeper soil pits, we believe that our 20-cm coarse fragment data is generally indicative in a comparative way of rooting zone soil conditions. However, it is also important for evaluating soil movement and conditions for seedlings or shallowly rooted herbaceous vegetation. Bedrock type was assigned to each plot based on field notes and geologic mapping (Tabor and Cady 1978).

Statistical Analysis

TEMPERATURE DATA PREPARATION AND DESCRIPTIVE STATISTICS—For most statistical analyses of temperature data, we used the 3 years with the most complete records (September 2011 through August 2014). This dataset included 29 plots for air temperatures, 19 plots for soil surface temperatures, and 22 plots for soil temperatures. This is the basic dataset for our statistical analyses of temperature, unless otherwise stated, and we refer to it as the “3-year dataset.” The coverage of these plots in terms of elevation, aspect, and other physical site parameters was representative of the study area.

We calculated 65 mean temperature variables for each of the air, soil surface, and soil datasets over the 3 years of record for each plot. Included were 1 overall mean annual temperature, 4 overall quarter-day means, 12 overall monthly means, and 48 monthly by quarter-day means. For descriptive purposes, we present these data in graphical and tabular formats; we also used the 65 means as input for other statistical procedures (described below). For some analyses we made similar calculations using maximum and minimum temperature data. In all cases, we calculated standard deviations of the means.

ELEVATION BANDS AND ASPECT GROUPS—For some analyses we grouped the data by site aspect (three groups) or elevation (three bands). The elevation bands were thirds of the range in elevations from our lowest to our highest plots (1420 to 1578 m, 9 plots; 1578 to 1735 m, 18 plots; 1735 to 1892 m, 13 plots).

To group our plots by azimuth, we first divided the 360° azimuth (true north) in half along a base line running between 22° and 202°, as all our plots except for one lay in the western half of this division. We then divided this western half into three sectors of 60° each. The first sector included three plots that were between 328° and 360° and represented our coolest aspects. The second sector lay between 262° and 322° and included 17 plots. The third sector, which represented our warmest aspects, lay between 202° and 262° and included 18 plots. This left the one plot at 192°, which we added to the third sector.

1.5- AND 3-M-HIGH AIR TEMPERATURES—Because of iButton sensor failure, we combined the air temperature data for the sensors at 1.5-m height with that of the sensors at 3-m height in the 3-year dataset for a more complete air temperature record. Whenever there was data for both sensors, we selected the one with the lowest temperature, which was generally the 3-m-high sensor. If only one sensor was recording, then that was the one we used. We wanted to know, however, whether the differences between these two recording heights were significant. We used ANOVA to compare the data from the 1.5- and 3-m-high sensors for each of the 29 plots in the 3-year database. We did this based on the entire year and separately for the snow-free season (June through October) and the season of heaviest snowpack (January through March).

MICROCLIMATIC OVERVIEWS—Each of the sections on air, soil surface, and soil temperatures begins with an overview of general microclimatic data. We graphically present the mean monthly temperature data calculated for each year of the 3-year dataset. We also present the mean, minimum, and maximum annual temperature data calculated for each of the 3 years and the standard deviation of the mean for each year. We provide dates and times for the maximum and minimum annual temperatures for each of the 3 years.

TEN MAXIMUM AND TEN MINIMUM TEMPERATURES—To examine the frequency and distribution of temperature extremes, the 10 maximum temperature readings were taken from each plot for air, soil surface, and soil temperature datasets for each of the 3 years. Thus, there were up to 30 measurements per plot for each dataset. For this analysis, to achieve the most comprehensive representation of the study area, we included plots with just 1 or 2 years of data. Thus, there were 29 plots included for air, soil surface, and soil temperature datasets. We calculated the percentage of the maximum temperature measurements that occurred in each month over all plots for each dataset. Also, we calculated the mean of the maximum temperature measurements by month as well as the number of plots that contributed to each monthly percentage or mean. We present these data graphically. In the same way, we also examined the 10 minimum temperature recordings from each plot for each year using the 30 minimum air, soil surface, and soil temperatures per plot.

FREEZING TEMPERATURES—We extracted all the temperature measurements that were at or below 0 °C from the 3-year air temperature dataset and calculated the mean percentage of freezing air temperature measurements for each plot by month over the 3 years of record. We used these means to calculate the mean percentage of freezing days per month and the associated standard deviation over all the plots, which we present graphically.

We did not do the same analysis for soil surface and soil temperatures. These temperature locations spent much of their time under snowbanks close to freezing. We were not confident that the sensors in these locations accurately measured the fractions of a degree necessary to distinguish freezing from not freezing, nor did we feel that such precision is necessarily important. Instead, we have chosen other ways to illustrate winter temperatures experienced at these locations.

FROST-FREE INTERVALS—For each plot, we determined the longest number of days between air temperature recordings that were above 0 °C for each year in our 3-year dataset. We averaged these three values for each plot and used these plot means to calculate the average number of frost-free days by solifluction group and by plant association or community type.

SNOTEL AND MOUNT TOWNSEND DATA ANALYSIS—We present, in tabular format, general features of the SNOTEL station locations and calculated their recorded mean, maximum, and minimum air temperatures over the same 3-year period as our temperature data (September 2011 through August 2014). We also used the air temperature/elevation relationship (lapse rate) that we developed for our study site (see below) to estimate the mean annual air temperature at the elevation for each of these sites and compared this estimation to the actual mean calculated from SNOTEL data. We similarly estimated and compared the mean annual air temperature for the Mount Townsend dataset. For the Mount Townsend site, we calculated the mean annual temperatures (based on its 5-year record) for each of the sensor locations (air and at soil depths of 3, 20, 50, and 100 cm) and determined the date of snowmelt from each of the years of record according to when daily temperature fluctuation resumed in spring from a thermocouple placed 3 cm deep in the soil. We used these data to compare with data from our site for context.

TEMPERATURE PULSE MOVEMENT—We estimated the rate of movement through the soil for a temperature pulse by calculating the difference in time between daily peak soil surface and peak soil (at 20-cm depth) temperatures for the month of July 2012. We selected one open-canopy plot (i.e., low percentage of canopy closure) (plot 3) and one closed-canopy plot (i.e., high percentage of canopy closure) (plot 32) and subtracted the average time recorded for all the daily soil surface temperature peaks in July from the average time recorded for all the daily soil temperature peaks in July. As our recording intervals are about 4 hours long, we probably missed the actual peaks; however, because the recording interval migrates several minutes each day, we feel the average has meaning beyond what would be obtained with fixed intervals.

SOIL TEMPERATURE REGIME—We used methods in *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys* (USDA NRCS 1999) to determine soil temperature regimes, which are based on the mean annual soil temperature, the mean summer (June through August) soil temperature, and the mean winter (December through February) soil temperature at 50-cm depth. As our soil temperature data came from a 20-cm depth, we estimated the 50-cm-deep temperatures. According to USDA NRCS (1999), the mean annual soil temperature changes only negligibly with depth, and in mid-latitudes, summer and winter temperature gradients are about 0.5 °C per 10 cm of depth. Also relevant

to soil temperature regime determination are the presence of an O horizon (surficial layer that is dominated by organic material), presence of soil saturation during summer, and depth to a lithic contact (a boundary between soil and underlying bedrock). We collected data on the O horizon, which often consisted of a shallow, loose, and intermittent layer of litter. In these cases, we did not consider the plot to have an O horizon. Only when the litter layer was continuous (regardless of depth) did we consider it to be an O horizon for the purposes of soil temperature regime determination. All our soils were well drained except for plot 18, so we assumed they were not saturated during summer. We did not dig soil pits because of wilderness regulations, so we do not know the depth to a lithic contact. We believe that most of our soils were of relatively deep colluvium and assumed the lithic contacts were deeper than 50 cm.

We used the 3-year dataset to determine soil temperature regime for as many plots as possible (22 plots). For plots that did not have continuous 3 years of data, we resorted to the use of other data. Whenever we were able to piece together the equivalent of at least 1 full year from the full 5-year dataset, we assigned a soil temperature regime to that plot. In this way, we estimated the soil temperature regime for an additional 14 plots. We also determined the soil temperature regime for the Mount Townsend site and for the Buckinghorse SNOTEL weather station site. We also used the differences in 20- and 50-cm-deep soil temperatures calculated for these two sites to determine the soil temperature regimes of our plots instead of using the difference indicated by the soil taxonomy guide (see above). Thus, we made three estimates for the soil temperature regime.

RELATIONSHIPS BETWEEN ANNUAL AND DAILY TEMPERATURE PATTERNS AND OVERSTORY CANOPY CLOSURE—It was advantageous in some analyses to group the data by overstory canopy closure (closed canopy and open canopy). Overstory canopy closure is the collective percentage of overstory species canopy cover as if all overstory species constituted a single entity. Depth of the canopy, or the overlapping canopies from different trees or species, does not count; a point on the ground either has or does not have tree canopy over it. Canopy closure is never higher than 100 percent. This is different from total canopy cover, in which the sum of the covers of the individual species can total to greater than 100 percent if there is canopy overlap. Closed canopy refers to plots with >55 percent canopy closure, while open canopy refers to plots with ≤55 percent canopy closure.

As an initial means of exploring the relationship between plot temperature and elevation, we made scatterplots of mean annual air, soil surface, and soil temperature data by elevation data. These scatterplots revealed two distinct populations that could be distinguished by different amounts of overstory canopy closure (fig. 3), which we refer to as open-canopy and closed-canopy plots. This division was most apparent in the soil temperature data and least obvious in the air temperature data. In the soil temperature data, five closed-canopy plots were grouped separately from the remaining open-canopy plots. Only two of the closed-canopy plots were present in the soil surface temperature data, but they were both grouped separately from the remaining open-canopy plots. The same five closed-canopy plots plus a 6th plot (plot 33 for which there was no soil or soil surface temperature data) were grouped separately with the air temperature data. Examination of the data revealed that all except one plot in the smaller closed-canopy group of plots had between 75- and 90-percent canopy closure of trees. One plot in the closed-canopy group had only 10 percent overstory canopy closure, but it was in a topographically shaded location (plot 7). Although plot 7 was on a moderately steep, western aspect, it was in the bottom of a talus-filled basin in the shadow of

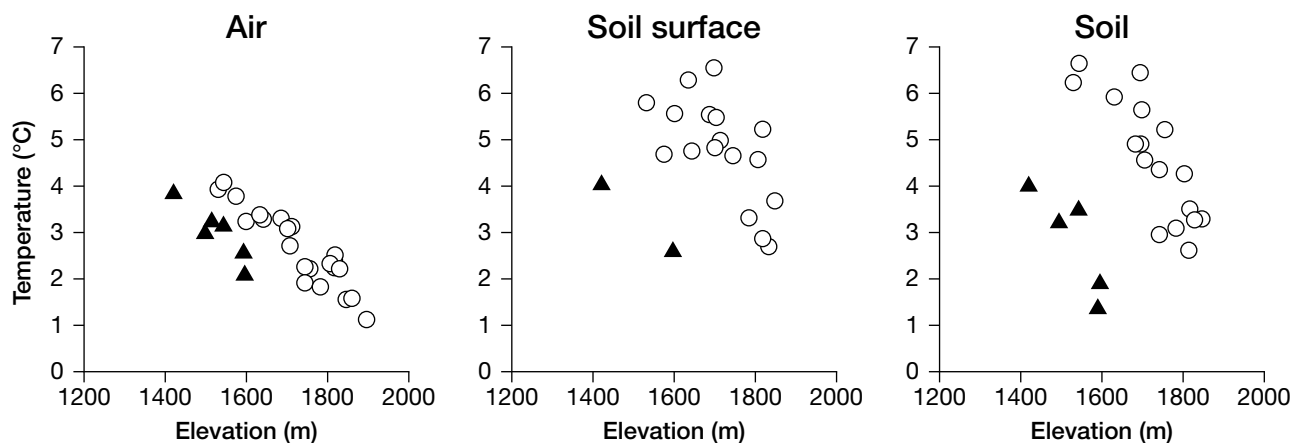


Figure 3—Mean annual air, soil surface, and 20-cm-deep soil temperatures of sample plots in the Olympic Mountain whitebark pine communities study by elevation showing two separate populations of points. The triangles are closed-canopy plots, and circles are open-canopy plots.

a precipitous high ridge that rises about 350 m above it immediately to the south. All except one of the more open-canopy plots had 50 percent or less overstory canopy closure. One plot had 80 percent overstory canopy closure, but 10 percent of that cover came from small trees <10 cm in diameter at breast height (plot 17). This stand was a small subalpine tree island of about 500 m² in an otherwise open landscape.

We calculated the mean monthly air, soil surface, and soil temperatures for closed-canopy and open-canopy plots. We present these data graphically for comparison between overstory canopy closure groups and times of the day (quarter-days).

RELATIONSHIPS BETWEEN TEMPERATURE AND TOPOGRAPHY—We used linear regression to model the relationship between mean annual temperature and elevation (lapse rate) by using the 3-year air, soil surface, and soil temperature datasets. We similarly calculated lapse rates for mean annual air, soil surface, and soil temperatures by quarter-day and for mean monthly air, soil surface, and soil temperatures. To compare the effect of canopy closure, we repeated this modeling analysis with the open- and closed-canopy groups already described. Thus, we calculated separate linear regressions for air, soil surface, and soil temperatures as a function of elevation separately for open- and closed-canopy groups.

When separated by canopy closure, seasonal progressions of lapse rates were apparent following snowmelt. To describe these trends, we used linear regression to model the monthly lapse rates as a function of time, beginning with spring snowmelt and ending just before the spring snowmelt in the following year. The increments of time were months.

We also wanted to know the relationship between seasonal changes in weather and insolation to these progressions. The potential explanatory variables that we explored were cloudiness by month, the number of cloudy days each month, and the number of clear days each month. These variables were measured at the Naval Air Station Whidbey Island, Washington, in Puget Sound, which was the nearest weather station with these data. We also obtained monthly direct solar radiation measured at the Waterhole SNOTEL weather station in the Olympic Mountains. We calculated the potential direct solar radiation for each plot and its standard deviation for each month and plot by using ArcMap version 10.5.1 (ESRI 2017). This program uses topographic data to estimate the potential duration of direct solar radiation for a point on the ground, assuming no cloud cover. We averaged these plot data

over the sample area by month to provide both a seasonal progression of potential direct solar radiation and calculated its standard deviation as a measure of its topographic heterogeneity. Finally, we calculated the percentage of time that plots were covered with enough snow to eliminate daily temperature fluctuations of the surface temperature sensor for each plot in each month. These plot data were averaged together for each month to provide a monthly index of the total sample area that was snow covered. We refer to these seven variables as: cloudiness, cloudy days, clear days, MD solar (measured direct solar in watts per square meter), PD solar (potential direct solar), SD solar (standard deviation of PD solar), and percentage of snow (percentage of ground covered by snowpack). We modeled monthly lapse rates as a function of these seven variables by using stepwise regression. We included all seven variables in an initial model that used a selection criterion of $P = 0.15$.

RELATIONSHIPS BETWEEN TEMPERATURE AND ASPECT—To explore relationships between temperature and aspect, we first converted all azimuths to degrees deviation from north-northeast (22°). All our plots except one lay in the western half of an arc of azimuths running between 22° and 202° . We used this deviation from 22° for all analyses involving aspect and refer to this new variable as aspect unless otherwise stated. This assumes that aspects facing north-northeast are the coolest and aspects facing south-southwest are the warmest. We used linear regression to model the mean annual air, soil surface, and soil temperatures of plots with their aspects. We used multiple linear regression to model the combined effects of aspect and elevation on mean annual air, soil surface, and soil temperatures, as well as by quarter-day, as functions of elevation and aspect. We then divided the data into open- and closed-canopy groups, although at this level we did not have enough data in the soil surface temperature dataset for analysis. We also used multiple regression to model the highest soil surface temperature recorded for each plot as a function of elevation, aspect, and the summed percentages of overstory and understory canopy cover (total canopy cover).

OTHER ANNUAL SOIL SURFACE AND SOIL TEMPERATURE RELATIONSHIPS—We used multiple regression to explore the relationship between mean annual soil surface temperature and the combined effects of elevation, aspect, and the percentage of overstory canopy closure. To better understand the factors that affected the mean annual soil temperature, we used simple linear regression to model the effects of the following variables on mean annual soil temperature: mean annual air temperature, elevation, aspect, slope steepness (percentage), total canopy cover, overstory and understory canopy closure, PAR at 1.3-m height and ground level and their standard deviations, and the duration of winter snow cover in days. We then selected the most promising variables and performed three multiple regressions: (1) mean annual soil temperature as a function of mean annual air temperature, elevation, and snow season duration; (2) mean annual soil temperature as a function of elevation, overstory canopy closure, and aspect; and (3) mean annual soil temperature as a function of aspect and the standard deviation of ground-level PAR.

SEASONAL CORRELATION BETWEEN OVERSTORY CANOPY CLOSURE AND SOIL TEMPERATURE—To examine the seasonal relationships between overstory canopy closure and soil temperature, we first calculated the Pearson product-moment correlation between overstory canopy closure and each mean monthly soil temperature using the 3-year dataset. Marginal or significant relationships were found for June, July, and August. We then used linear regression to model the effect of overstory canopy closure on mean monthly soil temperatures in June, July, and August.

For each year, we also summed the number of days with soil temperatures above 9°C . Temperatures below 9°C have been implicated with poor root growth (Alvarez-Uria and

Körner 2007). We used linear regression to show the relationship between overstory canopy closure and elevation and the total number of days above 9 °C each year.

RELATIONSHIPS BETWEEN ALPINE TREE LINE POSITION AND TEMPERATURE—Körner and Paulsen (2004) postulated that alpine tree lines form when the mean growing-season soil temperature drops below about 6.7 °C at 10-cm depth, thus restricting root growth. The value of 6.7 °C is an average of a worldwide range of temperatures (6.4 to 7.8 °C) where they found that tree lines formed. They defined the growing season as the period between when the soil first warms to 3.2 °C at 10-cm depth in spring and when it drops below this temperature in fall.

We explored this relationship with our temperature and vegetation data. Although our soil temperatures were taken at 20-cm depth, in terms of timing during the abrupt seasonal changes, this would only make a difference of hours or at most a few days in spring and again in fall, so we believe that using our 20-cm-deep soil temperatures would make little difference in terms of season length. Over the entire summer, the mean soil temperature will be about 0.5 °C lower for each 10 cm of depth (USDA NRCS 1999). Thus, we subtracted 0.5 °C from Körner and Paulsen's (2004) tree line temperature standards for comparisons with the temperatures we calculated from our 20-cm-deep soil temperature data (thus, a mean of 6.2 °C and a range of 5.9 to 7.3 °C).

We extracted from our 5-year dataset all temperatures between the period from when the soil temperature first exceeded 3.2 °C in spring to when it dropped below this temperature threshold in fall. Thus, we had from one to four seasons of data for 36 plots. We averaged multiple seasonal datasets from individual plots to provide a single mean growing-season soil temperature for the plot.

We regressed mean growing-season soil temperature on overstory canopy closure for each plot to estimate the temperature change caused by each 1-percent increase in overstory canopy closure ($\Delta T/\Delta C$). For each plot, we then calculated the percentage of open area and multiplied this percentage by the previously calculated $\Delta T/\Delta C$ to estimate how much temperature change would occur if overstory canopy closed over the plot. We then subtracted this number from the mean growing-season soil temperature to estimate soil temperature, assuming complete canopy closure for each plot.

WINTER SNOW ACCUMULATION—Although we were not present on our plots during winter, we were able to deduce the arrival and departure of snow on our plots by examining the behavior of temperature data, especially that from our soil surface temperature sensors (fig. 4). In figure 4, the flat areas in the plotted data at or near 0 °C signify the presence of a deep snowpack. The lowest soil surface temperatures occurred in November before a deep snowpack accumulated, and the abrupt return to daily temperature fluctuations in spring (often in May) signifies the point in time when the snow melted over the sensor. Also visible in late 2013 are several instances of short-duration snow cover before the continuous winter snowpack set in; and in 2015, similar episodes can be observed after the main winter snowpack melted in February, earlier than usual. This was also useful in determining the effect of tree wells on snow accumulation with our 1.5-m-high sensors. We used observations such as these from all our plots to describe seasonal trends in temperature. Zhang et al. (1997) also found this to be a reliable method of detecting the first and last days of snow on the ground and showed that the results were consistent with results from the U.S. Department of Commerce National Oceanic and Atmospheric Administration's National Weather Service records.

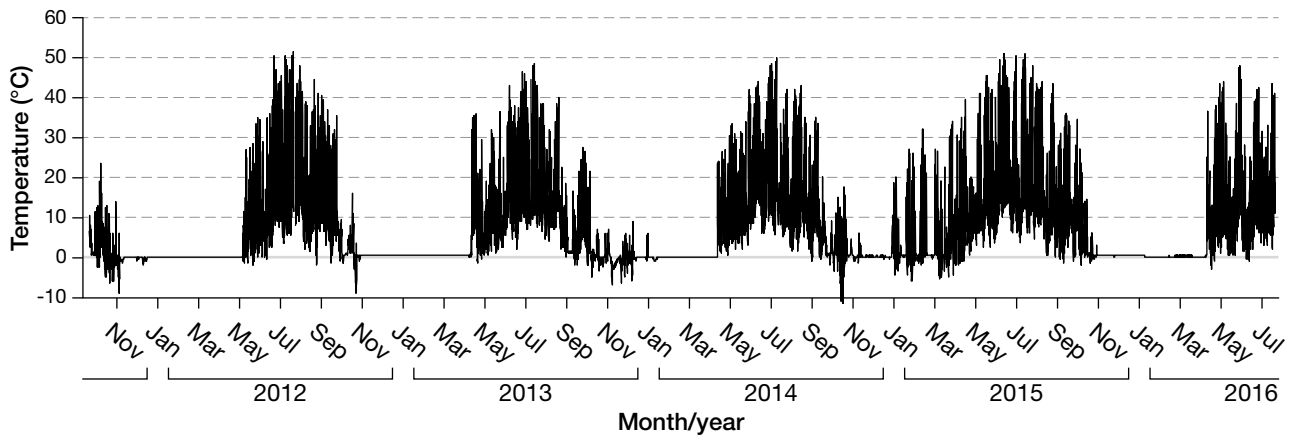


Figure 4—Continuous soil surface temperatures recorded on plot 37 of the Olympic Mountain whitebark pine communities study. This was the only plot on which we successfully recorded soil surface temperatures for the entire 5-year period. This plot had an elevation of 1814 m, an azimuth of 233°, and a slope steepness of 67 percent. Total overstory canopy cover on this plot was 40 percent, and the recording location was exposed.

Because snow is a good insulator, once covered, the daily fluctuations of temperatures recorded by the sensors were damped and eventually ceased altogether. Shallow snow depths could be detected by decapitated daily temperature fluctuations (i.e., fluctuations that only occurred in the negative direction, below 0 °C). This occurred primarily at night. During the warmth of day, temperatures were maintained at 0 °C by melting snow while the snow remained. When the snow over the sensor melted entirely, daily temperature fluctuation resumed both above and below 0 °C. Under a sufficiently deep snowpack, all daily temperature fluctuation ceased. Because we were not present to measure the snow, we do not know at what depth this occurred, but fewer than half of our 1.5-m-high sensors were so affected, and only one of the 3-m-high sensors was affected in this way.

We explored the factors important to the duration of the winter snowpack on our plots with a model. In examining the first plots to accumulate a winter snowpack and the first plots to lose their winter snowpack on maps and air photos, we found several possible determinants of where the deepest snowpacks occurred. For example, it appeared that more plots with deep snowpacks occurred on northern aspects, especially where the plot was close to a ridge crest running approximately east to west. We reasoned that the effect of aspect on the duration of the winter snowpack was related to reception of solar radiation as modified by several other factors, and we used stepwise linear regression to explore these factors. Thus, we input aspect, elevation, and proximity to a ridgetop (expressed as meters from the nearest ridge to the northeast [positive number] or southwest [negative number]). We estimated potential direct solar radiation (output from ArcMap version 10.5.1) (ESRI 2017) for October, November, and December as well as March, April, May, June, and the year in total. We also estimated overstory canopy closure. The significance level for entry into the model was $P = 0.15$.

We also calculated the Spearman correlation coefficients for the correlations between the mean annual temperatures, mean monthly temperatures, and mean annual temperatures by quarter-day and the Julian day of the first snow of the season, the Julian day of snowmelt in spring, and for the total number of days the site was under snow cover. This was done for the air, soil surface, and soil temperature datasets.

SOLIFLUCTION—To examine how plots with signs of active solifluction differed from those in which we saw no such evidence, we used ANOVA to compare the two groups in terms of coarse fragment content (percentage), elevation, slope steepness, mean annual air temperature, standard deviation of the mean annual air temperature, mean annual soil surface temperature, standard deviation of the mean annual soil surface temperature, mean annual soil temperature, standard deviation of the mean annual soil temperature, Julian day of when the daily soil temperature fluctuation stopped in fall or winter (day of winter snowpack establishment), mean of the annual minimum soil temperatures over the period of record, mean number of frost-free days, and aspect.

We also used ANOVA to compare species cover on plots with visual signs of solifluction and those that had no such signs. In this comparison, we used only the plant associations where solifluction was observed. These associations were spreading phlox (*Phlox diffusa*), subalpine fir/common juniper (*Juniperus communis*), and subalpine fir/broadleaf lupine (*Lupinus latifolius*). There were also two krummholz plots with signs of solifluction, but these were not used as they were complex plots with more than one plant association present. There were 13 plots with visual evidence of solifluction that were used for this comparison and 11 plots that had no such evidence.

SOIL TEXTURE, COARSE FRAGMENTS, AND BEDROCK TYPE—Different kinds of bedrock decompose in different ways and produce different kinds of rubble and weathering products because of differences in hardness, density, and chemical properties. We used ANOVA to test whether coarse fragment content and soil moisture (see below) differed between bedrock types.

SOIL MOISTURE—We used ANOVA to compare soil moisture in 5 closed-canopy plots with that of 22 open-canopy plots. We used Spearman correlation analysis to explore the relationships between 7 physical, 42 solar, and 560 temperature variables and the mean soil moisture on each plot. Following the identification of significantly correlated variables, we used linear regression to model how some of the more highly correlated physical, solar, and temperature variables affected soil moisture.

The seven physical site variables included in the correlation analysis were elevation, aspect, slope steepness, coarse fragment content, and three variables to describe the shape of the ground surface at the plot level: horizontal microtopography and vertical microtopography (codes ranking the concavity or convexity of the plot surface in horizontal or vertical directions to the slope), and overall microtopography (a combination of the horizontal and vertical rankings into a single, overall plot surface shape).

We used ArcMap version 10.5.1 (ESRI 2017) to calculate 40 solar radiation variables including the potential solar radiation (watt hours per square meter) by month in terms of direct solar exposure, diffuse light exposure, and duration of direct solar exposure (hours). We also included our field measurements of PAR at ground level and 1.3-m height for each plot.

The temperature variables included in the correlation analysis were mean, maximum, and minimum annual, monthly, and quarter-day air, soil surface, and soil temperatures (555 total). We also included two variables related to the persistence of snowpack: the duration in days from the first detectable snow to the last detectable snow (or melting of the snowpack, whichever was later) and the duration in days in which daily temperature fluctuations were undetectable. In addition, we calculated the number of freezing measurements recorded for the air, soil surface and at 20-cm depth in the soil (three variables). In all, this sums to 560 variables that we used in correlation analyses. We present the number of significant monthly temperature correlations graphically and report the means of the significant monthly correlation coefficients.

Vegetation and Biological Relationships

Field Data Collection

CANOPY COVER AND CANOPY CLOSURE—Using methods described in Henderson et al. (1989), we employed ocular estimation of canopy cover for each species on the plot to describe vascular plant vegetation. We collected these data in 2007 through 2010. The canopy cover of the plot area was described separately for each species by projecting a polygon around the outer tips of each plant to the ground. Thus, the sum of any one species cannot exceed 100 percent, but the sum of multiple species can exceed 100 percent because of canopy overlap. We also distinguish between canopy closure and total canopy cover. Canopy closure is the percentage of the plot covered by all vegetation (treating all vegetation as if it were a single species). Thus, this estimation cannot exceed 100 percent, and a closure of less than 100 percent indicates the presence of bare ground, rock, or duff openly exposed to the sky. We also refer to canopy closure of overstory species and canopy closure of understory species. Total canopy cover is the sum of the individual covers of all species; thus, this variable can and often does exceed 100 percent because of canopy overlap.

TREE MEASUREMENTS—For all trees ≥ 1.3 m tall (live and dead) on each plot, we recorded species and measured stem diameter at breast height (d.b.h., measured at 1.3-m height) to 0.1-cm precision. Each stem at 1.3-m height was considered a separate tree. We measured height to the nearest 10 cm for a subset of about 30 percent of the trees on the plot. These trees were distributed over all sizes but always included some dominant and codominant trees.

We sampled live and dead trees < 1.3 m tall (hereafter, seedlings) in 2-m-radius nested plots 8 m north of plot center. We tallied small trees in the following height classes: 0 to 10 cm, 10 to 50 cm, 50 to 100 cm, and 100 to 130 cm (separately for live and dead). In some cases, when small trees were few, and the larger main plot was mostly open, we counted the three tallest size classes on the entire northeast quarter of the plot. In addition to measuring seedlings and saplings during initial plot measurement, we also remeasured the seedling subplots in 2014 and 2016. Because of the small sample size and large plot variability, we combined these size classes into a single seedling category for most analyses.

TREE AGE—We collected core samples from each tree on the plot that was measured for height, provided the tree was large enough to bore. We collected these cores from a height of 1.3 m (hereafter, breast height) and occasionally also from the base of the tree.

In 2013, we used an increment borer to sample at least two additional trees on each plot that had trees. We bored these trees at breast height and between 0 and 20 cm above the base. The height to the basal bore hole was recorded. Whenever possible, we sampled one subalpine fir and one whitebark pine tree, but if only one of these species was present, we sampled at least two trees of the species that was present. In this way, we sampled a total of 60 trees at both base and breast heights. Of these, 31 were subalpine fir and 29 were whitebark pine.

Also, we located several specimens of small trees about the same size as those in the various size classes in the 2-m-radius subplot off the larger main plot. We measured their heights and collected a basal stem segment for later age determination in the laboratory. We sampled basal stem segments from 44 seedlings, including 24 from subalpine fir, 17 from whitebark pine, 2 from shore pine, and 1 from Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*).

DEAD TREES AND DOWN WOOD—We recorded all dead trees on each plot that were ≥ 1.3 m tall and measured their diameter at breast height. In most cases, we were able to identify them to species. We recorded the cause of death if it was obvious, but this was not possible

in all cases. In most cases of recent white pine or whitebark pine mortality, we were able to attribute death to white pine blister rust. Each dead tree was also assigned a decay class (same as indicated below for down wood).

We used the methods of Brown (1971, 1974) to sample and calculate the volume of coarse woody debris (CWD), which we report in cubic meters per hectare. Pieces of down wood with a diameter of at least 10 cm at its small end were assessed on each of the four cardinal lines emanating from plot center by using a tape measure stretched from the plot center to the plot edge. For each piece, we recorded species (when possible), slope distance to center, and diameter to the nearest centimeter at the point where the tape crossed the center of the piece of down wood. We recorded length from the large end to a point 10 cm in diameter. For snags <1.3 m tall and ≥ 10 cm in diameter at the top of the snag, we recorded the length of the line that intercepted the snag, measured at the root collar. We recorded decay class (1 to 5) for each piece as follows (Maser et al. 1979):

1. Bark intact and tight, branches and fine twigs present, bole shape round, wood hard, log elevated above ground on support points.
2. Bark mostly present but may be loose, large branches present, fine twigs generally absent, bole shape round, wood hard to partly soft, log elevated above ground but slightly sagging.
3. Bark loose and missing in many places, fine twigs absent, wood mostly hard and in large pieces with some decay, shape round to oval, all of log on ground.
4. Bark generally absent, small branches and fine twigs absent, wood soft and in blocky pieces, shape round to oval, all of log on ground.
5. Bark entirely absent, branches and fine twigs absent, wood soft and powdery, shape oval, all of log on ground.

WHITE PINE BLISTER RUST ASSESSMENT—We assessed white pine blister rust infections in several ways. Each stem forking below breast height was assigned a rust infection severity code from 0 through 4, with 0 equal to no infection and 4 equal to a severe infection. An additional code (i.e., rux) was assigned to trees that had been killed by blister rust. We made these measurements at the same time as the tree measurements. The Olympic National Forest provided the protocol they use, and the codes are as follows:

Code	Blister rust assessment
ru0	No rust observed
ru1	Canker >61 cm from the tree bole
ru2	Canker >15 cm from the tree bole
ru3	Canker on tree bole or within 15 cm of bole
ru4	Top killed because of a canker on the bole
rux	Tree killed by blister rust

In 2013 and 2016, we repeated the blister rust assessments. Because the study was conducted in a wilderness area, we could not permanently mark the trees during the measurements, so the later measurements were not relatable to the previous measurement at the tree level. In 2013, we also recorded the percentage of the crown that was dead and the percentage that appeared to be dying.

LITTER DEPTH—In 2010, we measured litter depth (total organic material depth) on each cardinal direction at 10 m from the plot center. In 2011, we remeasured litter depth on all the plots 6 m from the plot center at azimuths of 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315° (8 measurements per plot). We present the mean of all the measurements in 2010 and 2011 for each plot.

FOLIAR NITROGEN AND CARBON—In 2011 (September 12 through 17), we collected foliar samples from two to three subalpine fir and two to three whitebark pine trees (when available) on each plot for nitrogen and carbon analysis. Each sample included four to six current-year shoots, each collected as a terminal segment of a primary shoot clipped to provide a 10- to 20-cm length. We collected shoots from the lowest sun-exposed limbs on the south side of each tree if possible. Each sample was placed in a sealed plastic bag and kept shaded and cool until they could be dried and processed in the laboratory.

Laboratory Processing, Pre-analysis, and Data Preparation

AGE DETERMINATION FROM FIELD COLLECTED SPECIMENS—We counted tree rings on 378 core samples and 44 seedling stem segments in the laboratory under a stereoscopic dissecting microscope. We carefully planed each core at right angles to the grain with a razor blade to make narrow rings more visible. We sanded stem segments to a high polish. Most core samples included or narrowly missed the pith. When the pith was narrowly missed, the pith age was estimated by observing the ring curvature on the inside of the core to determine the distance to the center of the tree, similar to the method of Villalba and Veblen (1997). Then by determining the rings per centimeter of the innermost rings on the core, we estimated the missing rings. We encountered rotten wood in cores from two Douglas-fir trees between plots 3 and 4. For these trees, we estimated breast-height pith age by extrapolating the innermost rings per centimeter to the center of the tree by using the difference of the core length and the inside bark diameter of the tree to determine the missing core length. We estimated the inside bark diameter of the stem (wood diameter) from the outside bark diameter and an estimate of the bark thickness made in the field.

TREE AGE ESTIMATION—One of the important pieces of data that we analyzed was tree age. However, because we could not determine all the tree ages in the field, we needed a way to estimate the ages of trees on our plots from which a core sample was not obtained. The following sections describe the methods we used for these estimates.

Of the 44 basal stem sections that we obtained from seedlings (see table A2.1), we used 34 (20 subalpine fir and 14 whitebark pine) to derive relationships between tree age and height. Two subalpine fir from krummholz stands were excluded because it was not possible to determine where the point of germination was, and thus it was not possible to assign a height (length) for the sample point. Two subalpine fir trees, which were older than their heights suggested, were considered outliers and were not used—one from a subalpine fir/broadleaf lupine plant association and one from a black alpine sedge (*Carex nigricans*) meadow. Likewise, two whitebark pine tree ages were discarded that came from the same black alpine sedge meadow. One whitebark pine from a subalpine fir/broadleaf lupine plant association (Henderson et al. 1989) was discarded because a tree height had not been recorded. There was also one Douglas-fir and two shore pine basal stem sections.

We used the ages and measurements of these subalpine fir and the whitebark pine seedlings to estimate the age of seedlings by regressing the age of each seedling on its height. We fit both linear and power curves to the data and found that the power curve produced a better fit. The power curve forces the origin through the intercept at 0, which in this case, provides a better estimate of age for small trees. We fit three curves—one for subalpine fir grown under a more closed canopy (plots with >55 percent canopy closure), one for subalpine fir grown under a more open canopy (plots with ≤55 percent canopy closure), and one for whitebark pine (fig. 5).

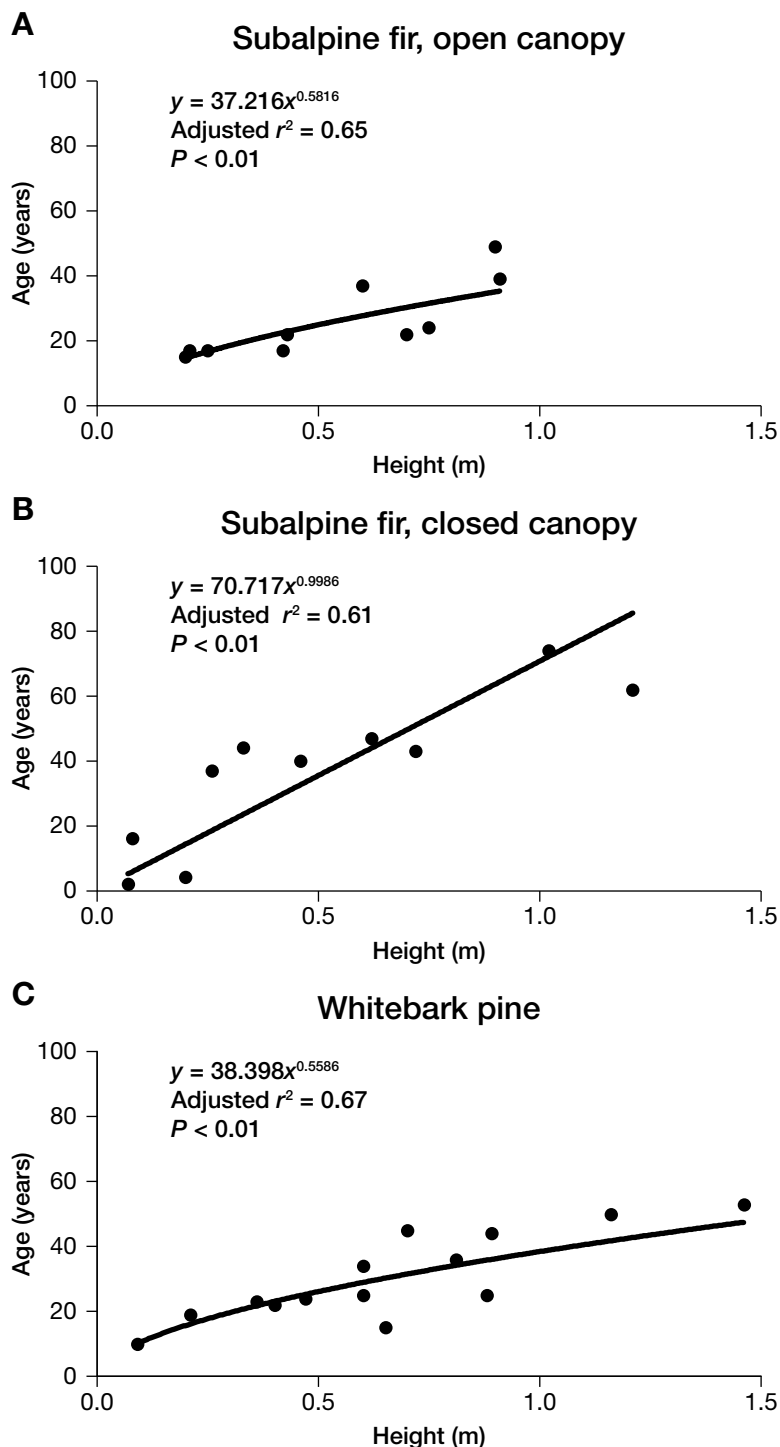


Figure 5—Relationships between age and height of subalpine fir seedlings (<1.3 m tall) in (A) open-canopy plots and (B) closed-canopy plots and (C) whitebark pine seedlings for the Olympic Mountain whitebark pine communities study. P = probability value; r^2 = coefficient of determination.

To represent trees that were counted by size class but not aged, we used these relationships to estimate ages for each of the seedling size class mid-point heights. Because we did not have a sufficient sample size for the other species, we estimated their ages by using these relationships as well. For Alaska cedar (*Callitropsis nootkatensis*), we used the subalpine fir relationships (depending on the seedling's overstory conditions). For western white pine, shore pine, and Douglas-fir, we used the whitebark pine relationship.

For trees ≥ 1.3 m tall, we sampled a subset of trees at breast height and as close to the soil surface as we were able. For trees sampled at the base, the age of the tree is the number of rings on the basal core. However, for various reasons, some of the sample cores were from up to 20 cm above the base. For these trees, we used the relationships derived from the seedling data (see fig. 5) to estimate the age to the height of the basal core-sample hole.

We sampled 29 subalpine fir and 28 whitebark pine trees at the base and at breast height and used this data to estimate age from stem diameter at breast height (table A2.2). One whitebark pine, which was much older than its diameter at breast height would suggest, was considered an outlier and not used. This tree grew in a cluster of whitebark pine and may have suffered from shade suppression for much of its life.

To estimate the age of trees ≥ 1.3 m tall that were not sampled, we used a relationship calculated from the trees that we had measured and bared at the base (see above). We fit separate linear regression curves for the basal age as a function of diameter at breast height for subalpine fir and whitebark pine (fig. 6). A strong linear regression model for subalpine

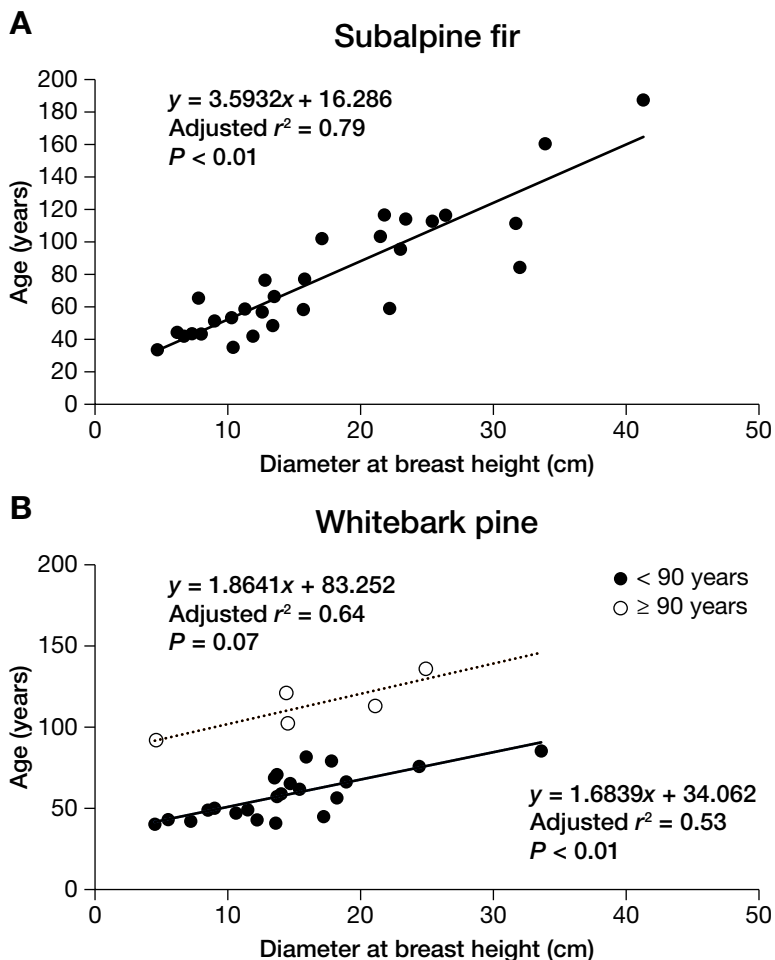


Figure 6—Relationships between age and diameter at breast height of (A) subalpine fir and (B) whitebark pine trees (≥ 1.3 m tall) for the Olympic Mountain whitebark pine communities study. For whitebark pine, the data was separated into two groups based on age. P = probability value; r^2 = coefficient of determination.

fir was derived (adjusted $r^2 = 0.79$). However, the relationship for whitebark pine was weak. A scatter graph of whitebark pine age to diameter at breast height suggested two separate populations existed, with a small population of 5 older trees (≥ 90 years) requiring a separate relationship from the larger, younger population of 23 trees (< 90 years) (fig. 6).

For trees with a breast-height core sample but no basal core sample, we used the mean number of years between the basal and the breast-height ages from the trees where both had been determined as an add-on. The add-on for subalpine fir was 28 years, and for whitebark pine, it was 26 years for trees < 90 years old and 41 years for trees ≥ 90 years old.

We used the relationships in figure 6 to calculate age estimates for trees that had not been core sampled. In the case of whitebark pine, we first calculated ages using the young tree formula. For trees estimated at ≥ 90 years, we recalculated ages with the older tree formula. However, there were only three whitebark pine trees ≥ 90 years old that did not have a core sample-derived age and therefore had to be estimated with the relationship for trees < 90 years old.

We core sampled 24 Douglas-fir trees at breast height. In addition, we sampled a 102-year-old Douglas-fir that was 23.1 cm d.b.h. at 10-cm height. The age of the 10-cm-high sample was 21 years older than the breast-height sample. One 0.5-m-tall Douglas-fir seedling had a basal age of 7 years. For trees sampled at breast height, the estimated number of years needed to reach 1.3-m height that was derived from the young whitebark pine data of 26 years was added to the rings counted at breast height to estimate total age. The age for the tree with the 10-cm-high basal core sample was used with no further correction and assumed to be a basal age. The estimated total ages for the 24 trees core sampled at breast and 10-cm heights were used together to estimate age from the diameter at breast height of trees that had not been sampled. We fit a linear regression through these points (fig. 7).

We used the relationship described in figure 7 to estimate the age of each tree on each plot that we measured for diameter at breast height but did not core sample. We used the measured age for core sampled trees but calculated the age for others. Species that did not have enough data to calculate separate relationships included western white pine, Alaska cedar, and shore pine. We used relationships for other species believed to be most appropriate to estimated ages for these species; for Alaska cedar, we used the subalpine fir equation, and for western white pine and shore pine, we used the whitebark pine equation for younger trees. We determined an origination date by subtracting the age of the tree from the year the core sample was extracted.

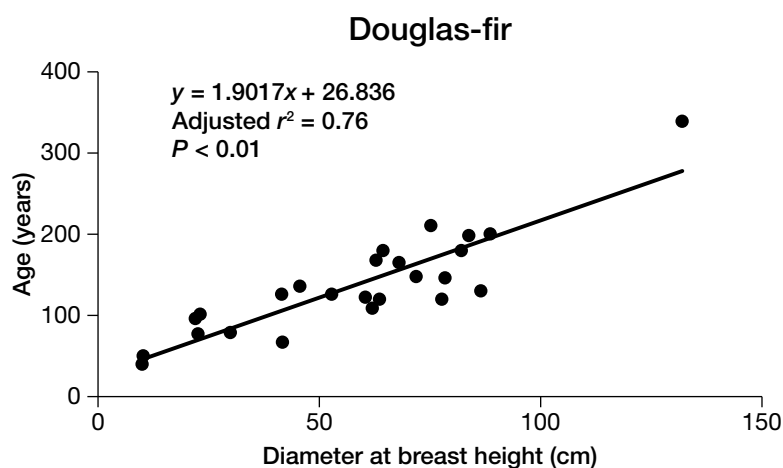


Figure 7—Relationship between Douglas-fir age and diameter at breast height of trees (≥ 1.3 m tall) for the Olympic Mountain whitebark pine communities study. P = probability value; r^2 = coefficient of determination.

FOLIAR NITROGEN AND CARBON—In the laboratory, the foliar samples for each plot and species were cleaned of materials older than the current season tissues. Also, buds and reproductive organs were removed. We dried the foliar samples in a 65 °C oven to a stable weight in paper bags. Then, we removed 100 fully intact needles from each sample, placed them in a paper envelope, and returned them to the oven. These were dried to a stable weight, which was recorded to the nearest 0.001 g. The percentage of carbon and percentage of nitrogen of the samples were determined with combustion analysis based on the dry weight of the samples by the Oregon State University Central Analytical Laboratory (Corvallis, Oregon).

Statistical Analysis

AGE CLASSES AND CALCULATION OF TREE DENSITIES—For trees ≥ 1.3 m tall, we calculated tree densities separately for live and dead trees. All the plots except for plot 4 were 0.05-ha plots, so each tree on the plot represented 20 trees per hectare. Plot 4 was a 0.1-ha plot, so each tree on that plot represented 10 trees per hectare. Each tree on a plot was assigned to a 10-year age class (0 to 10 years = age class 0, 10 to 20 years = age class 10, etc.). Thus, the age class is named for the lowest age in its range. The trees per hectare for each age class was the number of trees assigned to the class multiplied by the expansion factor appropriate for the plot size.

We used the diameter at breast height of the trees in each age class to calculate the total basal area per hectare by calculating the basal area represented by each tree, multiplying that basal area by the plot-appropriate expansion factor, and summing the expanded basal areas in the age class. We also calculated the average diameter at breast height and age for each age class. We used these calculated values to represent the age, size, and basal area structure graphically.

We examined the relationships between 12 temperature and physical site variables as well as summer soil moisture and the age of the oldest tree on the plot and stand basal area with Pearson product-moment correlation. We then selected the five strongest correlating variables and further analyzed their combined relationships using multiple linear regression. From this analysis we derived a strong explanatory model with two variables. We similarly analyzed the basal area of subalpine fir and whitebark pine separately.

For seedlings, we used the averages of the seedling plot data from 2014, 2016, and the original measurements done in 2007 through 2010 for all calculations and procedures. To calculate trees per hectare for each plot, we used the method described above for trees ≥ 1.3 m tall, except that the expansion factors appropriate for the seedling-nested plot were used (e.g., 3183.1 for 2-m-diameter subplot data). Many plots had no seedlings. Quantile-quantile plots indicated that the small-tree density per plot data had a decidedly nonnormal distribution. We analyzed the distribution of subalpine fir and whitebark pine seedlings within our study area with a Kruskal-Wallis nonparametric ANOVA. Specifically, we analyzed differences between the plot densities of seedlings of each species by aspect and elevation band. Similarly, we compared the plot densities of seedlings of subalpine fir with those for whitebark pine.

CORRELATIONS BETWEEN SPECIES CANOPY COVER AND AIR, SOIL SURFACE, AND SOIL TEMPERATURES—We selected 20 species from the total 194 for correlation analysis with temperature data. The species we selected met one of the following criteria: (1) occurred on at least 20 plots (14 species); (2) averaged at least 1 percent canopy cover over all plots (including 0 values) and had at least five occurrences (5 species); or (3) the species thinleaf

huckleberry (*Vaccinium membranaceum*), which had eight occurrences, and a mean canopy cover of 0.3 percent was added because of its plant community indicator value (Henderson et al. 1989).

To better understand the relationships between these species and their environments, we correlated species canopy cover with mean annual and monthly air, soil surface, and soil temperatures. Because of concerns over linearity and skewness of some of the data, we used Spearman correlation. Scatter graphs showed a mix of linear and nonlinear monotonic relationships. Also, some species canopy cover data was strongly skewed because of the presence of many zero values, and some temperature data was similarly skewed.

We calculated 65 mean temperature variables for each of the air, soil surface, and soil datasets over the 3 years of record for each plot. Included were 1 overall mean annual temperature, 4 overall quarter-day means, 12 overall monthly means, and 48 monthly by quarter-day means. For descriptive purposes, we present these data in graphical and tabular formats; we also used the 65 means as input for other statistical procedures (described below). For some analyses we made similar calculations using maximum and minimum temperature data. In all cases, we calculated standard deviations of the means.

The canopy cover for each of the 20 species was correlated with each temperature variable, producing 65 correlations per species. This was done for air, soil surface, and soil temperature data. To summarize these data, we graphically presented the number of significant correlations out of the 65 by air, soil surface, or soil temperature. At $P = 0.05$, we expect 3.3 falsely significant results among the 65 correlations purely by chance per species. We graphically presented the number of significant correlations for each species by month and quarter-day.

CORRELATIONS BETWEEN SPECIES CANOPY COVER AND SOLAR RADIATION—With the same 20 species described in the previous section, we used Spearman correlation to correlate species canopy cover from each plot with the mean annual and mean monthly potential direct and diffuse solar radiation and duration of direct solar radiation associated with each of the plots (calculated in ArcMap version 10.5.1) (ESRI 2017). We graphically presented the number of significant correlations by species.

EFFECTS OF SNOWPACK—To explore species preferences for growing in places where the snowpack melts in spring at different times, we calculated the mean Julian day and its standard deviation for when the snowpack melted (date of snowmelt) for all of the plots on which each of the 20 species was present and displayed this graphically. We also calculated the mean canopy cover for each of the 20 species from 36 plots where the snowpack melted in April, May, or June. Only one of these plots (plot 23) had its snowmelt occur in March, and because that was on the last day of March, it was included with the April data. For each species, we compared the canopy cover from the plots that melted out in each month with Kruskal-Wallis ANOVA to explore whether the species preferred sites based on month of snowmelt.

RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND SUMMER SOIL MOISTURE—We used the same set of 20 species used in the temperature analysis to look at the relationships between the percentage of canopy cover for each species and soil moisture. We also included the sum of the of canopy covers for species thought to be alternate hosts for white pine blister rust, which included harsh Indian paintbrush (*Castilleja hispida*), giant red Indian paintbrush (*Castilleja miniata*), mountain Indian paintbrush (*Castilleja parviflora*), elephanthead lousewort (*Pedicularis groenlandica*), sickletop lousewort (*Pedicularis racemosa*), mapleleaf

currant (*Ribes acerifolium*), and prickly currant (*Ribes lacustre*). Of these species, giant red Indian paintbrush and sickletop lousewort were by far the most common. We also summed the canopy covers of all species on each plot as an index of total vegetation (total canopy cover). For this analysis, we calculated Spearman correlation coefficients and their statistical significance. We ranked the species by their correlations and displayed them graphically to show their relationship to each other. We also examined the correlations between species richness and the age of the oldest whitebark pine tree on the plot with soil moisture.

RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND SUMMER SOIL MOISTURE AND TEMPERATURE—Using only the plots that had both soil moisture and temperature data and only species with at least three occurrences, we calculated a mean summer soil moisture for each species for all the plots on which each was present. Similarly, we calculated the 3-year mean air, soil surface, and soil temperatures for each of these species for the period of June through August. There were 29 plots and 73 species that met the criteria and were included in this analysis.

We then calculated the Spearman correlation coefficient for the correlations between canopy covers for each species and the mean soil moisture on the plot. We did the same for the correlations between canopy covers and mean soil temperatures for the period of June through August for each species. We graphically presented the correlations between species canopy covers and mean soil moistures and mean soil temperatures, and we indicated on the graph which values were significant at $P = 0.05$.

ORDINATION OF PLOTS BY SPECIES AND RELATIONSHIPS WITH OTHER VARIABLES—We used information in Henderson et al. (1989) as our starting point for the identification of plant associations. We used the term “plant association” to describe vegetation that was clearly similar to existing plant association descriptions, such as those described by Henderson et al. (1989). This publication provides keys, which we used to assign forested plots to a plant association. For other recognizable kinds of vegetation within our study area, we used the term “community type.” In some cases, others have recognized similar kinds of vegetation, but no other formal classifications of vegetation have been produced for the Olympic Peninsula.

Of the 40 plots where we recorded detailed vegetation data, 23 fit into the plant association classification of Henderson et al. (1989). However, theirs was a classification only of forested plant associations, and many of our plots were either alpine or other nonforested plant communities, and a few plots were unique forested communities that would not key to any association in Henderson et al. (1989).

Because we located our plots at random, some plots overlapped more than one plant community or fell on landforms not encountered by Henderson et al. (1989). Two plots overlapped a talus boulder field and vegetation developing along its edge, two plots overlapped subalpine fir krummholz and alpine subshrub communities, and two plots partially overlapped a riparian community but otherwise represented upland vegetation.

Assuming cohesiveness within plant communities and that their relationships to other communities are partly or largely functions of environmental gradients, we used ordination to analyze all species over multiple plots. Ordination enables the generation of hypotheses about environmental gradients from species abundances because major environmental gradients are generally few and simultaneously affect numerous species (Gauch 1982). The interpretation of ordination results rests on data and insight external to the ordination analysis itself, and toward that end, we employed joint plots and individual species correlation analyses. Although individual species tell us a lot about the physical environment in

which they are found, they are at the same time responding to competitive and historical influences, which in this context represent noise. Environmental variation generally affects numerous species in complementary or parallel ways, whereas noise involves uncoordinated or random variations in single species (Gauch 1982).

We used nonmetric multidimensional scaling (NMDS) for our ordinations, which uses a nonparametric rank order correlation approach that makes few assumptions about the nature of the data. Thus, it is suited to nonnormal data and tends to linearize the relationship between environmental distance and sociological distance (Beals 1984), while relieving the zero-truncation problem, which is present in all ordinations of heterogeneous datasets (McCune and Mefford 2006). NMDS is not an eigenvalue-eigenvector technique that ordination axis 1 explains the greatest amount of variance, and ordination axis 2 explains the next greatest amount, etc. As a result, an NMDS ordination can be rotated, inverted, or centered as desired (Holland 2008).

To explore the relationships between temperature, snowpack, solar radiation, physical site, and vegetation variables and the ordination axes, we used 26 plots with 179 species associated with the 3-year dataset, as those were the plots with continuous and consistent temperature data. We included in this ordination a secondary matrix consisting of 209 variables to investigate in conjunction with the ordination axes. These variables included 192 temperature-related variables, including mean annual, monthly, and quarter-day air, soil surface, and soil temperature measurements. Also, mean soil moisture data measured in July or August were used. We also included elevation, slope steepness, aspect, two measurements of snow duration, coarse fragment content, litter layer depth, PAR measured at ground level and 1.3-m height, overstory and understory canopy closure, total canopy cover on the plot, maximum diameter at breast height and height of trees on the plot, and canopy covers of subalpine fir and whitebark pine.

To evaluate the relationship between the variables in the secondary matrix and the floristic ordination, we used the joint plot (biplot) procedure in PC-ORD version 5.31 (McCune and Mefford 2006). This procedure calculates a correlation coefficient for each variable with each ordination axis. A diagram called a joint plot is produced to show the relationships between the variables and ordination scores consisting of lines radiating from the centroid of the ordination. The angle and length of each line indicate the direction and strength of the relationship. For a given variable, the line forms the hypotenuse of a right triangle with the two other sides being r values between the variable and the two axes. The r values determine the relative scaling of the vectors. The absolute scaling is arbitrary. Weak variables are eliminated from the diagram by selecting a joint plot r^2 cutoff value, which we set at $r^2 = 0.5$.

ORDINATION OF ALL PLOTS BY ALL SPECIES—We also used PC-ORD version 5.31 (McCune and Mefford 2006) to conduct NMDS ordination with all the plots and species to reveal floristic relationships among the plots. The data input for the ordination were canopy cover for the 220 species found on 40 plots. We specified acceptance of all default settings for the slow and thorough mode, including Sorensen distance measure, three axes, and a step length of 0.20.

SPECIES RICHNESS—We used Pearson product-moment correlation analysis to examine relationships between species richness and 7 physical site variables; 7 measured light or canopy cover variables; 40 potential solar variables; and 560 air, soil surface, and soil temperature variables. These variables were previously described in the soil moisture section. Also included in the analysis were 20 plot-level tree variables (such as size, age,

nutrient status, canopy cover and closure) and 5 indicators of white pine blister rust impact. There were 34 plots included in this analysis. Given a significance level of $P < 0.05$, we would expect 5 percent of the tests to yield significant results purely by chance. In the case of the 560 air, soil surface, and soil temperature correlations, this would be 28 of the tests.

TREE GROWTH AND AGE—To estimate tree growth in diameter as a function of age, we used the same data that we used to determine tree age as a function of diameter (previously described). We used linear relationships to estimate the height of seedlings from the measured age of subalpine fir seedlings grown in closed- or open-canopy plots as well as for whitebark pine seedlings, which were all grown in open-canopy plots. For larger trees, we also fitted separate linear regression curves for stem diameter at breast height as a function of basal age for subalpine fir, whitebark pine (<90 years and ≥ 90 years separately), and Douglas-fir.

BASAL AREA RELATIONSHIPS—We defined the stem basal area per plot as the total basal area from all trees on the plot that were ≥ 1.3 m tall. We calculated the stem basal area in square centimeters for each measured tree from its diameter at breast height measurement as the area of the circle with a diameter equivalent to the tree's diameter at breast height. Because all trees ≥ 1.3 m tall on the plot were measured, we could calculate the total basal area for the plot as a summation of the individual tree basal areas or the total for each species by summing their basal areas separately. As we knew the plot area, we were also able to calculate these values on a per hectare basis.

We used Pearson product-moment correlation analysis to explore relationships between plot-level basal area and physical and biological plot-level characteristics, including elevation; aspect; slope steepness; summer soil moisture calculated from 5 years of data; the number of frost-free days in the growing season; the mean annual air temperature based on 3 or 5 years of data; the mean growing-season air temperature; the mean annual soil temperature based on 3 or 5 years of data; the mean monthly air temperatures for June, July, August, and September; the mean monthly temperatures for June, July, August, and September; the mean summer soil temperatures (June through August); the plot overstory canopy closure; the maximum tree height for the plot; and the maximum tree age for the plot. This analysis was carried out for total plot basal area and the basal area of the two main tree species, subalpine fir and whitebark pine.

We used simple and multiple linear regression to describe basal area per hectare as a function of some of the same physical variables. We report the strongest linear relationship that we found for total basal area and also for subalpine fir and whitebark pine basal areas.

STAND STRUCTURE BY AGE CLASS, ELEVATION, AND ASPECT FOR TREES ≥ 1.3 M TALL—We used tree data from our plots to calculate the density of trees ≥ 1.3 m tall overall in the study area by species. We then stratified the tree density data by species into decadal age bins to present the overall age class structure of the study area by species. We further stratified these data into three elevation bands (previously described) and three aspect groups (previously described) to show fundamental habitat preferences and establishment patterns for each species in terms of tree density as a function of decadal age class. We also calculated the basal area in square meters of each measured tree, summed them by the decadal age class, and used the appropriate expansion factor for the plot to give the basal area in terms of square meters per hectare. We graphically presented basal area by age class for each species by elevation and aspect. We calculated the Spearman correlation coefficients for the correlations between plot-level density of trees ≥ 1.3 m tall and plot elevation for each species, which we presented in tabular format. We also calculated the Spearman correlation coefficients for the correlations between sample tree age and elevation by species.

HABITAT RELATIONSHIPS FOR SEEDLINGS (REPRODUCTION)—We used Kruskal-Wallis nonparametric ANOVA to compare the number of live or dead subalpine fir seedlings (trees <1.3 m tall) that we found on our plots with the number of whitebark pine seedlings on our plots. The number of seedlings on our plots had a highly nonnormal distribution due to many plots having no seedlings at the time of record. We also used the same technique to compare the data from each tree species (live and dead trees separately) by three aspect groups and three elevation bands (previously described).

We further examined habitat preferences of subalpine fir and whitebark pine seedlings by correlating the plot-level density of trees <1.3 m tall (seedlings per hectare) with several indicators of site conditions. We calculated the Pearson product-moment correlation coefficient and probabilities for correlations between seedling density and ground-level PAR; overstory canopy closure; density of all trees ≥ 1.3 m tall (trees per hectare); basal area of trees ≥ 1.3 m tall (square meters per hectare); mean annual soil temperature; mean seasonal soil temperature (defined by the period between when the soil temperature rose above 3.2 °C in spring and when it dropped below that temperature in fall); mean summer (over June through August) air temperature; and mean monthly air temperatures for July, August, and September.

STANDING DEAD TREES (SNAGS ≥ 1.3 M TALL)—We used graphical and tabular methods to compare the overall tree density and the tree density by 10-cm-d.b.h. size classes of live and dead trees ≥ 1.3 m tall by species. We used these figures to calculate the percentage of dead trees for further comparison. We also graphically presented dead stem density data by 10-cm-d.b.h. size classes according to a matrix of three elevation bands by three aspect groups (previously described).

COARSE WOODY DEBRIS—We presented our coarse woody debris (CWD) data graphically and in tabular format in terms of its volume (cubic meters per hectare) by decay class (previously described), 10-cm stem diameter size classes, and species, in combination with aspect and elevation. We also graphically presented the volume of CWD by plant association. We used ANOVA to compare the mean diameter of all CWD by three elevation bands and three aspect groups (previously described). We further used ANOVA to compare the mean volume of all CWD among the seven combinations of the aspect and elevation bands that were populated in our sample. When there was a significant difference, we used a Tukey honestly significant difference (HSD) test to locate the differences in the seven groups.

SURFICIAL ORGANIC LAYER (LITTER) DEPTH—We investigated potential factors that influenced accumulation of litter with linear regression. We selected fifteen variables including several temperatures, mean summer soil moisture, physical site variables, stand basal area, and the age of the oldest tree on the plot. We calculated the Pearson correlation coefficient for correlations between litter depth and each of these variables and selected the five variables with the strongest correlations for further analysis. We used combinations of these five variables in multiple linear regression models and selected the strongest model, which had just two variables. We also calculated the mean litter depth for each plant association and compared the results graphically. For plant associations with at least four plots, we used ANOVA and Tukey HSD tests to compare their means.

FOLIAR NITROGEN AND CARBON—We compared percentages of nitrogen and carbon and the carbon-to-nitrogen ratios of subalpine fir and whitebark pine foliage by using ANOVA. We used Pearson product-moment correlation to explore the similarities and differences in how the two species responded to their environments in terms of their nitrogen, carbon, and carbon-to-nitrogen ratios. We also used Spearman correlation to examine the relationships between the foliar percentages of nitrogen and carbon from these species and various site, temperature, and vegetation variables.

WHITE PINE BLISTER RUST INFECTION OF WHITEBARK PINE—In most of our analyses, we used individual tree (stem) data, or if aggregated, we aggregated the data by plot. However, whitebark pine often grows in clumps, which result from multiple, separate stems emerging from the ground, or in some cases, simply by lower stem branching (Weaver and Jacobs 1990). Some surveys and studies of whitebark pine have been conducted at the clump level (Shoal and Aubry 2004, 2006; Weaver and Jacobs 1990). We present our results in separate sections for clump-, tree-, and plot-level data.

For the clump-level analysis, we assigned each stem to a clump at the time of data collection on all but one plot (plot 29). Trees growing as single stems were considered single-stemmed clumps. The white pine blister rust infection severity code assigned to the clump was the most severe code given to any stem in the clump, which follows previously established methods (Shoal and Aubry 2004). We calculated the mean and standard deviation of the blister rust infection severity codes for all clumps at our site for comparison with similar calculations by stem (tree level) and with previously published data.

For the tree-level analysis, we reported the percentage of infected whitebark pine trees in each of the blister rust infection severity codes (1 through 4) as well as the overall percentage of all whitebark pine trees that were infected for data collected in the first plot measurements (2007 through 2010) and in 2013 and 2016. For infected trees, we similarly reported the percentage of the crown that was dying or dead (data collected only in 2013 and 2016). We reported the mean and standard deviation for the blister rust infection severity code of all infected trees in the 2007 through 2010, 2013, and 2016 datasets.

We calculated the mean and standard deviation for whitebark pine age and diameter at breast height (cm) for the trees in each blister rust infection severity code (0 through 4). For each tree, we assigned the plot elevation (m), slope steepness, aspect, and summer soil moisture and calculated mean and standard deviation by blister rust infection severity code (thus, plots with many infected trees are weighted more heavily). We used ANOVA to compare the means for each variable by blister rust infection severity code for each variable and report the *P* value for each of the comparisons.

For the plot-level analysis, we calculated three white pine blister rust infection severity indicators for the 27 plots on which whitebark pine was found: (1) the average blister rust infection severity code of all the infected whitebark pine stems on the plot, (2) the number of infected whitebark pine trees on the plot, and (3) the average percentage of each whitebark pine tree's crown estimated to have died of the infection on each plot. We used Spearman correlation to explore the relationships of these three indicators with each other and to several plot-level physical and biological parameters.

The plot physical parameters that we analyzed were elevation, slope steepness, aspect, PAR at ground-level and 1.3-m height, and summer soil moisture. The biological parameters included whitebark pine canopy cover on the plot, species richness, and the summed canopy cover of all potential alternate host species for white pine blister rust.

Similarly, we also used Spearman correlation analysis to explore the relationships between the three blister rust severity indicators and potential direct solar radiation, the calculated direct duration of potential solar radiation, and potential diffuse solar radiation by month and year (total of 40 variables).

We also used Spearman correlation analysis to explore the relationships between air, soil surface, and soil temperature and the three blister rust severity indicators. We analyzed temperature variables annually, monthly, and monthly by quarter-day (a total of 540

variables). We present the temperature analysis as tallies of significant correlations by month or quarter-day.

According to Hansen and Patton (1975), white pine blister rust germ tube development is most vigorous between 9 and 15 °C, and because of light and moisture sensitivity, most germination occurs at night. We reasoned that more infections, and ultimately more serious infections, would occur in areas where these temperature conditions are more common. We examined this idea by using correlation analysis. We selected the air temperature records for June through November from the 3-year dataset for plots on which whitebark pine was found, as this encompasses the snow-free period when white pine blister rust is most physiologically active. From these months, we selected the first and fourth quarters of the day (hereafter quarter-days 1 and 4), as these represent the period from 1800 to 0600, which encompasses the night hours. We calculated the total number of air temperature measurements taken during these hours for each month and the total number of air temperature measurements between 9 and 15 °C in this period for each month. With these, we calculated the percentage of temperatures each month that fell in the 9 to 15 °C temperature range. Also, for each month, we calculated the mean of the temperatures that fell in the 9 to 15 °C temperature range for each month.

We calculated Pearson product-moment correlation coefficients for correlations between mean white pine blister rust infection severity code for each plot and the mean monthly (July, August, September, October, and November) percentage of time in quarter-days 1 and 4 that temperatures fell between 9 and 15 °C for each plot.

FIRE AND ESTABLISHMENT HISTORY—We did not conduct a formal fire history study of the area. Nevertheless, we recorded some relevant observations. Most of these observations were of a qualitative nature in the form of notes made on and off plots. We made notes of bark char, the lack of soil charcoal, and apparent scars on some Douglas-fir trees. We also noted pitch-soaked rings and other evidence of potential fire scarring on core samples. These observations allowed us to determine the presence or absence of recent fire in the study area and if present, where it had occurred.

The large numbers of trees that we measured and for which we determined age provided a way to study the establishment history, which revealed further clues relative to fire history. By graphically displaying the establishment year of each tree, periods when more or fewer trees established can be visualized, which formed the basis for our analysis. These observations allowed us to look for abrupt cohort signatures that generally follow stand-replacement fires as opposed to more gradual occupation suggestive of a primary invasion associated with changing climate.

Results

Physical Environment

Tables A2.3 and A2.4 provide general physical and geological characteristics of each plot. Although the sample area is only 144 ha, there is considerable variation in physical characteristics because of the steep and complex topography. The plot elevation ranged from 1420 to 1893 m (mean = 1673 m). Aspects were limited to the western hemisphere, but they ranged from 192 to 360°, while slope steepness ranged from 10 to 82 percent. There were two rock types present: basalt and argillite. Coarse fragment content varied from 1 to 100 percent, and the soil texture consisted mostly of loamy sands, sands, or sandy loams, but two

plots consisted mostly of boulders. Summer soil moisture measurements varied from 0 to 12.7 percent in the top 12 cm of soil, the mean annual air temperature varied from 1.1 to 4.1 °C, and the number of frost-free days ranged from 48 to 132.

Air Temperature

1.5- AND 3-M-HIGH TEMPERATURES—

- Air temperatures came primarily from 3-m-high sensors.
- Temperature at 3-m height averaged 0.24 °C lower than at 1.5-m height but differed slightly more in winter.

We reported the lesser of air temperatures recorded by 1.5- and 3-m-high sensors. In practice, this means that they were primarily from the 3-m-high sensor, as that sensor typically recorded the lower temperature of the two. Over all plots and years, the 3-m-high sensor averaged 0.24 °C lower temperatures than the 1.5-m-high sensor, and 3-m-high sensor temperatures were, on average, lower than the 1.5-m-high sensor temperatures in all months of the year. Although we saw no pattern relative to the physical environment, there was a seasonal pattern. The difference was greatest during the period of deepest snow depth, from January through March (0.5 to 0.8 °C) and least during the period without snow, from June through October (0.1 to 0.2 °C).

The temperatures at 1.5- and 3-m heights were significantly different on some but not all plots (table 1). In winter, almost half of the plots yielded significant temperature differences between sensor heights, but in summer, it was fewer than one-quarter of the plots. Thus, the difference between the 1.5- and 3-m-high temperatures was small but larger in winter than in summer. The plots with significant differences included some of our lowest and highest elevation plots, some of the coolest and warmest aspects, and they included both closed- and open-canopy plots.

Table 1—Number of Olympic Mountain Whitebark Pine Community study plots showing differences between air temperatures recorded at 1.5- or 3-m heights by significance using the indicated test statistic from analysis of variance with 3-year data based on 29 plots

Period	Significance ^a		
	<i>P</i> = 0.05	<i>P</i> = 0.10	<i>P</i> > 0.10
	NUMBER OF PLOTS		
June through October	7	2	20
January through March	14	5	10
All months	8	1	20

P = probability value.

Note: Differences were tested using analysis of variance with 3-year data based on 29 plots.

^a *P* = 0.05 is significant, *P* = 0.10 is marginally significant, and *P* > 0.10 is not significant.

Air microclimatic overview

- The mean annual air temperature varied 1.4 °C over 3 years.
- Over the 3 years, the maximum air temperature recorded was 31.1 °C, and the minimum was −21.5 °C.
- Mean monthly air temperature standard deviations among plots varied little.

Year 1 (September 2011 through August 2012) was generally the coolest year, but the three sample years were similar, especially years 2 (September 2012 through August 2013) and 3 (September 2013 through August 2014) (fig. 8). Year 1 was cooler than years 2 and 3 in all months except December and February.

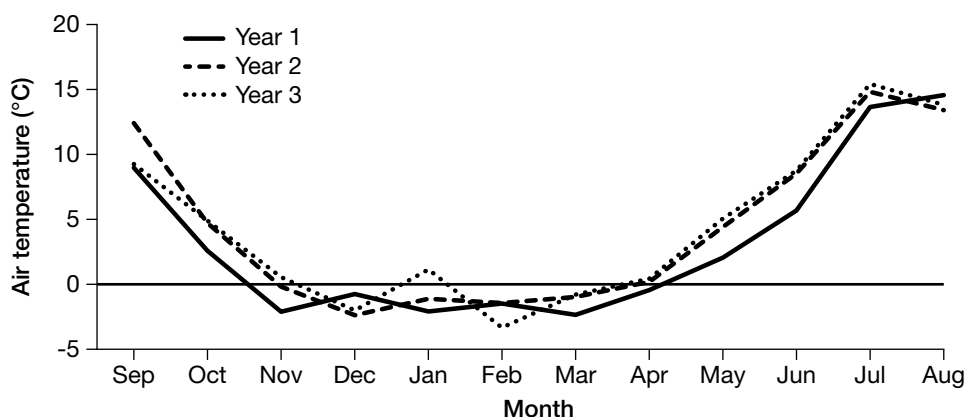


Figure 8—The annual cycle of mean monthly air temperatures for the Olympic Mountain whitebark pine communities study. Each mean is based on all the recorded temperatures (day and night) over the course of the month. Year 1 = September 2011 through August 2012, year 2 = September 2012 through August 2013, and year 3 = September 2013 through August 2014.

Over all plots, the mean annual air temperatures of the 3 years varied by 1.4 °C (table 2). In year 1, the maximum air temperature recorded (30.5 °C) occurred on August 17 at 1846 on plot 8. In year 2, the maximum air temperature (29 °C) occurred on June 30 at 1531 on plot 11. In year 3, the maximum air temperature (31.1 °C) occurred on August 9 at 1602 on plot 11. In year 1, the minimum air temperature recorded (−19.5 °C) occurred on January 16 at 0642 on plot 18 (table 2). In year 2, the minimum air temperature (−15.5 °C) occurred on January 11 at 0946 on plot 37. In year 3, the minimum air temperature (−21.5 °C) occurred on December 7 at 0653 on plot 29. This temperature occurred again on February 9 at 0048 on plots 29 and 30 and again at 0452 on plot 31. The plots exhibiting these minimum temperatures were in the upper third of elevation in our study area.

The standard deviation of mean monthly air temperatures among plots varied little across the year (ranging from 1.1 °C in May to 0.61 °C in December) compared to standard deviations of mean monthly soil surface and soil temperatures (fig. 9). At the soil surface, the standard deviation of the mean monthly air temperature ranged from 3 °C in July to 0.4 °C in March, and for soil temperatures, the range was 3.4 °C in July to 0.7 °C in January (fig. 9).

Table 2—Annual air, soil surface, and 20-cm-deep soil temperatures measured September 2011 through August 2014 for the Olympic Mountain whitebark pine communities study

Year	Air temperature			Soil surface temperature			Soil temperature		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max	Mean (SD)	Min	Max
DEGREES CELSIUS									
1	2.1 (7.2)	−19.5	30.5	4.1 (8.6)	−11.5	58.5	3.7 (5.9)	−7.0	27.5
2	3.3 (7.4)	−15.5	29.0	5.4 (9.0)	−12.5	57.5	5.1 (6.0)	−1.0	27.0
3	3.5 (7.4)	−21.5	31.1	4.3 (8.2)	−16.0	56.5	3.8 (5.5)	−14.0	27.0

SD = standard deviation.

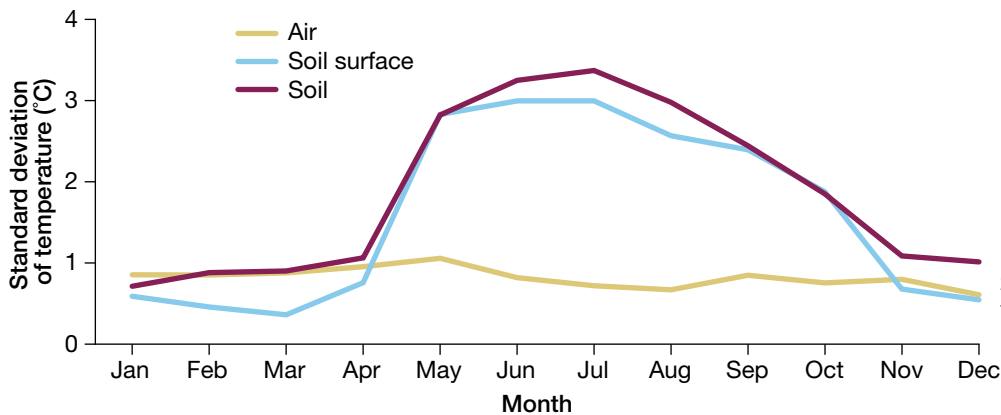


Figure 9—Standard deviations of mean monthly air, soil surface, and 20-cm-deep soil temperatures for the Olympic Mountain whitebark pine communities study.

TEN MAXIMUM AND TEN MINIMUM AIR TEMPERATURES FROM EACH PLOT AND YEAR—

- August had more of the maximum air temperatures than any other month, but July was the warmest on average.
- January had more of the minimum air temperatures than any other month, but December and February were colder on average.
- Nearly all the plots contributed to the dataset of the 10 maximum and 10 minimum air temperatures.

The 10 maximum air temperatures for each year occurred in the months of June through September. The greatest proportion of the 10 maximum air temperatures occurred in August, although this peak was only slightly higher than in July (fig. 10). Of the 29 plots with the maximum air temperature data, all contributed at some point in July through September, and 24 plots contributed in June (fig. 10).

The 10 minimum air temperatures from each plot and from each of 3 years occurred from October through April, but more occurred in January than in any other month (fig. 11). The mean of the minimum monthly air temperatures was lower in February and December than in January (fig. 11). Most of the plots contributed to the 10 minimum air temperatures from November through March, but only one plot each contributed in April and October (fig. 11). Most of the plots contributed to the 10 minimum soil surface temperature and 10 minimum soil temperatures only in November through January.

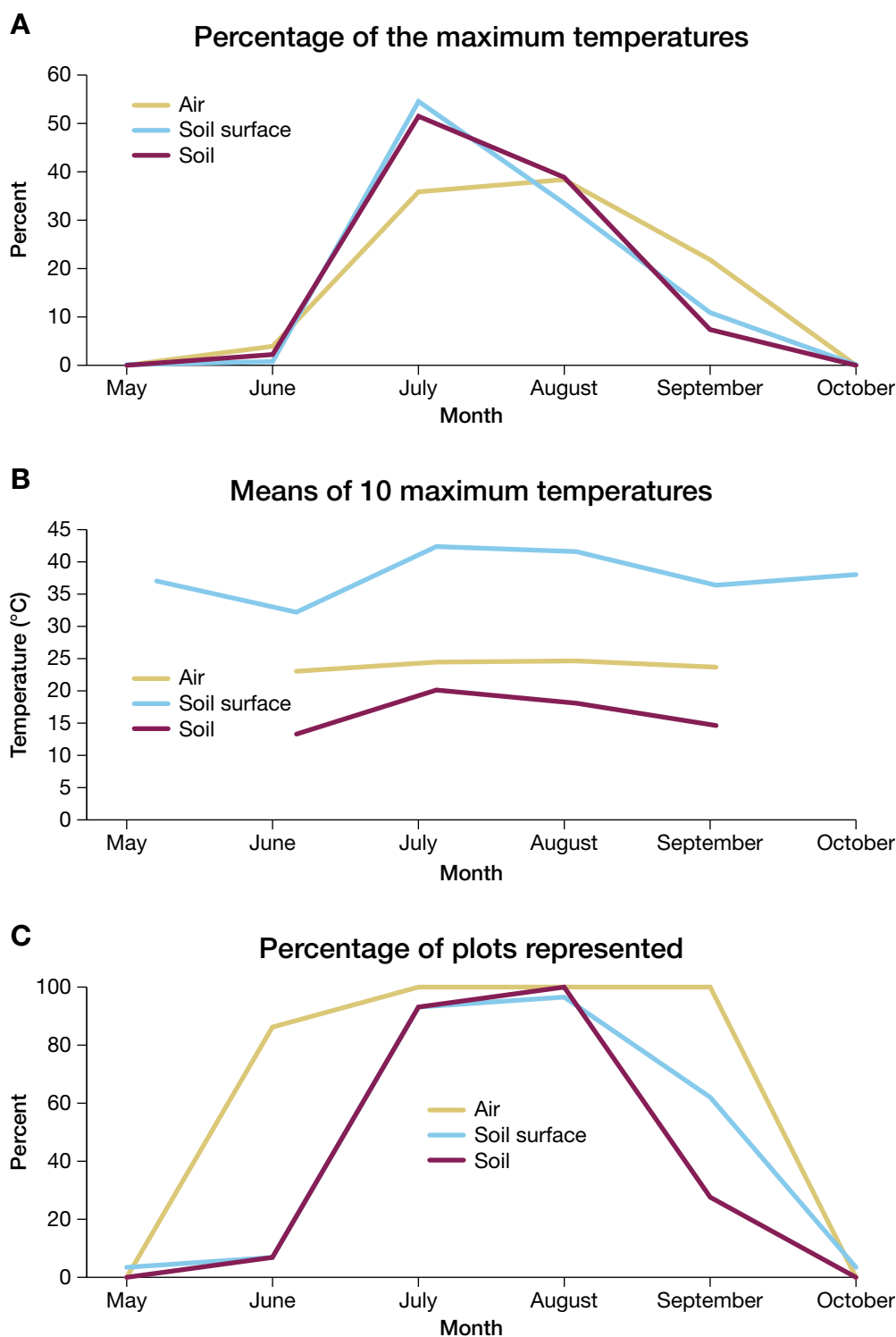


Figure 10—(A) The percentage of maximum air, soil surface, and 20-cm-deep soil temperatures that occurred in each month based on the 10 maximum temperatures recorded for each plot in each of 3 years (30 total measurements) of the Olympic Mountain whitebark pine communities study. (B) Means of the 10 maximum air, soil surface, and 20-cm-deep soil temperatures from each plot in each of 3 years that occurred in each month. (C) Percentage of plots over which the above monthly data was distributed.

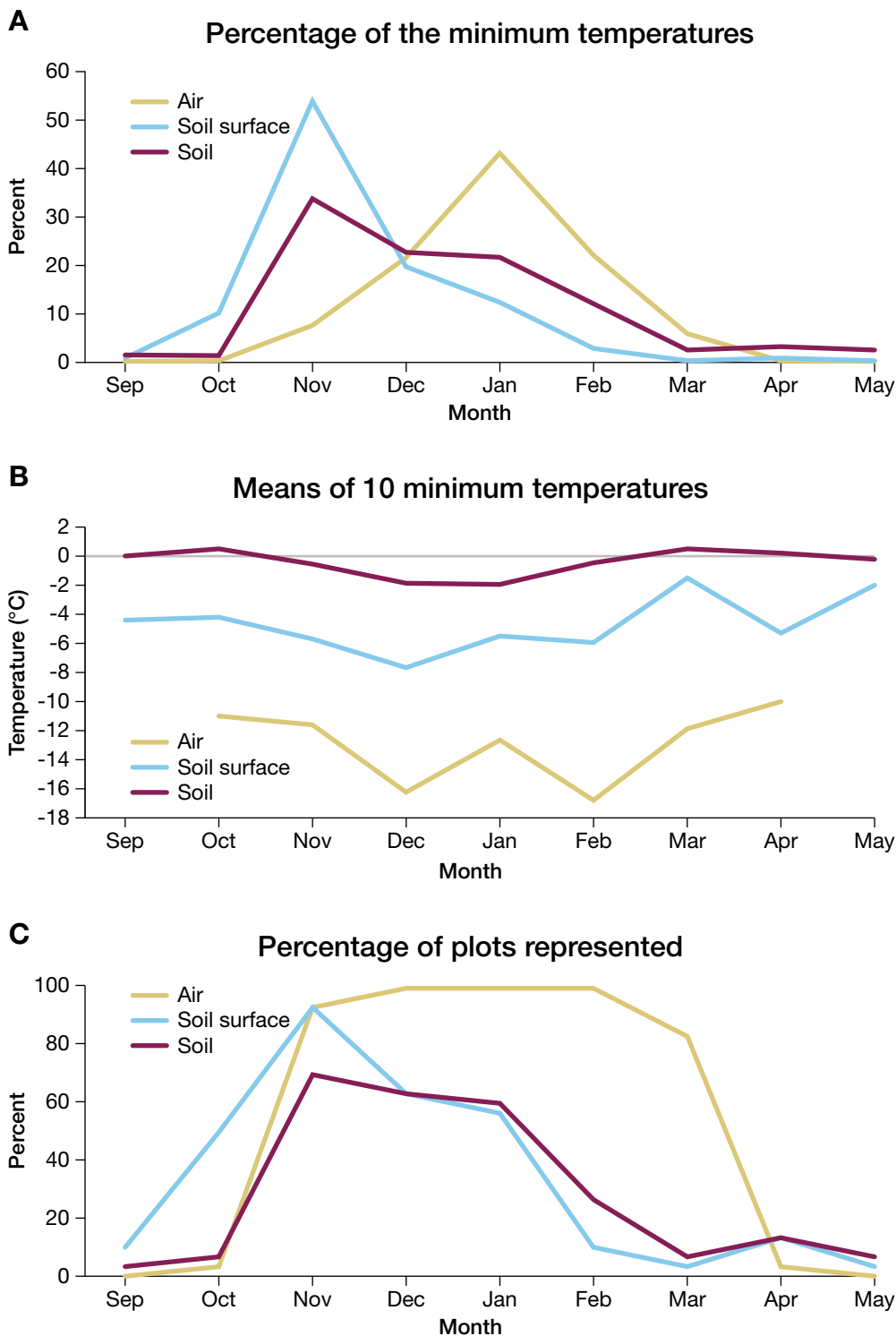


Figure 11—(A) The percentage of minimum air, soil surface, and 20-cm-deep soil temperatures that occurred in each month based on the 10 minimum temperatures recorded for each plot in each of 3 years (30 total measurements) of the Olympic Mountain whitebark pine communities study. (B) Means of the 10 minimum air, soil surface, and 20-cm-deep soil temperatures from each plot in each of 3 years that occurred in each month. (C) Percentage of plots over which the above monthly data was distributed.

FREEZING AIR TEMPERATURES—

- Freezing air temperatures occurred somewhere in the study area in all months of the year but were fewest in August.
- From November through April, air temperatures were freezing more than 60 percent of the time (81 percent in February).

Freezing air temperatures were recorded in all months of the year, although in August, they occurred on only three plots (plots 8, 30, and 35) (fig. 12). Plot 8 received cold-air drainage, and plots 30 and 35 were ridgetop plots with considerable exposure for radiative heat loss at night. From November through April, air temperatures were freezing more than 60 percent of the time, and in February, they were freezing 81 percent of the time (fig. 12). The greatest variation among the plots in terms of freezing frequency occurred in April, but in general, the variation was higher from January through May than at other times of the year.

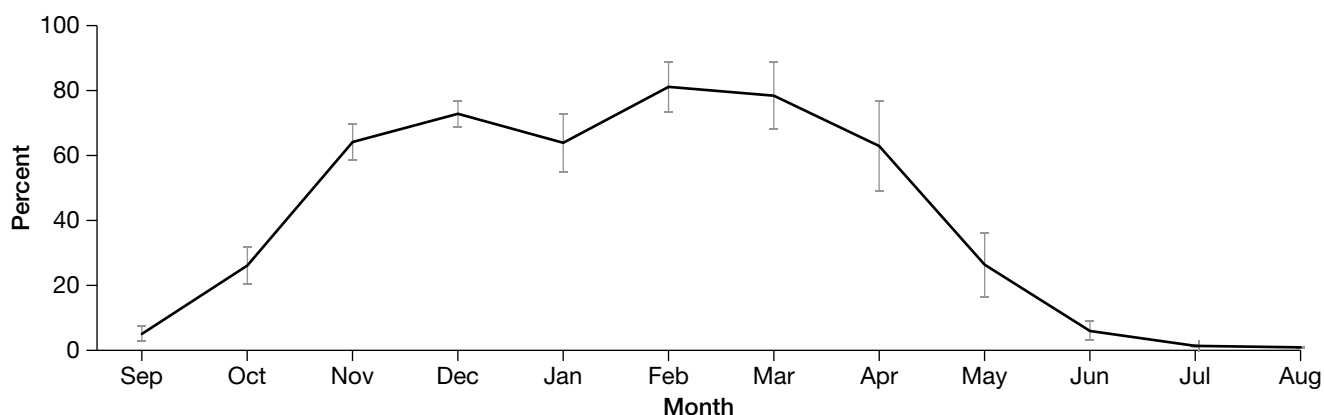


Figure 12—Mean percentage of air temperature measurements at or below 0 °C in each applicable month across all plots over 3 years of the Olympic Mountain whitebark pine communities study. Error bars show one standard deviation above and below the mean.

FROST-FREE INTERVALS—

- Frost-free intervals on plots varied from 48 to 132 days and averaged 94 days.

Of the 29 plots for which we had continuous air temperature data, the minimum frost-free interval (48 days) occurred on plot 7, the maximum frost-free interval (132 days) occurred on plot 23, and the average of all plots was 94 days (SD = 18.9) (table A2.3). All the plots with a frost-free season of fewer than 90 days were in frost pockets (plots 7, 8, 13, and 18) or on an open upper slope of a ridge (plots 12, 28, 29, 30, 31, and 35). Other plots in frost pockets and ridge positions also tended to have short frost-free seasons. For example, plots 32 and 6 were near ridgetops with frost-free seasons of 92 and 96 days, respectively. Plot 23, with the longest frost-free season, was the lowest elevation plot and was situated on a lower slope (but well above the valley bottom) facing southwest. Nine of the twelve lowest elevation plots had frost-free seasons of at least 100 days.

SNOTEL AND MOUNT TOWNSEND DATA ANALYSES—

- Of the four SNOTEL weather station sites from which we collected mean, maximum, and minimum annual temperatures, Waterhole was most similar to the study area (mean annual air temperature = 3.6 °C compared to 1.1 to 4.1 °C for plots in the study area).
- The study area lapse rate estimated the annual air temperature at Waterhole within 0.1 °C.
- The record from Mount Townsend was similar to those from our cooler forested sites, and our overall lapse rate estimated a mean annual air temperature at Mount Townsend that was 0.5 °C higher than the measured mean annual air temperature.

The four SNOTEL sites in the Olympic Mountains are all lower in elevation and had higher mean annual air temperatures than our site (table 3). The Waterhole site was closest to our site in terms of elevation and mean annual air temperature. Waterhole's mean annual air temperature of 3.6 °C lay within the range of our plot mean annual temperatures (1.1 to 4.1 °C). By using our site-level lapse rate (see below) to predict the mean annual air temperature of the SNOTEL sites, two of the four were estimated within 0.1 °C (table 3).

Table 3—Environmental variable data for four SNOTEL sites in the Olympic Mountains and the Olympic Mountain whitebark pine communities study site for comparison

Variable	Dungeness	Mount Crag	Waterhole	Buckinghorse	Study site
Distance from the study site (km)	8	10	26	26	0
Direction from the study site	NE	SE	NW	SW	NA
Elevation (m)	1222	1207	1527	1484	1673
Mean annual air temperature (°C)	6.0	5.1	3.6	5.1	2.7
Maximum air temperature (°C)	29.9	29.7	27.8	27.3	30.2
Minimum air temperature (°C)	−15.9	−16.6	−19.9	−17.4	−18.8
Mean annual soil temperature (°C)	—	—	—	3.0	—
Maximum soil temperature (°C)	—	—	—	12.1	—
Minimum soil temperature (°C)	—	—	—	0.1	—
Estimated mean annual air temperature (°C)	5.0	5.1	3.5	3.7	—
PRISM model precipitation (mm)	1320	1884	1759	2604	1810 to 2404

— = no data; PRISM = Parameter-elevation Relationships on Independent Slopes Model.

Note: SNOTEL site mean temperatures were based on 3-years of data, and soil temperatures were taken at 20-cm depth.

The record from Mount Townsend, although from different years and 9 km away, is similar to that of cooler forested sites in the study area (fig. 13). The mean annual temperatures for the period of record were 2.4 °C for air and 2.8 °C for 3-cm-deep soil, 2.8 °C for 20-cm-deep soil, 2.7 °C for 50-cm-deep soil, and 2.6 °C for 100-cm-deep soil. All the mean temperatures, including the air temperature, were similar in early October and late April through late May (fig. 13). These data indicate that snowmelt occurred on May 4, 1994; May 23, 1995; May 25, 1996; May 21, 1998; and July 12, 1999.

The overall relationship we derived to calculate the lapse rate for our study site (see below) predicts that the mean annual air temperature at the Mount Townsend site was 2.9 °C (0.5 °C higher than the measured mean annual air temperature).

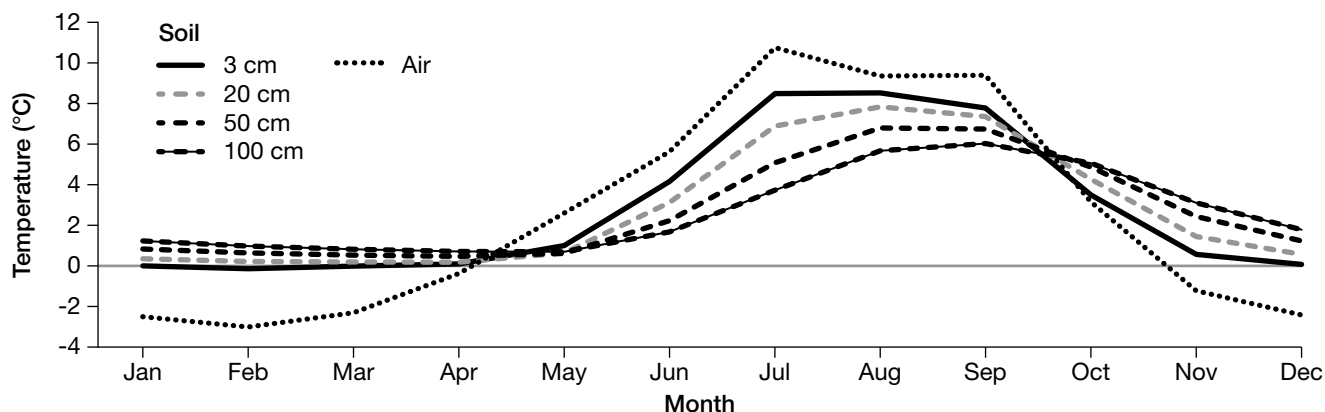


Figure 13—Mount Townsend mean monthly air and soil (at 3-, 20-, 50-, and 100-cm depths) temperatures averaged over 5 years of the Olympic Mountain whitebark pine communities study.

Soil Surface Temperature

SOIL SURFACE MICROCLIMATIC OVERVIEW—

- Soil surface temperatures varied little in winter, warmed rapidly after snowmelt, and peaked in July.
- Over the 3 years, the maximum soil surface temperature was 58.5 °C, and the minimum was –16 °C.
- Snow began to moderate soil surface temperatures in November and December and lasted into April on most plots and into June on a few plots.

The mean soil surface temperatures were lower in most months of year 1 than in years 2 and 3, which were similar to each other (fig. 14). The differences among years from December through March were negligible. Variation in the mean monthly surface temperatures among plots, as measured by the standard deviation of the mean, was low in winter but rapidly increased in May as snowpack began to melt. The standard deviation peaked in July before tapering off through November (fig. 9).

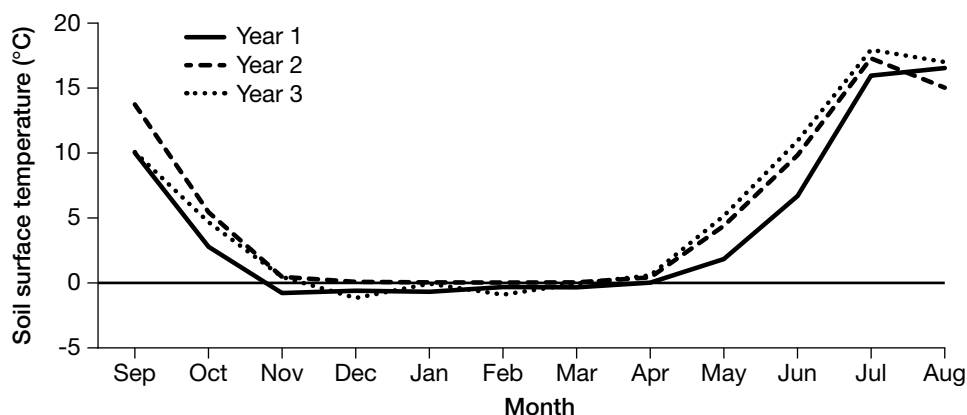


Figure 14—Annual cycle of mean monthly soil surface temperatures for the Olympic Mountain whitebark pine communities study. Each mean is based on all the recorded temperatures (day and night) over the course of the month. Year 1 = September 2011 through August 2012, year 2 = September 2012 through August 2013, and year 3 = September 2013 through August 2014.

In year 1, the maximum soil surface temperature recorded (58.5 °C) occurred on August 13 at 1531 on plot 11 and on August 17 at 1301 on plot 5. In year 2, the maximum soil surface temperature (57.5 °C) occurred on July 23 at 1433 on plot 9 and at 1550 on plot 11. In year 3, the maximum soil surface temperature (56.5 °C) occurred on July 15 at 1523 on plot 31 (table 2).

In year 1, the minimum soil surface temperature recorded (−11.5 °C) occurred on December 10 at 0747 on plot 40. In year 2, the minimum soil surface temperature (−12.5 °C) occurred on November 11 at 0601 and at 1016 on plot 7. In year 3, the minimum soil surface temperature (−16 °C) occurred on December 8 at 0407 on plot 7 (table 2).

Snow began to affect mean soil surface temperatures in November and December, as shown by a flattening of the curve in figure 14, although this varied by plot. The snowpack lasted into April on most plots and into May and June on some, as shown by the upward inflections in the soil surface temperature curve at those times. Soil surface temperatures rose rapidly after snowmelt to a peak in July (fig. 14). The standard deviation of mean monthly soil surface temperatures increased greatly from spring through fall, indicating large temperature differences among plots in these times (see fig. 9).

TEN MAXIMUM AND TEN MINIMUM SOIL SURFACE TEMPERATURES FROM EACH PLOT AND YEAR—

- High soil surface temperatures were most common in July.
- Most of the plots contributed to the dataset of the 10 maximum soil surface temperatures in July and August.
- Low soil surface temperatures were most common in November, but the lowest occurred in December.

The greatest proportion of the 10 maximum soil surface temperatures occurred in July (see fig. 10), but some of these maximum soil surface temperatures were recorded in each month from May through October. The highest monthly means of the maximum soil surface temperatures during this time ranged from 32.2 to 42.4 °C (fig. 10). Most plots contributed to this dataset in July and August, but many fewer contributed in June, September, and October (fig. 10).

More of the 10 minimum soil surface temperature measurements occurred in November (fig. 11) than in other months, but at least a few were recorded in each month from September through May. On average, the soil surface temperatures in this dataset were coldest in December (fig. 11). The number of plots contributing to the soil surface temperature dataset peaked in November and then tapered off through March (fig. 11).

Soil Temperature

SOIL MICROCLIMATIC OVERVIEW—

- Mean annual soil temperatures ranged from 3.7 to 5.1 °C.
- Among-plot soil temperature variation was low in winter, rapidly increased after snowmelt, and peaked in July.
- Over the 3 years, the maximum soil temperature was 27, and the minimum was −14 °C.
- Snowpack moderated most soil temperatures from November to April through June, but winter melt-out permitted intermittent soil freezing on shallowly covered plots.

Like air and soil surface temperatures, soil temperatures were coolest in year 1, and years 2 and 3 were more like each other than year 1 (fig. 15). The mean annual soil temperatures ranged from 3.7 to 5.1 °C. Variation in the mean monthly soil temperatures among plots, as measured by the standard deviation of the mean, was low in winter but rapidly increased in May as snowpack began to melt. The standard deviation peaked in July before tapering off through November (fig. 9).

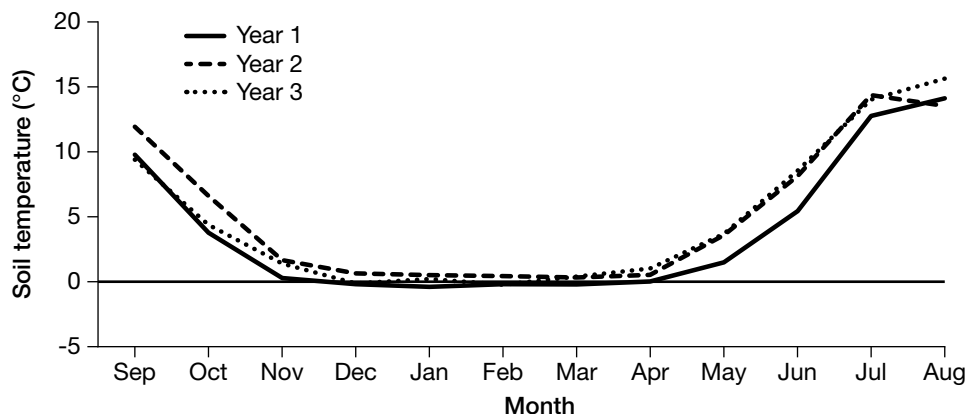


Figure 15—The annual cycle of mean monthly 20-cm-deep soil temperatures for the Olympic Mountain whitebark pine communities study. Each mean was based on all recorded temperatures (day and night) over the course of the month. Year 1 = September 2011 through August 2012, year 2 = September 2012 through August 2013, and year 3 = September 2013 through August 2014.

In year 1, the maximum soil temperature recorded (27.5 °C) occurred on August 6 at 2236 on plot 5. In year 2, the maximum soil temperature (27 °C) occurred on July 23 at 2136 on plot 5. The maximum soil temperature for year 3 (27 °C) was recorded on July 15 at 2136 on plots 5 and 35 (table 2).

In year 1, the minimum soil temperature recorded (−7 °C) occurred on January 18 at 0327, 0742 and at 1157 on plot 12. In year 2, the minimum soil temperature (−1.0 °C) occurred on December 10 and 11 from 2301 to 0731. In year 3, the minimum soil temperature (−14 °C) occurred on December 8 at 0408, 0823, 1238, and 1652 on plot 7 (table 2).

Snow began to affect mean soil temperatures in November and December, as shown by a flattening of the mean monthly soil temperature curve in figure 15, although this varied by plot. The snowpack lasted into April on most plots and into May and even June on some, as shown by the upward inflections in the soil temperature curve at those times. Soil temperatures and their standard deviations rose rapidly after snowmelt and tended to peak in July and August (fig. 15).

When snow accumulated rapidly, the transition from daily soil temperature fluctuation to virtually no soil temperature fluctuation occurred suddenly (fig. 16: plot 5). In figure 16, plot 5 shows a typical plot on which rapid snow accumulation prevented nearly all frost penetration of the soil. The plot's elevation was 1630 m, its aspect was 230°, its slope steepness was 59 percent, and its soil was a loamy sand with 16 percent coarse fragment content. The permanent winter snowpack arrived on December 5, 2013 (Julian day 339). Plot 7 had the most frost penetration of any plot in the study area. The lowest temperature was −14 °C, which occurred on December 8, 2013 (Julian day 342). The plot's elevation was 1591 m, its aspect was 262°, its slope steepness was 49 percent, and its soil was pockets of gravelly sand within almost 100 percent boulder talus. Large air-filled gaps between the boulders allow deep penetration of cold air before they are bridged and covered by snow. Note the midwinter thaw that affected plot 7 but not plot 5. This suggests that plot 7 had a shallower snowpack than plot 5.

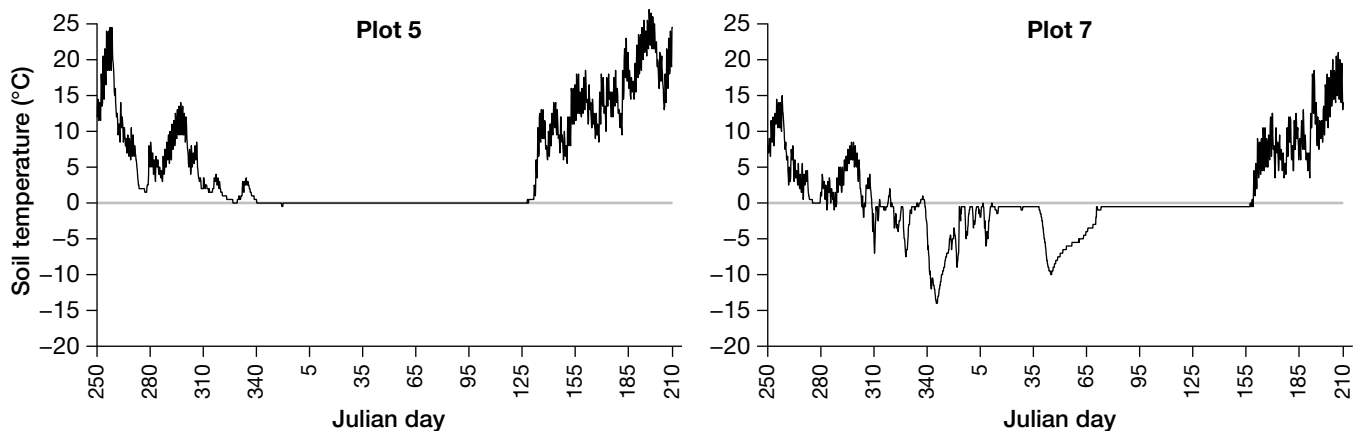


Figure 16—Twenty-cm-deep soil temperatures for winters of 2013 to 2014 and 2014 to 2015 (4-hour recording interval) for two contrasting plots in the Olympic Mountain Whitebark Pine Community study.

TEN MAXIMUM AND TEN MINIMUM SOIL TEMPERATURES FROM EACH PLOT AND YEAR—

- More of the maximum soil temperatures in this dataset occurred in July than in other months.
- More of the minimum soil temperatures in this dataset occurred in November than in other months.

The greatest proportion of the maximum soil temperatures occurred in July, which is also when the highest mean monthly maximum soil temperature occurred (fig. 10). All the highest soil temperatures occurred from June through September, but the greatest number of plots contributed in July and August (fig. 10).

More of the minimum soil temperatures occurred in November (fig. 11), although at least some occurred in each month from October through May. The lowest mean monthly minimum soil temperatures occurred in December and January (fig. 11). The number of plots contributing to the minimum soil temperature dataset peaked in November and then tapered off through March (fig. 11).

TEMPERATURE PULSE MOVEMENT—

- On average, the soil temperature pulse moved down into the soil at 3.93 cm per hour.

On plot 3 (an open-canopy plot), the mean daily soil surface temperature peak in July (35.1 °C) occurred, on average, at 1519, and the mean daily soil temperature peak in July (18.3 °C) occurred, on average, at 2029. Thus, the lag between peaks was 5 hours and 10 minutes, for a rate of 3.87 cm per hour. On plot 32 (a closed-canopy plot), the mean daily soil surface temperature peak in July (16.8 °C) occurred, on average, at 1545, while the mean daily soil temperature peak in July (9.6 °C) occurred, on average, at 2046. Thus, the lag between peaks was 5 hours and 1 minute for a rate of 3.99 cm per hour. The average of the estimates is 3.93 cm per hour. The lowest July temperature for both plots occurred at about 1015 on average. The mean daily soil temperature amplitude in July for plots 3 and 32 were 3.9 and 1.5 °C, respectively.

SOIL TEMPERATURE REGIME—

- Soil temperature regime is based on soil temperatures at 50-cm depths, which we did not have.
- Our mean annual soil temperature at 20-cm depth was between 1.4 and 6.6 °C.
- Adjusting our data to a 50-cm depth by using adjustments suggested by the USDA NRCS (1999) or relationships we derived from Buckinghorse or Mount Townsend data suggested that nearly all our plots had a cryic soil temperature regime with a few frigid soil temperature regimes.
- The Buckinghorse SNOTEL weather station and the Mount Townsend site also had cryic soil temperature regimes.

According to USDA NRCS (1999), a well-drained mineral soil at 50-cm depth with no organic surface horizon and that has a cryic soil temperature regime has a mean annual temperature less than 8 °C and a mean June through August (summer) temperature of less than 15 °C. If an organic surface horizon is present, then summer temperature criterion drops from 15 to 8 °C. For a frigid soil temperature regime, the soil is warmer in summer than a cryic regime but still has a mean annual 50-cm-deep soil temperature lower than 8 °C. In a further refinement of a frigid regime, if the difference between the June through August and December through February mean temperatures is less than 6 °C, the regime is called isofrigid. To classify our soils by using this system, we first must estimate what the 50-cm-deep soil temperature would be from our 20-cm-deep soil temperatures. According to USDA NRCS (1999), the temperature at 50-cm depth should be about 1.5 °C lower in summer and 1.5 °C higher in winter than at 20-cm depth. The data relevant to classifying our plot soil temperatures with this system is presented in table A2.5.

The mean annual 20-cm-deep soil temperature of our plots was between 1.4 and 6.9 °C (table A2.5). Based on this alone, and assuming the mean annual 50-cm-deep soil temperature was similar, all our plots have either a cryic or frigid temperature regime. Applying the USDA NRCS (1999) temperature adjustment to our 20-cm-deep soil temperature data for a 50-cm depth resulted in all but two of our plots having a cryic soil temperature regime. The other two plots (plots 3 and 5) had a frigid soil temperature regime.

Of the four SNOTEL weather stations, soil temperature monitoring was only carried out at Buckinghorse, which had a mean annual soil temperature of 3 °C at 46-cm depth (table 3). For our purposes, we assume this is close enough to 50-cm depth to stand uncorrected. The mean winter soil temperature at 46-cm depth was 0.5 °C. The mean summer soil temperature at 46-cm depth was 5.1 °C, so this site has a cryic soil temperature regime. The June through August mean soil temperature at 50-cm depth was only 1.1 °C lower than what was recorded at 20-cm depth, as opposed to the estimated difference of 1.5 °C suggested by USDA NRCS (1999). Also, the December through February mean soil temperature at 50-cm depth was only 0.3 °C higher than that measured at 20-cm depth, as opposed to the 1.5 °C suggested by USDA NRCS (1999). However, using these values to correct our 20-cm-deep soil temperatures to a 50-cm depth still provides little change from the USDA NRCS (1999) values—all plots but three had cryic regimes. Plots 3 and 5 had a frigid temperature regime, while plot 23 had an isofrigid regime.

At Mount Townsend, the mean annual soil temperature at 50-cm depth for the period of record was 2.7 °C. The mean summer soil temperature at 50-cm depth was 4.7 °C. The mean

winter soil temperature at 50-cm depth was 0.9 °C. The soil temperature regime is thus cryic (USDA NRCS 1999). The mean summer soil temperature at 50-cm depth was only 1.2 °C lower than at 20-cm depth, and the mean winter soil temperature at 50-cm depth was only 0.5 °C higher than at 20-cm depth. These are similar to those from the Buckinghorse SNOTEL weather station site, and if used instead of the suggested depth adjustment from USDA NRCS (1999), provide the same results as the SNOTEL Buckinghorse adjustments.

Thus, the area of our study site has predominantly a cryic soil temperature regime. The microsites that were not cryic had a frigid or isofrigid regime. The plots that were frigid were at relatively low elevations with west-southwestern aspects and had open tree canopies. Plot 23, with the isofrigid regime, was our lowest elevation plot, had a west-southwestern aspect, and a nearly closed overstory canopy.

Relationships Between Annual and Daily Temperature Patterns and Overstory Canopy Closure

- Mean annual air, soil surface, and soil temperatures were lower in closed-canopy plots than in open-canopy plots.
- Soil and soil surface temperatures under snow were similar, but after melting, soils in openings warmed faster than under trees and differed the most in July and August.
- During summer, afternoon soil surface temperatures in open-canopy plots were higher than in closed-canopy plots because of direct solar exposure, but because of open sky radiational heat loss, the reverse is true in the early morning hours.
- Summer air temperatures in closed- and open-canopy plots were similar because of convective mixing of the air.
- The number of days with soil temperatures above 9 °C (which is conducive to good root growth) ranged from 40 to 131 days, with overstory canopy closure and elevation accounting for 73 percent of the variation.

The mean annual temperature from air, soil surface, and soil temperature sensors was lower over a range of elevations in closed-canopy plots than at comparable elevations in open-canopy plots. During winter, while under a snowpack, soil surface and soil temperatures were similar regardless of overstory canopy closure group (fig. 17). Air temperatures during winter were lower than soil surface or soil temperatures, but they were similar between the two overstory canopy closure groups.

Beginning in April, as the snowpack melted, the soils began to warm, and daily differences began to appear between air, soil surface, and soil temperatures, as well as between open- and closed-canopy plots. Daily temperature fluctuation patterns for the soil surface and soil were strikingly different between open- and closed-canopy plots from April through November (fig. 17).

In the first of the four quarters of the day (hereafter quarter-days 1 through 4), the mean monthly air, soil surface, and soil temperatures in the closed-canopy plots were similar to each other as well as to air and soil surface temperatures in open-canopy group plots. However, soil temperatures in open-canopy plots were higher than any other temperature in the open- or closed-canopy plots from April through October (fig. 17). The difference began small in April, increased to more than 5 °C in July and August, and then gradually decreased.

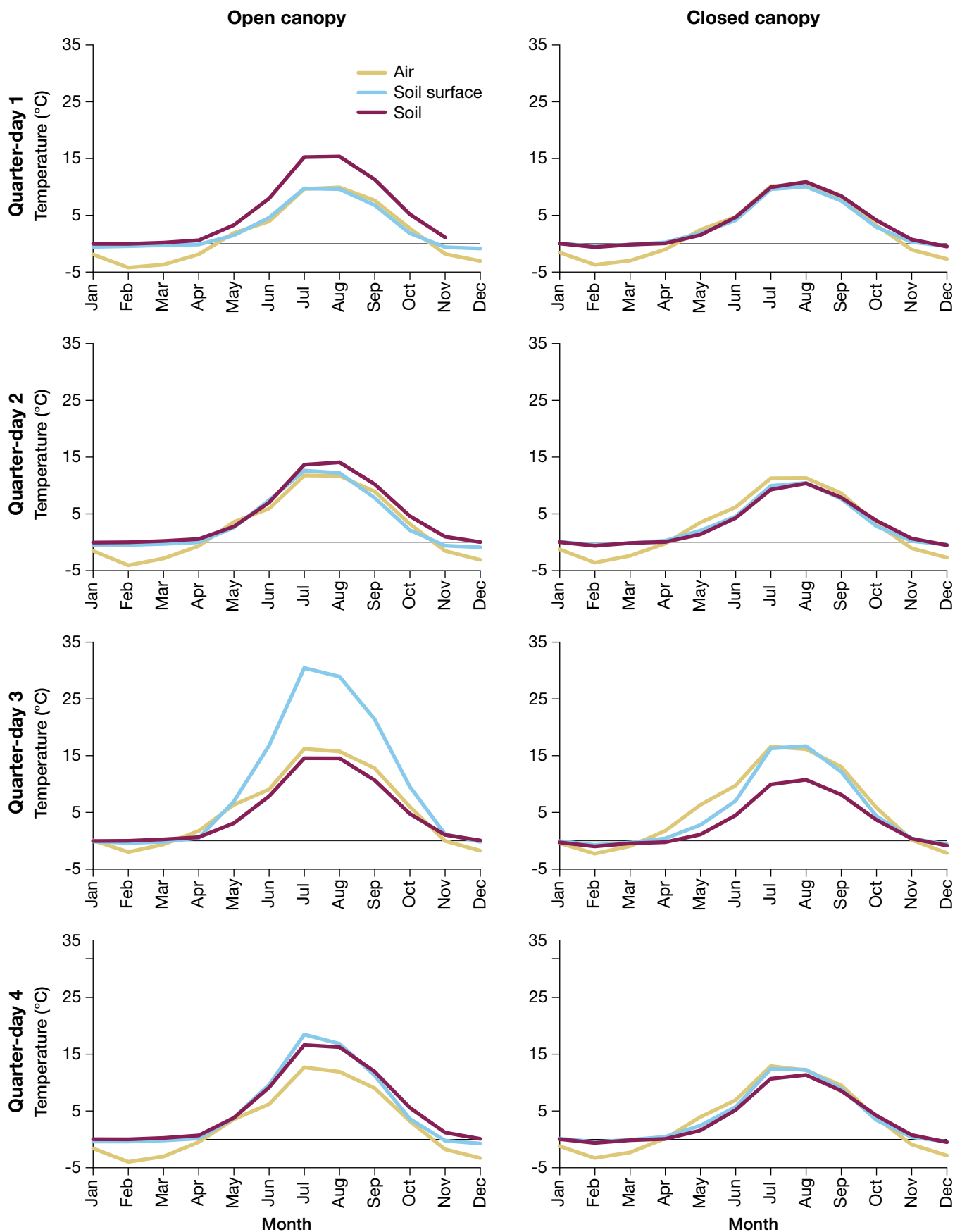


Figure 17—Annual cycle of mean monthly air, soil surface, and 20-cm-deep soil temperatures by quarter-day for open- and closed-canopy plots in the Olympic Mountain whitebark pine communities study. Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

In quarter-day 2, the mean monthly air and soil surface temperatures in open-canopy plots rose in tandem to approximate soil temperatures, which had cooled slightly from the night (fig. 17). At the same time, there was little change in closed-canopy plots. At this time of day, all temperatures within each canopy group were like each other, but temperatures in the open-canopy plots were slightly higher than temperatures in closed-canopy plots.

In quarter-day 3, mean monthly soil surface temperatures became much higher than air or soil temperatures in open-canopy plots (fig. 17). By July and August, soil surface temperatures in open-canopy plots averaged 14 to 15 °C higher than air or soil temperatures. Because of the high angle of the sun during summer, some radiation penetrated to the forest floor in the closed-canopy plots, causing a similar but muted seasonal increase in soil surface temperatures compared to 20-cm-deep soil temperatures. However, because of convective mixing, mean air temperatures were similar between closed- and open-canopy plots.

In quarter-day 4, mean monthly air, soil surface, and soil temperatures equilibrated and closely approximated each other in closed-canopy plots (fig. 17). However, there was a protracted decay of the much greater amount of surficial heat absorbed by the soil in open-canopy plots both to the air above and to deeper soils below. Thus, soil surface temperatures remained higher than air temperatures at this time but gradually approximated air temperatures in the next quarter-day 1. In the soil, the highest temperatures of the day occurred in quarter-day 4, as the afternoon temperature pulse that began at the soil surface passed through.

Because most root growth occurs above 9 °C (Alvarez-Uria and Körner 2007), we calculated the average number of days in a year that each plot had temperatures above this threshold at 20-cm depth in the soil. Note this does not imply that the soil remained above this threshold throughout the day—only that at least one of the six daily measurements was above this threshold. The number of days ranged from 40 to 131 days (table 4). We investigated site factors responsible for variation in days with soil temperatures above 9 °C with multiple linear regression. A strong explanatory multiple linear regression model included overstory canopy closure and elevation (adjusted $r^2 = 0.73$, $P < 0.01$) (table 5).

Table 4—Environmental variable data and average number of days each plot had 20-cm-deep soil temperatures above 9 °C per year for the Olympic Mountain whitebark pine communities study

Plot	Days above 9 °C	Overstory canopy closure	Elevation	Slope steepness	Aspect
	DAYS	PERCENT	METERS	PERCENT	DEGREES
17	40	80	1814	61	213
41	46	85	1497	25	230
11	57	80	1543	32	266
32	59	75	1595	46	0
6	75	35	1816	72	222
23	75	90	1420	52	228
13	75	30	1781	62	291
31	82	29	1845	72	295
28	83	14	1828	50	300
20	93	15	1682	69	192
19	99	10	1705	73	222
35	102	28	1742	55	265
12	103	3	1803	50	273
4	112	15	1696	58	251
24	114	3	1754	63	255
9	116	5	1698	71	238
5	122	35	1630	59	230
3	129	50	1529	58	251
40	131	<1	1693	63	216
22	131	35	1543	58	206

Note: Data is sorted from fewest to most days above 9 °C.

Table 5—Multiple linear regression model summary of the number of days with 20-cm-deep soil temperatures above 9 °C as a function of overstory canopy closure and elevation for the Olympic Mountain whitebark pine communities study

Variable	Coefficient	$P > t$
Intercept	380.80	<0.01
Overstory canopy closure	-1.01	<0.01
Elevation	-0.15	<0.01

P = probability value; t = t value.

Relationships Between Temperature, Topography, and Canopy Closure

RELATIONSHIPS BETWEEN AIR TEMPERATURE, ELEVATION, AND CANOPY CLOSURE—

- Mean annual air temperatures decreased 4.94 °C per kilometer gain in elevation, but the rate varied with the time of day (−3.99 to −5.53 °C per kilometer) and the season (−3.83 to −6.29 °C per kilometer).
- Air temperature lapse rates for closed-canopy plots were steeper and more variable daily and seasonally than lapse rates for open-canopy plots.
- Air temperature lapse rates decreased from June through May, with the number of clear days and variation in potential direct solar radiation accounting for 77 percent of the variation.
- Alternatively, the seasonal decrease in air temperature lapse rates can be modeled for closed- or open-canopy plots with the percentage of time that plots were covered by snow deep enough to moderate daily temperature variation, and for closed-canopy plots, the amount of potential direct solar radiation (accounting for 67 percent of variation), or for open-canopy plots, the measured total solar radiation at the Waterhole SNOTEL weather station (accounting for 86 percent of variation).

Mean annual air temperature over all the plots decreased 4.94 °C for every kilometer gain in elevation (i.e., a lapse rate of −4.94 °C per kilometer) (adjusted $r^2 = 0.65$, $P < 0.01$) (fig. 18, table A2.6). This rate varied with the time of day (fig. 18). Thus, for quarter-day 1, the rate was −4.92 °C per kilometer (adjusted $r^2 = 0.71$, $P < 0.01$). For quarter-day 2, the rate was −3.99 °C per kilometer (adjusted $r^2 = 0.54$, $P < 0.01$). For quarter-day 3, the rate was −5.53 °C per kilometer (adjusted $r^2 = 0.47$, $P < 0.01$). For quarter-day 4, the rate was −5.33 °C per kilometer (adjusted $r^2 = 0.73$, $P < 0.01$). Elevation accounted for half or more of the variation in annual air temperature data.

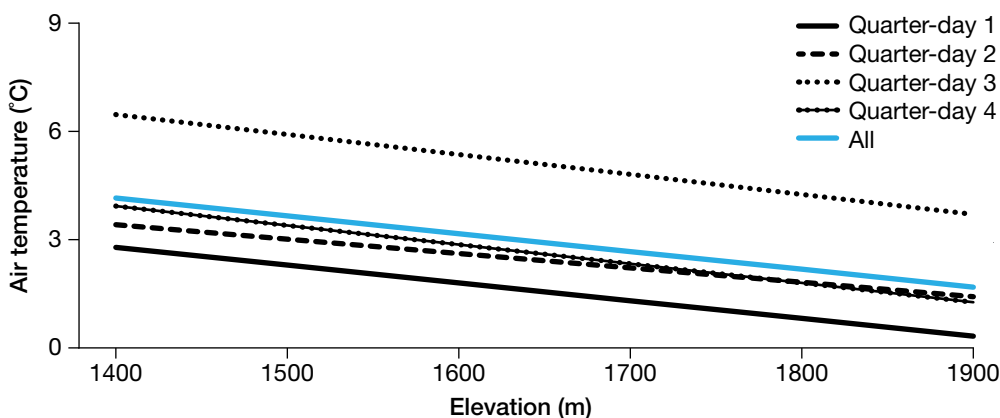


Figure 18—Annual air temperature lapse rates for the 3-year dataset of the Olympic Mountain whitebark pine communities study by quarter-day and the entire day. Note: quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

Throughout the year, the monthly air temperature lapse rate varied from −3.83 °C per kilometer in July to −6.29 °C per kilometer in April (fig. 19, table A2.7). The steepest rates were in spring and were centered on April, and in fall during November. Lapse rates were flatter in summer and early winter. The difference in temperature due to elevation was least during the growing season (July and August).

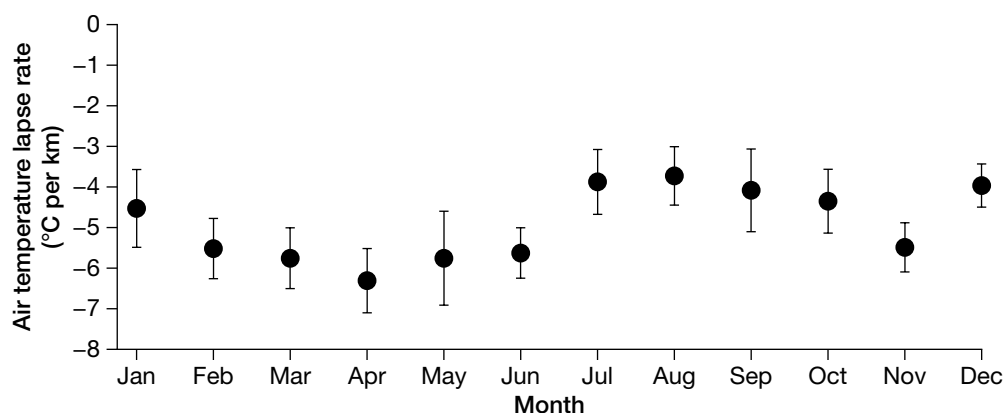


Figure 19—Monthly air temperature lapse rates (change per kilometer gain in elevation) for the 3-year dataset of the Olympic Mountain whitebark pine communities study with standard error bars. All 12 relationships were significant ($P < 0.01$). The adjusted r^2 for the relationships varied from 0.34 in September to 0.74 in November and averaged 0.56. The overall annual air temperature lapse rate for this dataset was -4.94 °C per kilometer.

Separating the data into closed- and open-canopy groups produced stronger linear regression models for both populations overall and by quarter-day than in the combined dataset (see table A2.6 for regression statistics and coefficients). The annual air temperature lapse rate was steeper for closed-canopy plots than open-canopy plots in all quarter-days except quarter-day 3 (table 6). Also, the annual air temperature lapse rate for closed-canopy plots was steepest in quarter-day 1 and flattest in quarter-day 3, which was nearly the opposite of the open-canopy plots.

Table 6—Mean annual air temperature lapse rates (decrease per kilometer gain in elevation) for all plots and by overstory canopy closure group and quarter-day for the Olympic Mountain whitebark pine communities study

Quarter-day ^a	Lapse rate, closed-canopy plots (n = 6)	Lapse rate, open-canopy plots (n = 23)	Lapse rate, all plots (n = 29)
DEGREES CELSIUS PER KILOMETER			
All	8.53	7.13	0.90
1	10.30	6.10	4.90
2	9.60	6.00	4.00
3	6.50	9.40	5.53
4	7.80	7.10	5.33

Note: Boldface type indicates significance of the lapse rate relationship at probability value (P) = 0.05. Regular type indicates nonsignificance.

^a Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

Most of the monthly air temperature lapse rate regressions by overstory canopy closure group (table A2.8) were significant. Monthly air temperature lapse rates for closed-canopy plots steepened from around -4 °C per kilometer in summer to -14.07 °C per kilometer in May, more or less steadily, but the rates for the open-canopy plots remained within about 2 °C per kilometer of each other throughout the year (fig. 20).

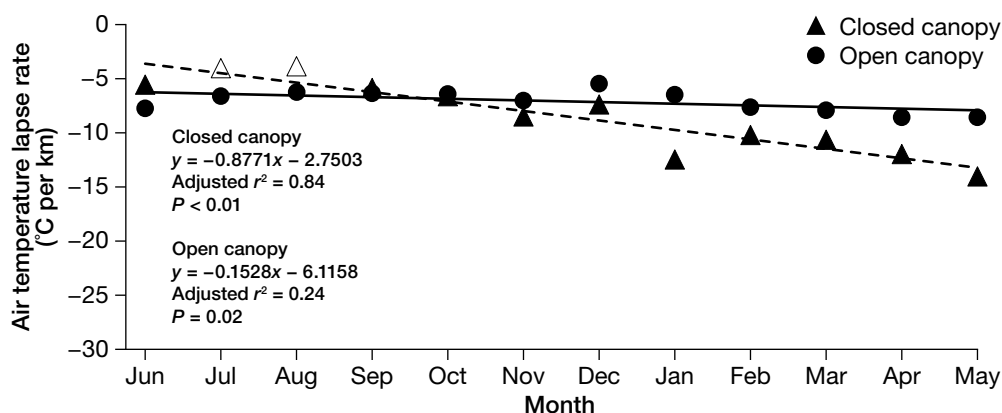


Figure 20—Seasonal progressions of monthly air temperature lapse rates (change per kilometer gain in elevation) by overstory canopy closure group for the Olympic Mountain whitebark pine communities study. The months are arranged to show the seasonal trend more clearly beginning after snowmelt. Regressions for the lapse rates represented by solid symbols were significant at $P = 0.05$, but regressions for lapse rates represented by hollow symbols were not significant.

There was daily variation in the seasonal progression of monthly air temperature lapse rates for the closed-canopy plots but relatively little variation for the open-canopy plots. For quarter-days 1 through 4, respectively, the slopes of the linear regression through the monthly air temperature lapse rates from June through May for closed-canopy plots were -0.42 , -0.64 , -1.5 , and -0.94 . For open-canopy plots, the slopes were -0.12 , -0.23 , -0.04 , and -0.21 . Thus, monthly air temperature lapse rates were steeper and more variable both daily and seasonally for closed-canopy plots than for open-canopy plots.

In working toward an explanation for the seasonal lapse rate patterns, we used stepwise regression to examine relationships between seven weather and solar seasonal variables and monthly air temperature lapse rates (table 7).

Table 7—Stepwise regression model summaries of monthly air temperature lapse rate, overall and by overstory canopy closure group, for the Olympic Mountain whitebark pine communities study (all the models were significant)

Model statistics				Summary of stepwise selection				
Model	Variable	Coefficient	P	Step	Enter/remove	Partial r^2	Model r^2	P
All plots (n = 29)	Intercept	-5.18212	<0.01	1	Clear days/	0.48	0.48	0.01
	Clear days ^a	0.56718	<0.01	2	SD solar/	0.30	0.77	<0.01
	SD solar ^b	-7.6E-05	<0.01					
Closed-canopy plots (n = 23)	Intercept	-13.33190	<0.01	1	%snow/	0.51	0.51	<0.01
	%snow ^c	0.07207	<0.01	2	PD solar/	0.17	0.67	0.06
	PD solar ^d	3.35E-05	0.06					
Open-canopy plots (n = 6)	Intercept	-8.86949	<0.01	1	PD solar/	0.54	0.54	<0.01
	MD solar ^e	0.01060	<0.01	2	%snow/	0.21	0.75	0.02
	%snow	0.01613	<0.01	3	MD solar/	0.11	0.86	0.04
				4	/PD solar	0.01	0.85	0.42

Note: For the overall all plots model, $P = 0.0013$, for the overall closed-canopy plots model, $P = 0.0065$, and for the overall open-canopy plots model, $P = 0.0002$.

P = probability value; r^2 = coefficient of determination.

^a Clear days were measured at Naval Air Station Whidbey Island, Washington, in the Puget Sound.

^b SD solar is the standard deviation of the calculated potential direct solar radiation among plots.

^c %snow is the mean over all plots of the percentage of time that each plot was covered by snow deep enough to damp (or moderate) daily temperature variation.

^d PD solar is the calculated potential direct solar radiation for each plot (ArcGIS) (ESRI 2017).

^e MD solar is measured direct solar radiation (watt hours per square meter) measured at the Waterhole SNOTEL site.

The monthly air temperature lapse rate model for all plots was highly significant and accounted for 77 percent of the variation ($P < 0.01$). The model included a positive relationship with the number of clear days and a negative relationship with the standard deviation of the mean potential direct solar radiation based on all the plots (table 7).

The closed-canopy plot model accounted for 67 percent of the variation ($P < 0.01$) but with different variables than the model based on all the plots. In this case, the model included a positive relationship with the percentage of time that plots were covered by snow deep enough to moderate daily temperature variation in each month and a positive relationship with the mean monthly potential direct solar radiation of the plots (table 7). The open-canopy plot model accounted for 85 percent of the variation ($P < 0.01$). In this case, the mean over all plots of the percentage of time that plots were covered with snow deep enough to moderate diurnal temperature variation in each month was also important, but the measured direct solar radiation at the Waterhole SNOTEL weather station was a better estimator than the standard deviation of the potential direct solar radiation (table 7).

RELATIONSHIPS BETWEEN SOIL SURFACE TEMPERATURE, ELEVATION, AND CANOPY CLOSURE—

- Mean annual soil surface temperature was not a simple function of elevation, rather it was a function of aspect, elevation, and overstory canopy closure, increasing toward the southwest but decreasing with elevation and overstory canopy closure.
- Open-canopy plots had a significant annual soil surface temperature lapse rate only when snow was covering the higher elevation plots but not the lower elevation plots. There was insufficient data to analyze closed-canopy plots in the same way.
- Of the variation in mean monthly soil surface temperature lapse rates for open-canopy plots, 74 percent was accounted for by the duration of the seasonal snowpack (positive relationship) and the variation in solar radiation (negative relationship).

The relationship between mean annual soil surface temperature and elevation was not significant. When mean annual temperatures by quarter-day were analyzed, significant relationships emerged only for quarter-day 1 (-4.1 °C per kilometer, adjusted $r^2 = 0.50$) and quarter-day 2 (-4 °C per kilometer, adjusted $r^2 = 0.27$). These are the two quarters of the day when an exposed surface most closely approximates the air temperature. Seasonally, there were significant monthly soil surface temperature lapse rates only in January (-2.72 °C per kilometer), October (-8.44 °C per kilometer), and November (-4.23 °C per kilometer), and marginally in December (-2.04 °C per kilometer, $P = 0.07$).

Modeling mean annual soil surface temperature as a function of overstory canopy closure group did not result in a significant model. Also, the model of mean annual soil surface temperature as a function of aspect accounted for only a modest portion of soil surface temperature variation (see below). However, a multiple linear regression model of mean annual soil surface temperature as a function of aspect, elevation, and percentage of overstory canopy closure was highly significant and strong (adjusted $r^2 = 0.72$, $P < 0.01$), and all three variables were highly significant (table 8). The mean annual soil surface temperature increased with increasing aspect (more south facing) and decreased with elevation and percentage of overstory canopy closure.

We did not have sufficient data to analyze mean annual soil surface temperature lapse rates for closed-canopy plots (only two such plots with data), but the mean annual soil surface temperature lapse rate for open-canopy plots was steepest in quarter-day 3 and

flattest during the night (table 9). For the open-canopy plots, lapse rates varied from near 0 °C per kilometer in spring before the snow melted to −17.42 °C per kilometer in June after the snow had melted in the lower but not the higher elevation plots (fig. 21). Thus, there appears to be a seasonal trend that is similar to the trend in the soil data (fig. 22), although several of the soil surface points were not significant (fig. 21).

We used stepwise regression to examine relationships between seven weather and solar seasonal variables and the monthly soil surface temperature lapse rates (table 10). None of the variables were significant estimators in the monthly soil surface temperature lapse rate model for all plots. The open-canopy plot model was significant, accounting for 74 percent of the variation ($P < 0.01$). The model included a positive relationship with snowpack and a negative relationship with the standard deviation of potential direct solar radiation (table 10).

Table 8—Multiple linear regression model summary of mean annual soil surface temperature as a function of aspect, elevation, and percentage of overstory canopy closure for the Olympic Mountain whitebark pine communities study

Variable	Coefficient	P
Intercept	12.15092	<0.01
Aspect	0.01585	<0.01
Elevation	−0.00508	<0.01
Canopy closure	−0.02901	<0.01

P = probability value.

Note: This regression used data from 19 plots.

Table 9—Mean annual soil surface temperature lapse rates (decrease per kilometer gain in elevation) for all plots and open-canopy plots in the Olympic Mountain whitebark pine communities study by quarter-day

Quarter-day ^a	Lapse rate, open-canopy plots (n = 17)	Lapse rate, all plots (n = 19)
DEGREES CELSIUS PER KILOMETER		
All	7.60	3.00
1	4.60	4.10
2	6.47	4.02
3	14.39	2.36
4	4.93	1.65

Note: Boldface type indicates significance of the lapse rate relationship at probability value (P) = 0.05. Italic type indicates marginal significance at P = 0.1. Regular type indicates nonsignificance.

^a Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

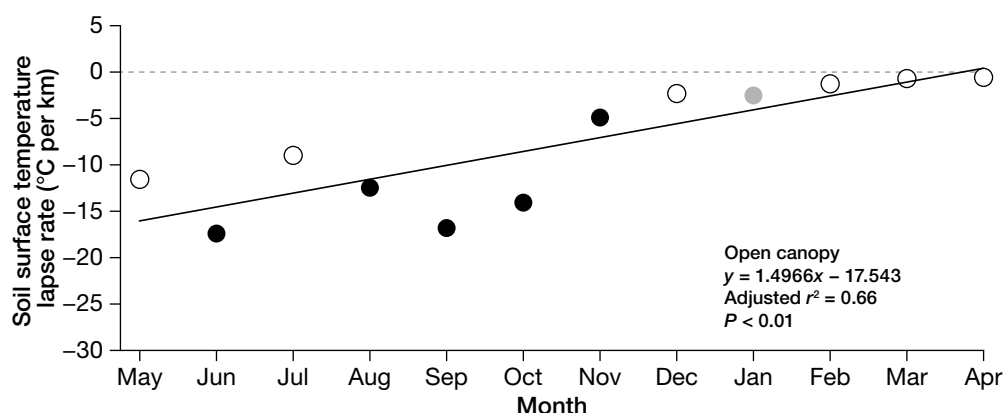


Figure 21—Seasonal progressions of monthly soil surface temperature lapse rates (change per kilometer gain in elevation) for open-canopy plots in the Olympic Mountain whitebark pine communities study. The months are arranged to show seasonal trend more clearly beginning with snowmelt in May. Regressions for lapse rates represented by solid symbols were significant at $P = 0.05$, regressions for lapse rates represented by gray symbols were significant at $P = 0.1$, and regressions for lapse rates represented by hollow symbols were not significant. Regression statistics and coefficients for each month are provided in table A2.9.

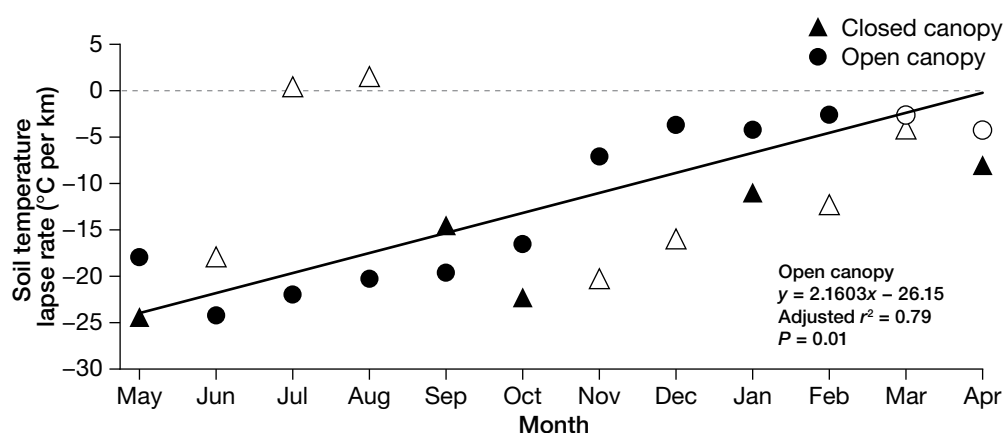


Figure 22—Seasonal progressions of monthly 20-cm-deep soil temperature lapse rates (change per kilometer gain in elevation) by canopy closure group for the Olympic Mountain whitebark pine communities study. The months are arranged to show the seasonal trend more clearly beginning with snowmelt in May. A regression line is shown only for the open-canopy plots because the regression for the closed-canopy plots was not significant. Regressions for the lapse rates represented by solid symbols were significant at $P = 0.05$, but regressions for lapse rates represented by hollow symbols were not significant. Regression statistics and coefficients are provided in table A2.10.

Table 10— Stepwise regression model summary of monthly soil surface temperature lapse rate for open-canopy plots ($n = 12$) in the Olympic Mountain whitebark pine communities study

Model			Summary of stepwise selection				
Variable	Coefficient	P	Step	Enter/ remove	Partial r^2	Model r^2	P
Intercept	-7.50590	0.05	NA	NA	NA	NA	NA
SD solar ^a	-0.00026	0.11	1	%snow/	0.65	0.65	<0.01
% snow ^b	0.12243	<0.01	2	SD solar/	0.09	0.74	0.11

Note: For the overall model, $P = 0.0022$.

NA = not applicable; P = probability value; r^2 = coefficient of determination.

^a SD solar is the standard deviation of the calculated potential direct solar radiation among plots.

^b %snow is the mean over all plots of the percentage of time that each plot was covered by snow deep enough to damp (or moderate) daily temperature variation.

RELATIONSHIPS BETWEEN SOIL TEMPERATURE, ELEVATION, AND CANOPY CLOSURE—

- Overall, annual or monthly soil temperatures mostly did not exhibit elevational lapse rates.
- Significant soil temperature lapse rates were obtained by separating the data into open- and closed-canopy closure groups.
- Closed-canopy plots tended toward steeper annual and annual by quarter-day soil temperature lapse rates than with open-canopy plots, and soil temperature lapse rates, in general, were steeper than air temperature lapse rates.
- Monthly soil temperature lapse rates tended to decrease from steep rates in May, when the snow is still melting at higher elevations but is gone from lower elevations, to nearly flat in winter, when most areas are covered with snow. This seasonal progression can be estimated with potential direct solar radiation and the percentage of the area under deep snowpack (both negative relationships).

Over the entire dataset, soil temperatures mostly did not exhibit elevational lapse rates (annual and monthly linear regressions were mostly nonsignificant). The relationship between mean annual soil temperature and elevation was not significant (table 11), nor were the relationships between mean annual soil temperatures by quarter-day and elevation significant. There was a significant monthly soil temperature lapse rate of -2.7°C per kilometer in January, and marginally significant ($P = 0.07$) monthly soil temperature lapse rates of -6.03°C per kilometer in October and -3.45°C per kilometer in November.

In modeling mean annual soil temperature as a function of elevation for closed-canopy plots, only the quarter-day 3 model was significant ($P = 0.05$) (table 11). However, the overall open-canopy model (all) and all of the open-canopy plots by quarter-day models were significant and mostly flatter than what the closed-canopy plot analysis suggested.

Most of the monthly soil temperature lapse rates for closed-canopy plots were not significant. Those that were significant varied from -8.03°C per kilometer in April to -24.40°C per kilometer in May (fig. 22). However, most of the monthly soil temperature lapse rates in the open-canopy closure group were significant, and they varied from -24.23°C per kilometer in June to -2.61°C per kilometer in February (fig. 22).

None of the seven explanatory variables that we analyzed with stepwise regression were significant estimators for the monthly soil temperature lapse rate pattern when closed- and open-canopy plot data were pooled. However, when separating the data into closed- and open-canopy plot groups, the closed-canopy plot model accounted for 67 percent of the variation ($P < 0.01$) and the open-canopy plot model accounted for 91 percent of the variation ($P < 0.01$). The significant variables for both groups were potential direct solar radiation and the percentage of time that plots were covered by snow deep enough to damp (or moderate) daily temperature variation averaged over all plots, and both were negative relationships (table 12). The measured direct solar radiation from the Waterhole SNOTEL weather station also had a significant positive relationship in the open-canopy plot model (table 12).

Table 11—Mean annual soil temperature lapse rates (decrease per kilometer gain in elevation) for all plots and by canopy closure group and quarter-day for the Olympic Mountain whitebark pine communities study

Quarter-day ^a	Lapse rate, closed-canopy plots (n = 5)	Lapse rate, open-canopy plots (n = 17)	Lapse rate, all plots (n = 22)
DEGREES CELSIUS PER KILOMETER			
All	13.39	11.79	1.94
1	13.50	11.85	1.89
2	14.82	10.69	2.20
3	13.43	11.27	1.89
4	11.79	13.34	1.77

Note: Boldface type indicates significance of the lapse rate relationship at probability value (P) = 0.05. Italic type indicates marginal significance at P = 0.1. Regular type indicates nonsignificance.

^a Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

Table 12—Stepwise regression model summaries of monthly soil temperature lapse rate by canopy closure group for the Olympic Mountain whitebark pine communities study (both models were significant)

Model statistics				Summary of stepwise selection				
Model	Variable	Coefficient	P	Step	Enter/remove	Partial r^2	Model r^2	P
Closed-canopy plots (n = 17)	Intercept	2.39728	0.42	1	%snow/	0.39	0.39	0.03
	PD solar ^a	-8.3E-05	0.02	2	PD solar/	0.28	0.67	0.02
	%snow ^b	-0.12969	<0.01					
Open-canopy plots (n = 5)	Intercept	1.68621	0.45	1	%snow/	0.69	0.69	<0.01
	PD solar	-0.00023	0.03	2	PD solar/	0.18	0.88	<0.01
	%snow	-0.18300	<0.01	3	MD solar/	0.03	0.91	0.14
	MD solar ^c	0.07133	0.14					

Note: For the overall closed-canopy model, P = 0.0064, and for the overall open-canopy model, P = 0.0002.

P = probability value; r^2 = coefficient of determination.

^a PD solar is the calculated potential direct solar radiation for each plot (ArcGIS) (ESRI 2017).

^b %snow is the mean over all plots of the percentage of time that each plot was covered by snow deep enough to damp (or moderate) daily temperature variation.

^c MD solar is measured direct solar radiation (watt hours per square meter) measured at the Waterhole SNOTEL site.

Relationships Between Temperature and Aspect

- Linear regression models of mean annual air, soil surface, and soil temperature data as a function of aspect were weak.
- Combining elevation and aspect in a model resulted in a strong linear regression model for air temperature but did not improve soil surface or soil temperature models.
- For open-canopy plots, linear regression models of air, soil surface, and soil temperatures by quarter-day, including aspect (positive relationship) and elevation (negative relationship) were strong for air and soil temperatures but were strong only in quarter-days 1 and 2 for soil surface models.
- The highest soil surface temperature for each plot was best modeled as a function of total canopy cover and aspect.

The linear regression model of mean annual air temperature as a function of aspect was significant but weak (table 13). Excluding plots with 75 percent or more overstory canopy closure improved the model (adjusted $r^2 = 0.45$), implying an effect of overstory canopy closure on air temperature. The linear regression model of mean annual soil surface temperature as a function of aspect was significant and of moderate strength, and the linear regression model of mean annual soil temperature as a function of aspect was significant but weak (table 13).

Table 13—Linear regression model summary of the change in mean annual air, soil surface, and 20-cm-deep soil temperatures as a function of aspect for the Olympic Mountain whitebark pine communities study

Model	n	Model <i>P</i>	Adjusted r^2	Intercept	Aspect coefficient	Intercept <i>P</i>
Air	29	0.01	0.18	1.47020	0.010	<0.01
Soil surface	19	<0.01	0.41	1.97457	0.021	0.02
Soil	22	<0.01	0.26	1.43580	0.021	0.16

P = probability value; r^2 = coefficient of determination.

Modeling mean annual air temperature as a function of both elevation and aspect resulted in a strong model (adjusted $r^2 = 0.79$) (table 14). The comparable regressions with soil surface and soil data were also significant but accounted for less variation, and only the aspect variable was significant in those models.

Table 14—Multiple linear regression model summaries of the change in mean annual air, soil surface, and 20-cm-deep soil temperature as a function of elevation and aspect (deviation from 22° azimuth) for the Olympic Mountain whitebark pine communities study

Model	n	Model <i>P</i>	Adjusted r^2	Intercept	Intercept <i>P</i>	Elevation coefficient	Elevation <i>P</i>	Aspect coefficient	Aspect <i>P</i>
Air	29	<0.01	0.79	9.61709	<0.01	−0.00471	<0.01	0.00825	<0.01
Soil surface	19	0.01	0.40	5.11471	0.16	−0.00178	0.36	0.01946	<0.01
Soil	22	0.03	0.23	2.64983	0.54	−0.00069	0.77	0.02095	0.01

P = probability value; r^2 = coefficient of determination.

We also analyzed mean annual air, soil surface, and soil temperatures by quarter-day as functions of elevation and aspect. Full model coefficients and statistics are provided in table A2.11. The overall pattern is like that of the full-day relationships in that mean annual air temperature relationships were generally stronger and had higher significance than mean annual soil surface temperature relationships that were, in turn, stronger and more significant than mean annual soil temperature relationships. For mean annual air temperature, the quarter-day 4 model was the strongest; for mean annual surface temperature, the quarter-day 1 model was the strongest; and for mean annual soil temperature, the quarter-day 2 model was the strongest, although in the latter case, the relationship was weak. With mean annual air temperature, the slopes of regression lines for elevation (negative relationship) and aspect (positive relationship) were steepest in the quarter-day 3 model, although

the slope for elevation in the quarter-day 4 model nearly equaled that of the quarter-day 3 model. This pattern was the same for the mean annual soil surface temperature models, except that only the aspect coefficient (and not the elevation coefficient) was significant in quarter-day 3 and 4 models, and for the mean annual soil temperature model, only the aspect coefficient was significant in all quarter-days.

Carrying the analysis one step further, we divided the data into closed- and open-canopy plot groups, although at this level we did not have enough data in the mean annual soil surface temperature dataset for a closed-canopy plot analysis (see table A2.11 for coefficients and statistics). For mean annual air temperature, open-canopy plot models were strong and highly significant, but closed-canopy plot models were mostly not significant, possibly because of the small sample size ($n = 6$). For mean annual air temperature in open-canopy plots, the quarter-day 4 model was the strongest, but all quarter-days had strong models. The slopes of regression lines for elevation (negative relationship) and aspect (positive relationship) were steepest in the quarter-day 3 model.

For mean annual soil surface temperature in open-canopy plots, the quarter-day 2 model was the strongest, but the model for quarter-day 1 was also strong. The slopes of regression lines for elevation (negative relationship) and aspect (positive relationship) were steepest in quarter-day 3 as was the case for mean annual air temperature; however, the models for quarter-days 3 and 4 were weak. In no case were mean annual soil surface temperature models as strong as the corresponding mean annual air temperature models.

For mean annual soil temperature, the closed-canopy plot models were not significant, possibly because of the small sample size ($n = 5$). However, the open-canopy plot models were significant and strong, but only the elevation coefficient was significant. The quarter-day 2 model was the strongest, but the slope of the regression line for elevation was steepest in the quarter-day 4 model.

We also modeled the highest soil surface temperature recorded for each plot ($n = 33$) as a function of the total canopy cover (summed overstory and understory canopy cover) and aspect. The highest soil surface temperature is strictly a summer, quarter-day 3 event. The total canopy cover and aspect were significant explanatory variables but not elevation (adjusted $r^2 = 0.41$, $P < 0.01$) (table 15).

Table 15—Multiple linear regression model summary estimating the highest soil surface temperature as a function of aspect and total canopy cover (overstory + understory canopy covers) for the Olympic Mountain whitebark pine communities study

Variable	Coefficient	P
Intercept	46.65820	<0.01
Aspect	0.09386	0.02
Total canopy cover	-0.14620	<0.01

P = probability value.

Other Annual Soil Temperature Relationships

- Linear regression models of mean annual soil temperature as a function of mean annual air temperature and elevation or as a function of aspect and the standard deviation of ground-level PAR were moderately strong.
- Models of mean annual soil temperature as a function of mean annual air temperature, elevation, overstory canopy closure, or aspect by themselves were weak or not significant.

The linear regression model of mean annual soil temperature as a function of mean annual air temperature from each plot was significant ($P < 0.01$), but the adjusted r^2 of the relationship was only 0.35. However, a multiple linear regression model of mean annual soil temperature as a function of mean annual air temperature, elevation, and the length of the snow season from the first detected snow to the last was significant ($P < 0.01$) with an adjusted r^2 of 0.58. In this model, mean annual air temperature and elevation (both positive relationships) were significant. Mean annual soil temperature was not significantly related to elevation or overstory canopy closure and was only weakly related to aspect.

Although mean annual soil temperature was not significantly related to canopy closure, it was related to the standard deviation (but not the mean) of the ground-level PAR (adjusted $r^2 = 0.16$, $P = 0.04$). Modeling mean annual soil temperature as a function of aspect and the standard deviation of ground-level PAR provided a stronger overall model (adjusted $r^2 = 0.40$, $P < 0.01$), and both variables had significant positive relations.

Seasonal Correlation Between Canopy Closure and Soil Temperature

- Neither PAR nor overstory canopy closure were significant linear regression explanatory variables for mean annual soil temperature.
- Correlation strength between overstory canopy closure and soil temperature changed seasonally, implying a weak warming effect of tree canopies in winter that changed to a stronger cooling effect in summer.
- Significantly warmer soils were estimated for plots with low percentage of overstory canopy closure compared to plots with high percentage of overstory canopy closure in June, July, and August; however, these relationships were weak.

Linear regression models of mean annual soil temperatures as a function of either overstory canopy closure or PAR (ground-level or 1.3-m height) were not significant, implying that shade does not strongly affect mean annual soil temperatures at 20-cm depth. Although there was no significant effect of overstory canopy closure on mean annual soil temperature, there were seasonal effects (fig. 23). The correlations between overstory canopy closure and mean monthly soil temperatures in July and August were both highly significant ($P < 0.01$), while the correlation with mean monthly soil temperatures in June was marginally significant. Although the other monthly correlations were not significant, there was an overall pattern that implied seasonal change and a weak positive effect of overstory canopy closure on soil temperature in winter that changes to a stronger negative effect in summer.

The linear regression of mean monthly soil temperature as a function of overstory canopy closure in June was marginally significant and weak (table 16), suggesting a modest warming of 3.9 °C in areas with no overstory compared to areas with completely closed canopies. The linear regression of mean monthly soil temperature in July as a function of overstory canopy closure was highly significant but of only moderate strength (table 16), implying a substantial warming of 7 °C in areas with no overstory compared to areas with completely

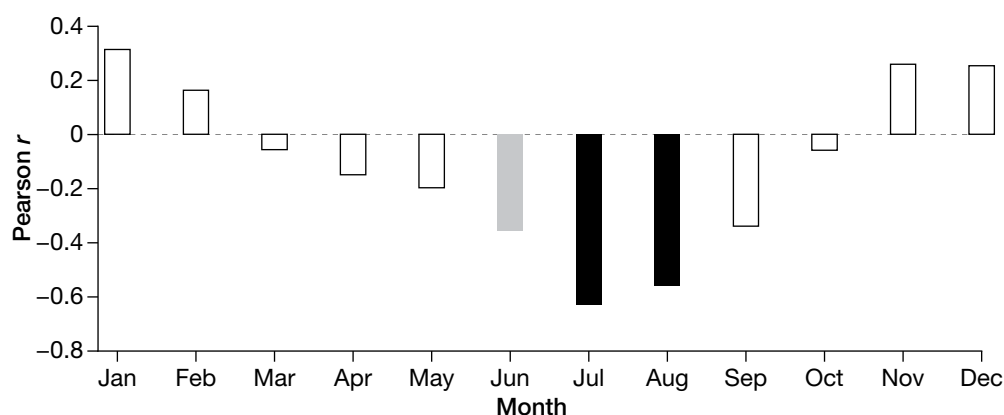


Figure 23—Monthly correlations between overstory canopy closure and mean monthly soil temperature (measured at 20-cm depth) for the Olympic Mountain whitebark pine communities study. Black bars indicate correlations that were significant at $P = 0.05$. Gray bars indicate marginal significance at $P = 0.1$. White bars indicate correlations that were not significant.

closed canopies. The addition of elevation, aspect, or slope steepness, alone or in combination, made only slight improvements in the model. The linear regression of mean monthly soil temperature in August as a function of overstory canopy closure was highly significant but relatively weak (table 16), suggesting a warming of 5.6 °C in areas with no overstory compared to areas with completely closed canopies.

Table 16—Linear regression model summaries of mean monthly 20-cm-deep soil temperature as a function of overstory canopy closure for the months of June, July, and August for the Olympic Mountain whitebark pine communities study

Month	n	Model P	Model adjusted r^2	Canopy cover coefficient	Intercept	Intercept P
June	22	0.10	0.09	-0.0387	8.65711	<0.01
July	22	<0.01	0.37	-0.0705	16.30430	<0.01
August	22	<0.01	0.28	-0.0555	16.04570	<0.01

P = probability value; r^2 = coefficient of determination.

Relationships Between Alpine Tree Line Position and Temperature

- Mean growing-season soil temperatures ranged from 7.4 to 14.5 °C, thus all were higher than 6.2 °C at 20-cm depth, which in Körner and Paulsen's (2004) model separates alpine from subalpine environments.
- A linear regression model of our mean growing-season soil temperatures suggested that there was a 4.4 °C difference between areas with no overstory and areas with completely closed canopies.
- Fourteen of 36 plots had mean growing-season soil temperatures ranging from 5.9 to 7.3 °C (*sensu* Körner and Paulsen 2004) where low soil temperatures could limit complete overstory canopy closure by inhibiting root growth.

We explored the temperature relationship put forth by Körner and Paulsen (2004) to explain the alpine tree line. None of our plots exhibited growing-season soil temperatures, as defined in their paper, that were as low as 6.7 °C at 10-cm depth (6.2 °C at 20-cm soil depth assuming a decrease of 0.5 °C for each 10 cm in depth as suggested by USDA NRCS [1999]). Similarly, none of our plots fell within the broader range that Körner and Paulsen (2004) provide (equivalent to 5.9 to 7.3 °C at 20-cm soil depth). Our mean growing-season soil temperatures ranged from 7.4 to 14.5 °C (plots 33 and 5, respectively). However, we wanted to know if any of our soils might get as cold as 6.2 °C should tree canopies close over them. After first calculating the mean growing-season soil temperature for each of our plots, we linearly modeled these temperatures on plot overstory canopy closure. This relationship was highly significant ($P < 0.01$) with an adjusted r^2 of 0.36. The intercept was highly significant (12.68 °C, $P < 0.01$) as was the overstory canopy closure coefficient (-0.04 , $P < 0.01$). Thus, should a complete overstory canopy develop on a fully open site, we would expect the mean growing-season soil temperature to decline by 4.4 °C compared to that of an entirely open area and by proportionately lesser amounts for less closure. Soil temperatures on plots 6, 7, 16, and 27 would fall to or below 6.2 °C under these conditions. Other plots that would fall within the broader range that Körner and Paulsen (2004) specified were plots 12, 13, 14, 17, 18, 19, 25, 29, 33, and 41. Thus, 14 of 36 plots for which we had data fall into the range where soil temperatures could limit complete overstory canopy closure by inhibiting root growth.

Winter Snow Accumulation

- Seasonal snowpack began in November following several melting and redeposition events usually spread over several days but in a few cases lasting into January, after which nearly all plots were covered through March and some as late as June.
- The first plots to receive a seasonal snowpack were among the last to have it melt.
- Aspect, proximity to a ridgetop, and elevation accounted for 41 percent of the variation in snowpack duration, with snowpack lasting longest on northern aspects at higher elevations close to the lee side of ridgelines that were oriented at high angles to approaching storm tracks from the southwest.
- The date of the first detected snow of the season was positively correlated with mean monthly air temperatures from September through December, especially at night. The date of the first snow of the season was positively correlated with mean monthly soil surface temperatures in September and October and mean monthly soil temperatures in November through January.
- The date of complete snowpack melt was negatively correlated with mean annual air temperatures, mean monthly air temperatures throughout the year, and mean annual air temperatures for all quarters of the day; mean annual soil surface temperature, mean monthly soil surface temperature in April through June, and mean annual soil surface temperatures in quarter-day 2; and mean annual soil temperature, mean monthly soil temperatures in April through July, September, and October, and all mean annual quarter-day soil temperatures.
- The duration of the seasonal snowpack was negatively correlated with mean annual air temperature; mean monthly air temperatures in December, January, and May; mean annual air temperatures in quarter-days 1, 2, and 4; mean annual soil surface temperature in quarter-day 4; and mean monthly soil temperatures in May and June.

The duration of the seasonal snowpack was positively correlated only with mean monthly soil surface temperature in February and was negatively correlated with mean monthly air temperatures in April and May.

At our study area, snow that was detectable with our techniques usually arrived in November, initially accumulating during the night more than in the day. In most cases, daily temperature fluctuation was much reduced from once to several times for a day or two at a time before being continuously flatlined for the season. In a few cases, reductions in daily temperature fluctuation came and went for a month or more, but all plot temperatures eventually flatlined for most of January, February, and March.

Plot 32 was the first plot to have seasonally damped temperature fluctuation (averaged over 3 years) on November 6. The elevation of this plot was only 1595 m, but it was located just below a ridgetop on a 0-degree aspect. This plot was heavily dominated by subalpine fir with a sparse Cascade azalea understory. Because most snow-bearing weather comes from the southwest in this area, it received snow that blew over the ridge in addition to direct snowfall.

On average, 1 to 2 days later, two other higher elevation plots (plots 13 and 31) in topographic positions similar to plot 32 (but farther from their ridgetops) and that had subalpine fir/broadleaf lupine plant communities were covered with snow for the season. At about the same time, two plots (plots 18 and 27) were also covered with snow for the season. Plot 18 was located on a pronounced bench, high on an otherwise west-facing ridge. The lip of the bench functioned like a ridgeline, trapping snow on the bench that was windblown up the west-facing slope. The community type here was a nonforested, black alpine sedge community. The other plot (plot 27) was very similar to plot 32 in terms of its plant community, elevation, and topographic position, but was somewhat farther from its associated ridgetop.

The last plot to accumulate a seasonal snowpack was plot 23, the lowest elevation plot (1420 m) on a southwest-facing slope, which (on average) achieved a seasonal snow cover on January 8. Aside from this plot, the five plots that were the latest to accumulate snow (plots 6, 15, 22, 38, and 40) were all on steep southwest-facing slopes but over a range of elevations, from 1543 to 1816 m.

In spring, the first plot to lose its seasonal snowpack (March 27) was plot 35 (1742-m elevation), which was on a highly exposed west-facing ridgetop. On the windward side, the community type was alpine tundra, and on top of the ridge, the community type was krummholz subalpine fir. Wind removed snow from the windward side and redeposited it in the krummholz and especially on the lee slope, which was also a nonforest community but due to late melting snow. The next three plots to lose their snowpack were plot 40 (April 2, 1693-m elevation, south-southwestern aspect), plot 23 (April 6, 1420-m elevation, west-southwestern aspect), and plot 12 (April 21, 1803-m elevation, western aspect).

The first 5 plots to receive a seasonal snowpack were among the last 10 plots to lose their snowpack. The snowpack stayed longest on plot 18 (June 24), the bench plot referenced above as one of the earliest to accumulate a seasonal snowpack. Plot 32, the first to accumulate a seasonal snowpack, was the second last to lose its snowpack (June 17). Plot 13, also one of the earliest plots to receive a seasonal snowpack, was the third latest to lose its snowpack (June 16). The highest elevation plot (plot 30, 1893-m elevation) also melted out on June 16, and the second highest plot (plot 29, 1857-m elevation) was the next to last to lose its snowpack (June 12).

Thus, aspect, elevation, proximity to a ridgeline running perpendicular or at a high angle to the approaching storm tracks (or other topographic feature that acted similarly) were important in the early-season accumulation of snow and in late-season loss of the snowpack and thus in the total duration of the seasonal snowpack.

Snow depth next to tree boles was mostly <1.5 m for the trees on which our temperature sensors were attached. Only 11 plots showed winter daily flattening of the 1.5-m-high air temperatures (table 17). This daily flattening was for a shorter duration than at the soil surface. The air temperature sensors affected by snow recorded nighttime freezing as low as -6°C , but during warmer periods, melting snow above the sensors kept the maximum temperature at 0°C . The lowest temperatures that were recorded invariably occurred early in the snow burial process, when the snow cover was shallow. As the snow over sensors accumulated, the air temperatures moderated to the range of -2 to 0°C . At the same time, air temperatures measured at 3-m heights ranged from -16.5 to 13°C .

These 11 plots suggest that the deepest snow occurred in winter of 2012 to 2013, and the shallowest snow accumulation occurred in winter of 2013 to 2014. The average period for which our 1.5-m-high air temperature sensors at the 11 plots were buried under snowpack was 74 days in winter of 2012 to 2013 and only 2 days in winter of 2013 to 2014 (table 17).

The plot with the longest duration of seasonal snowpack was plot 18, which over the 3 years of record, had its 1.5-m-high air temperature sensor covered with snow for an average of 97 days. The next longest snow covers were on plots 7, 13, 29, and 32, with 51 to 57 days of snow cover; plots 21, 31, and 39, with 26 to 34 days of snow cover; and plots 27, 28, and 30, with 3 to 13 days of snow cover (table 17).

Only plot 18 showed daily damping of the highest of the two air temperature sensors. However, the tree on which the sensor was attached was small (4-cm d.b.h. and 2.9 m tall). The air temperature sensor on this tree was placed at only 2.8-m height, and we cannot rule out that the tree was bent under the weight of the snow, further decreasing the height of both sensors, but especially the higher one.

With stepwise linear regression, we modeled the duration of the seasonal snowpack in days as a function of aspect; elevation; proximity to a ridgetop; potential direct solar radiation in fall, in spring, and in the entire year; and overstory canopy closure. The resulting model retained aspect, proximity to a ridgetop, and elevation (table 18). The model was highly significant ($P < 0.01$) with an overall adjusted $r^2 = 0.41$. Monthly direct solar radiation in spring or fall were not significant in the model, yet aspect was highly significant (negative relation) in the model and accounted for more variation than any other variable (table 18).

The date of snowmelt was negatively correlated with mean annual air temperature, mean air temperatures in all months, and mean annual air temperatures in all quarters of the day (tables 19 and 20). Mean annual air temperature and mean monthly air temperatures for December, January, and May were also negatively correlated with the total number of days of continuous snowpack. Similarly, all mean annual air temperatures by quarter-day, except quarter-day 3, were negatively correlated with the number of days of continuous snowpack (table 19). There were fewer mean monthly air temperatures that correlated with the date of the first snow, but all were positive and fell in fall and winter months (table 19).

The date of snowmelt was negatively correlated with the mean annual soil surface temperature, mean monthly soil surface temperatures in spring months, and mean annual soil surface temperatures in quarter-day 2 (tables 19 and 20). The number of days of continuous snowpack was positively correlated with mean monthly soil surface temperature in

Table 17—Olympic Mountain whitebark pine communities study plots where snow covered the 1.5-m-high air temperature sensor in at least 1 of the 3 years with the dates when daily fluctuations were first damped (first covered), when they resumed (last covered), and the duration of the seasonal snowpack in days

Plot	2011–2012			2012–2013			2013–2014			3-year mean duration covered
	First covered	Last covered	Duration covered	First covered	Last covered	Duration covered	First covered	Last covered	Duration covered	
	MONTH/DAY	MONTH/DAY	DAYS	MONTH/DAY	MONTH/DAY	DAYS	MONTH/DAY	MONTH/DAY	DAYS	
7	4/11	5/20	39	1/8	4/23	106	2/23	3/2	7	51
13	3/9	4/8	30	12/12	5/3	142	—	—	0	57
18	1/30	6/9	131	12/15	5/10	146	3/27	4/9	13	97
21	3/25	4/13	19	12/25	2/21	58	—	—	0	26
27	—	—	0	1/15	1/25	10	—	—	0	3
28	4/9	4/19	10	—	—	0	—	—	0	3
29	3/14	4/23	40	12/22	4/22	121	—	—	0	54
30	3/31	5/9	39	—	—	0	—	—	0	13
31	3/22	5/9	48	12/24	2/15	53	—	—	0	34
32	3/11	4/21	41	12/12	4/9	118	—	—	0	53
39	3/16	4/24	39	1/8	3/4	55	—	—	0	31
Annual mean (days)	NA	NA	39	NA	NA	74	NA	NA	2	NA

NA = not applicable; — = no data.

Note: There is some ambiguity in determining these events with the methods that we used, so the dates are only accurate within 2 or 3 days.

Table 18—Stepwise linear regression model summary of the duration of the seasonal snowpack in days as a function of aspect, proximity to a ridgetop, and elevation for the Olympic Mountain whitebark pine communities study (n = 36)

Model			Summary of stepwise selection				
Variable	Coefficient	P	Step	Enter/remove	Partial r^2	Model r^2	P
Intercept	118.24006	0.10	NA	NA	NA	NA	NA
Aspect ^a	-0.78491	<0.01	1	Aspect/	0.30	0.30	<0.01
Ridge ^b	0.05567	0.03	2	Ridge/	0.08	0.39	0.04
Elevation ^c	0.08239	0.05	3	Elev/	0.07	0.46	0.05

NA = not applicable; P = probability value; r^2 = coefficient of determination.

^a Aspect is deviation in degrees from 22° azimuth.

^b Ridge is the distance in meters from the nearest ridgetop with positive numbers indicating downwind and negative numbers indicating upwind.

^c Elevation is the elevation above sea-level in meters.

Table 19—Spearman correlation coefficients for relationships between snowpack indicators and mean annual and monthly air, soil surface, and 20-cm-deep soil temperatures for the Olympic Mountain whitebark pine communities study

	Air			Soil surface			Soil		
	First snow ^a	Days of snowpack ^b	Date of snowmelt ^c	First snow	Days of snowpack	Date of snowmelt	First snow	Days of snowpack	Date of snowmelt
n ^d	29	29	29	19	19	19	22	22	22
MAT ^e	—	-0.39	-0.52	—	—	-0.48	—	—	-0.65
Jan	—	-0.54	-0.67	—	—	—	0.54	—	—
Feb	0.38	—	-0.49	—	0.49	—	—	—	—
Mar	—	—	-0.41	—	—	—	—	—	—
Apr	—	—	-0.57	—	-0.64	-0.78	—	—	-0.56
May	—	-0.41	-0.62	—	-0.83	-0.88	—	-0.64	-0.91
Jun	—	—	-0.46	—	—	-0.48	—	-0.44	-0.70
Jul	—	—	-0.49	—	—	—	—	—	-0.43
Aug	—	—	-0.45	—	—	—	—	—	—
Sep	0.37	—	-0.45	0.57	—	—	—	—	-0.48
Oct	0.37	—	-0.46	0.54	—	—	—	—	-0.60
Nov	0.46	—	-0.42	—	—	—	0.60	—	—
Dec	0.38	-0.49	-0.59	—	—	—	0.51	—	—

— = no data.

Note: All correlations presented were significant at $P = 0.05$.

^a Mean Julian day of the first detectable snowfall.

^b Mean number of days of continuous snowpack.

^c Mean Julian day of the melting of the snow over the thermocouple, averaged over 3 years of record.

^d Number of plots on which the correlation is based.

^e Mean annual temperature.

February but was negatively correlated with mean monthly soil surface temperatures during the spring and with mean annual soil surface temperatures in quarter-day 4 (tables 19 and 20). The date of first snow was positively correlated with mean monthly soil surface temperatures in September and October.

The date of snowmelt was negatively correlated with mean annual soil temperature; as well as with some mean monthly soil temperatures during spring, summer, and fall; and with mean annual soil temperatures in all quarters of the day (tables 19 and 20). The number of days of continuous snowpack was negatively correlated only with mean monthly soil temperatures in May and June (table 19). The date of first snow was positively correlated only with mean monthly soil temperatures in November through January.

Table 20—Spearman correlation coefficients for correlations between several snowpack indicators and mean annual air, soil surface, and 20-cm-deep soil temperatures by quarter-day for the Olympic Mountain whitebark pine communities study

Quarter-day ^a	Air			Soil surface			Soil		
	First snow ^b	Days of snowpack ^c	Date of snowmelt ^d	First snow	Days of snowpack	Snowmelt	First snow	Days of snowpack	Date of snowmelt
1	0.44	-0.49	-0.55	—	—	—	—	—	-0.65
2	—	-0.40	-0.54	—	—	-0.55	—	—	-0.65
3	—	—	-0.47	—	—	—	—	—	-0.66
4	0.44	-0.38	-0.48	—	-0.46	—	—	—	-0.66

— = no data.

Note: All correlations presented were significant at $P = 0.05$.

^a Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

^b Mean Julian day of the first detectable snowfall.

^c Mean number of days of continuous snowpack.

^d Mean Julian day of the melting of the snow over the thermocouple averaged over 3 years of record.

Solifluction

- The 14 plots with visible evidence of solifluction were, on average, higher in elevation, steeper, and had more coarse fragments at the soil surface.
- Most plots with rock stripe solifluction had basaltic regolith, which produces more and larger coarse fragments than the local sedimentary rock.
- The mean annual air temperature of plots with solifluction was only marginally lower than those without.
- Solifluction was mostly observed in the spreading phlox, subalpine fir/common juniper, and subalpine fir/broadleaf lupine plant associations.

There was evidence of active solifluction (gradual movement of soils and rock down a slope due to freeze-thaw activity) on 14 plots (fig. 24): plots 4, 6, 9, 12, 13, 14, 19, 20, 24, 25, 28, 30, 31, and 38.

Plots with evidence of solifluction differed statistically from those without such evidence in terms of coarse fragment content ($P < 0.01$), elevation ($P < 0.01$), and slope steepness ($P = 0.01$) (table 21). Thus, plots with observed solifluction were, on average, higher in elevation,

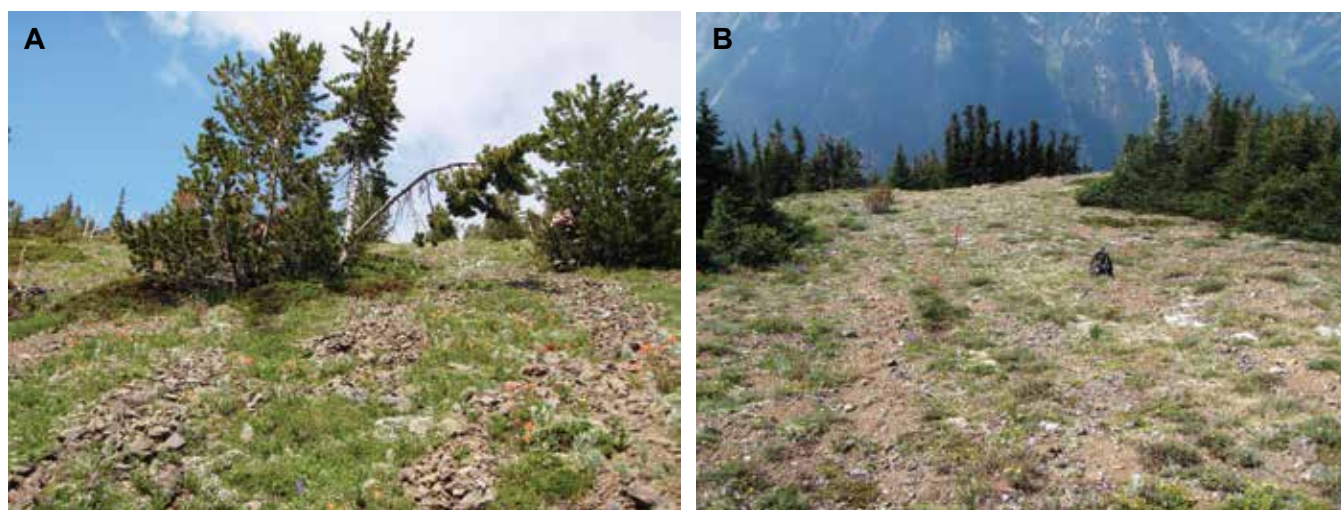


Figure 24—Two examples of solifluction striping on (A) plot 19 and (B) plot 30 of the Olympic Mountain whitebark pine communities study. The rock material in both cases is basalt. Photos by David H. Peter.

Table 21—Comparison of plots in the Olympic Mountain whitebark pine communities study with or without solifluction for several topographic and climatic variables with analysis of variance

Variable	With solifluction mean	Without solifluction mean	P	n
Coarse fragment content (%)	64.1	30.1	<0.01	14
Elevation (m)	1749.6	1639.0	<0.01	14
Slope steepness (%)	62.9	50.9	0.01	14
Mean annual air temperature (°C)	2.4	3.0	0.06	12
Standard deviation of mean annual air temperature (°C)	7.3	7.2	0.14	12
Mean number of frost-free days	88.0	98.2	0.16	12
Mean annual soil surface temperature (°C)	4.4	4.8	0.46	8
Standard deviation of mean annual soil surface temperature (°C)	9.0	8.3	0.44	8
Mean annual 20-cm-deep soil temperature (°C)	4.3	4.1	0.81	10
Standard deviation of mean annual 20-cm-deep soil temperature (°C)	5.8	5.4	0.42	10
Date of winter snowpack establishment	360.4	353.2	0.53	11
Mean annual minimum 20-cm-deep soil temperature (°C)	−2.6	−2.5	0.97	9
Aspect	125.9	118.1	0.58	14

steeper, and had more coarse fragments at the soil surface. Whereas the underlying bedrock on our plots was split almost equally between basalt and sedimentary rock, 67 percent of the plots with solifluction had underlying basalt. Also, the regolith on two of the five plots with underlying sedimentary rock consisted largely of basaltic rubble eroded from nearby basalt above the plot location. Thus, 88 percent of the plots with solifluction had mainly basaltic regolith. Basalt produces more and larger coarse fragments than the local sedimentary rock (see below). The mean annual air temperature of plots with solifluction was marginally lower than those without such evidence ($P = 0.06$) (table 21).

Seven species differed significantly between plots with visible evidence of solifluction and those without. This comparison was made only with plots in spreading phlox, subalpine

fir/common juniper, and subalpine fir/broadleaf lupine plant associations, as these were the principal associations in which solifluction was observed. There were no species with significantly more cover in plots with solifluction compared to plots without solifluction. The species with significantly more cover in the plots without solifluction were subalpine fir, lodgepole pine, Douglas-fir, common yarrow (*Achillea millefolium*), squirreltail (*Elymus elymoides*), broadleaf lupine, and Douglas' catchfly (*Silene douglasii*).

Soil Texture, Coarse Fragments, and Bedrock Type

- The dominant soil texture on plots was loamy sand.
- Bedrock was about half basaltic and half sedimentary in our plot sample.
- Coarse fragment content on sedimentary substrates averaged 22 percent, and on basaltic substrates, it averaged 66 percent.
- The average summer soil moisture of the fine soil fraction was similar in soils on the two bedrock types but was more variable in soils on basaltic substrates.

Of the 37 plots for which we had soil texture data, the soil texture on 7 plots was sandy, it was loamy sand on 27 plots, and it was sandy loam on 1 plot (table A2.4). Two plots had mostly rocky talus, with little surficial soil. These were the dominant texture classes for the plots, but small inclusions of others were often present. Thus, there were places in the talus plots where soil was present, and plants grew only in those places.

The coarse fragment content differed strongly by rock type but not the measured summer soil moisture (table 22). However, the summer soil moisture in soils on the basalt rock type varied more both within the plot and through the years than in soils on the sedimentary type.

Table 22—Analysis of variance probabilities for comparison of coarse fragments and summer soil moisture variables by bedrock type for the Olympic Mountain whitebark pine communities study

Variable	Sedimentary mean (n = 19)	Basalt mean (n = 18)	P > F
Coarse fragment content of soil (%)	21.6	65.5	<0.01
Summer soil moisture (%)	4.6	4.7	0.99
Standard deviation of summer soil moisture (%)	1.1	1.8	<0.01
Within-plot standard deviation of summer soil moisture (%)	1.1	1.5	<0.01

Summer Soil Moisture

CORRELATION ANALYSIS—

- Summer soil moisture was higher on concave or flatter slopes and on northern aspects.
- We found no obvious relationships between summer soil moisture and persistence, and relationships with solar radiation exposure were weak.
- Summer soil moisture was higher for closed-canopy plots than for open-canopy plots.
- Correlations between summer soil moisture and air, soil surface, and soil temperatures were negative.
- Most soil surface and soil temperature correlations occurred in the snow-free season, with the strongest in spring and summer.

The significant physical site correlations with summer soil moisture were slope steepness ($r = -0.59$), overall microtopography ($r = -0.51$), aspect ($r = -0.41$), and horizontal microtopography ($r = -0.37$).

Variables relating to the persistence of snow in spring were not significantly correlated with summer soil moisture. Although percentage of overstory canopy closure also did not significantly correlate with summer soil moisture, the mean summer soil moisture of closed-canopy plots (5.8 percent) was significantly higher than the mean summer soil moisture of open-canopy plots (4.5 percent, $P = 0.02$).

Of the 42 solar variables, only 3 were significantly correlated with summer soil moisture: duration of direct solar exposure in June ($r = 0.49$), duration of direct solar exposure in July ($r = 0.36$), and ground-level PAR ($r = -0.36$).

Of the 560 temperature variables, there were 38 significant correlations between summer soil moisture and air temperatures, 44 with soil surface temperatures, and 47 with soil temperatures (fig. 25). All were negative correlations. The strongest correlation among the temperature variables was with the mean June soil surface temperature in quarter-day 4 ($r = -0.78$) and following it was the mean September maximum air temperature in quarter-day 4 and the overall mean soil surface temperature in June, both at $r = -0.68$.

The air temperature correlations were distributed more-or-less equally among the months of the year (fig. 25). However, soil and soil surface temperature correlations were concentrated in summer, especially in July and August, suggesting a link between summer soil heating and drying.

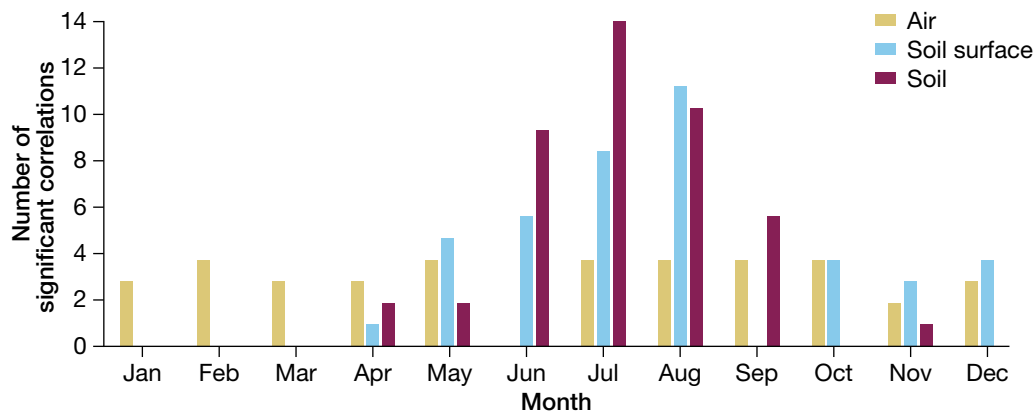


Figure 25—The number of significant correlations between monthly air, soil surface, and 20-cm-deep soil temperature means and mean summer soil moisture for the Olympic Mountain whitebark pine communities study. All correlations were negative.

Both the number and strength of the temperature correlations varied by month. The mean of the significant correlation coefficients for mean monthly air temperatures varied from a low in February ($r = -0.46$, $SD = 0.03$) to a high in December ($r = -0.58$, $SD = 0.10$). The mean of the significant correlation coefficients for mean monthly soil surface temperatures varied from a low in May ($r = -0.49$, $SD = 0.02$) to a high in June ($r = -0.63$, $SD = 0.09$), and the mean of the significant correlation coefficients for mean monthly soil temperatures varied from a low in April ($r = -0.45$, $SD = 0.004$) to a high in June ($r = -0.58$, $SD = 0.07$).

REGRESSION ANALYSIS—

- A linear regression model including the physical site variables of slope steepness, overall microtopography, and aspect accounted for 51 percent of the variation in summer soil moisture.
- A linear regression model including the mean June soil surface temperature in quarter-day 4, slope steepness, and overall microtopography accounted for 63 percent of the variation in summer soil moisture.

A linear regression model based on physical site variables accounted for 51 percent of the variation in summer soil moisture and included slope steepness, overall microtopography, and aspect (adjusted $r^2 = 0.51$, $P < 0.01$) (table 23: model 1). A stronger linear regression model accounted for the variation in summer soil moisture as a function of the mean June soil surface temperature in quarter-day 4, slope steepness, and the shape of the overall microtopography (i.e., convex, flat, or concave) (table 23: model 2) (adjusted $r^2 = 0.63$, $P < 0.01$).

Table 23—Linear regression model summaries of summer soil moisture as a function of environmental variables for the Olympic Mountain whitebark pine communities study

Model 1 (adjusted $r^2 = 0.51$, $P < 0.01$):	Coefficient	P
Intercept	9.87811	<0.01
Slope steepness (%)	−0.04430	<0.01
Overall microtopography ^a	−0.78105	0.12
Aspect	−0.00877	0.03
Model 2 (adjusted $r^2 = 0.63$, $P < 0.01$):	Coefficient	P
Intercept	9.71054	<0.01
June soil surface temperature in quarter-day 4 ^b	−0.09964	0.03
Slope steepness (%)	−0.03252	0.02
Overall microtopography ^a	−1.07527	0.02

P = probability value; r^2 = coefficient of determination.

^a Field coded as convex, flat, or concave.

^b Quarter-day 4 = 1800 to 2400.

Biological Relationships

For general reference and to assist in the interpretation of subsequent sections, appendix 1 provides a complete list of the plant species found on our plots (as well as plant species that appear in this report for other reasons), including scientific names, authorities, common names, and symbols (USDA NRCS, n.d.); table A2.14 provides species canopy cover by plot; and table A2.15 provides white pine blister rust statistics.

Correlations Between Species Canopy Cover and Temperature

- We used the number of significant temperature correlations (out of 65) between species canopy cover and air, soil surface, and soil temperatures to define warm, neutral, and cool site preferences of 20 species.
- Douglas-fir, shore pine, white hawkweed (*Hieracium albiflorum*), and Cascade desertparsley (*Lomatium martindalei*) were always in the warm habitat group; big huckleberry was always in the neutral habitat group; and Cascade azalea and cliff dwarf-primrose (*Douglasia laevigata*) were always in the cool habitat group.
- Whitebark pine was in the neutral habitat group for air and soil temperatures but was in the warm habitat group for soil surface temperature.
- Subalpine fir was in the neutral habitat group for air and soil surface temperatures but was in the cold habitat group for soil temperature.

Figure 26 summarizes the number of significant correlations between 65 temperature variables and the percentage of canopy covers for 20 species. The significant correlations for each species were either positive or negative—there were no cases where some were of one sign and others were of the opposite sign. The air temperature correlations suggested three groups of species were present, including species from locally warm environments—shore pine, white hawkweed, Douglas-fir, Oregon boxleaf, western white pine, and Cascade desertparsley; locally neutral species—subalpine fir, whitebark pine, common juniper, thin-leaf huckleberry, broadleaf lupine, and orange agoseris (*Agoseris aurantiaca*); and species from locally cool environments—littleflower penstemon (*Penstemon procerus*), Cascade azalea, spreading phlox, giant red Indian paintbrush (*Castilleja miniata*), hookedspur violet (*Viola adunca*), common yarrow, Roemer's fescue (*Festuca idahoensis* ssp. *roemeri*), and cliff dwarf-primrose. The relationships indicated by the air temperature correlations were generally, but not entirely, similar to those of the soil surface and soil temperatures. Shore pine, white hawkweed, Douglas-fir, and Cascade desertparsley all showed at least some positive correlation with air, soil surface, and soil temperatures, but only two species (Cascade azalea and cliff dwarf-primrose) were negatively correlated with air, soil surface, and soil temperatures.

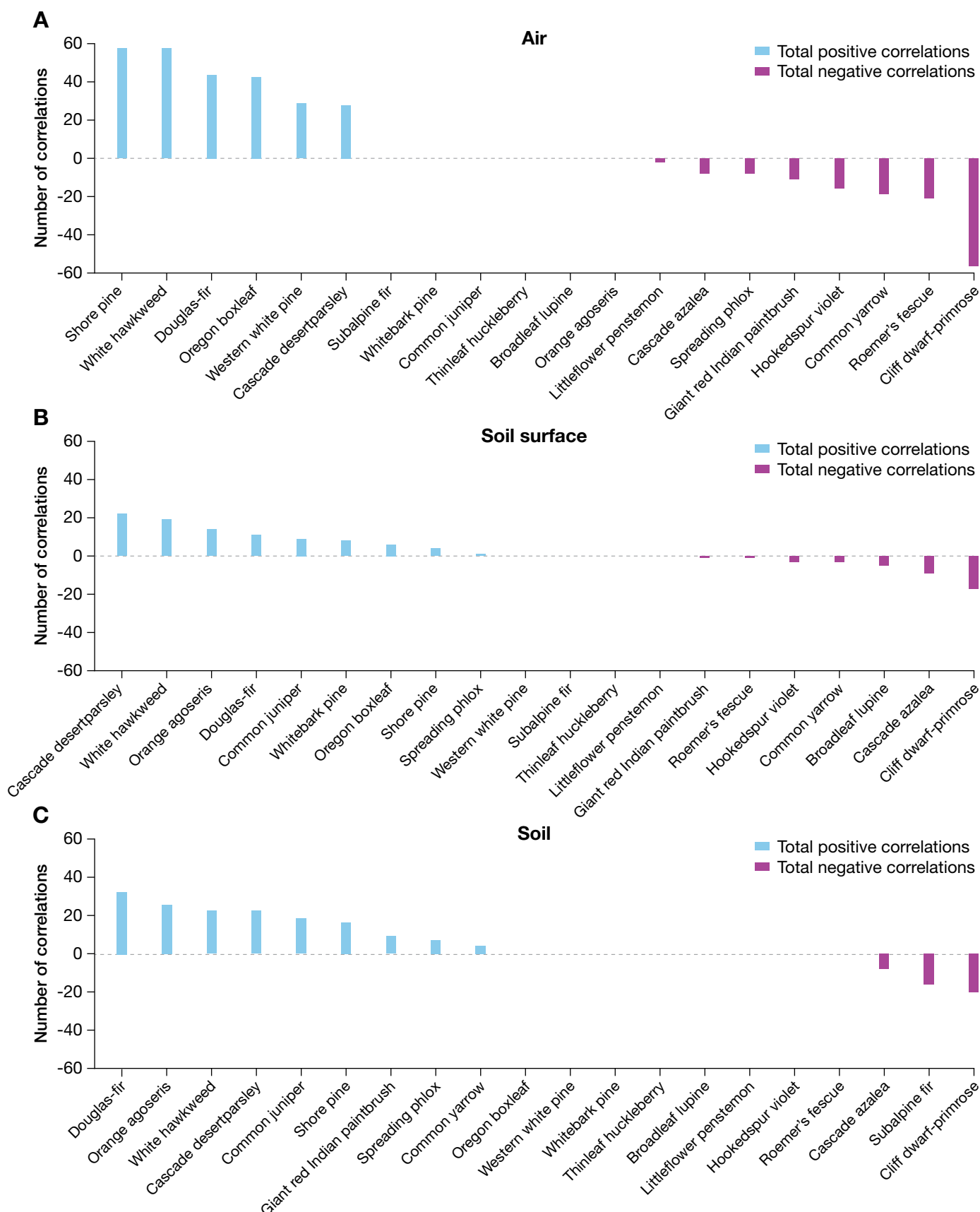


Figure 26—The number of significant Spearman correlations between the canopy cover and mean (A) air temperature, (B) soil surface temperature, and (C) 20-cm-deep soil temperature for 20 species in the Olympic Mountain whitebark pine communities study. There were 65 variables tested, including annual and monthly temperatures by quarter-days or entire days. The species are sorted in order of the number of significant correlations from positive to negative.

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND AIR TEMPERATURE—

- Subalpine fir, whitebark pine, thinleaf huckleberry, broadleaf lupine, and orange agoseris were not significantly correlated with mean air temperatures either monthly or by quarter-day.
- Western white pine, Oregon boxleaf, Cascade desertparsley, shore pine, Douglas-fir, and white hawkweed tended to be positively correlated with mean monthly air temperatures in the late afternoon, while Douglas-fir, shore pine, and white hawkweed were also positively correlated with mean air temperatures in nearly every month and in all quarters of the day.
- Cliff dwarf-primrose and Cascade azalea were negatively correlated with mean monthly air temperatures in nearly every month and in all quarters of the day.
- Other species that were negatively correlated with mean monthly air temperatures, especially during the night, included common yarrow, hookedspur violet, Roemer's fescue, spreading phlox, littleflower penstemon, and giant red Indian paintbrush—all species that occur in open environments.

Canopy covers for several species, including subalpine fir, whitebark pine, thinleaf huckleberry, broadleaf lupine, and orange agoseris were not significantly correlated with mean air temperatures, monthly or by quarter-day. However, some of these species were variously correlated with mean soil surface or soil temperatures. Shore pine and Douglas-fir canopy covers were significantly and positively correlated with mean air temperatures in every month and in all quarters of the day, although afternoon correlations were slightly stronger than for other times of the day (fig. 27). Western white pine canopy cover was positively correlated with mean air temperatures from March through December, especially in the afternoon (quarter-day 3), with the strongest correlations in summer months. Western white pine canopy cover was positively correlated with mean monthly air temperatures in the morning and evening but for fewer months and centered more or less on the solstice. White hawkweed and Oregon boxleaf canopy covers showed similar strong positive correlations with mean monthly air temperatures year-round. Oregon boxleaf canopy cover tended to be more strongly correlated with mean monthly air temperatures in the afternoon. Cascade desertparsley canopy cover was also positively correlated with mean monthly air temperatures but only in the daytime and evening hours. Also, mean monthly air temperatures in the morning were only important in spring and fall months, suggesting that a longer growing season is more important than a warmer growing season for this species.

Cliff dwarf-primrose canopy cover was negatively correlated with mean monthly air temperatures in every month and in all quarters of the day but especially at night. Cascade azalea canopy cover was also negatively correlated with mean monthly air temperature throughout the year and day but especially in the afternoon. Roemer's fescue, common yarrow, giant red Indian paintbrush, and probably hookedspur violet canopy covers were more negatively correlated with nighttime than daytime temperatures, although there was little seasonality in their correlations. Littleflower penstemon may be similar, but with only two significant correlations, it is difficult to say.

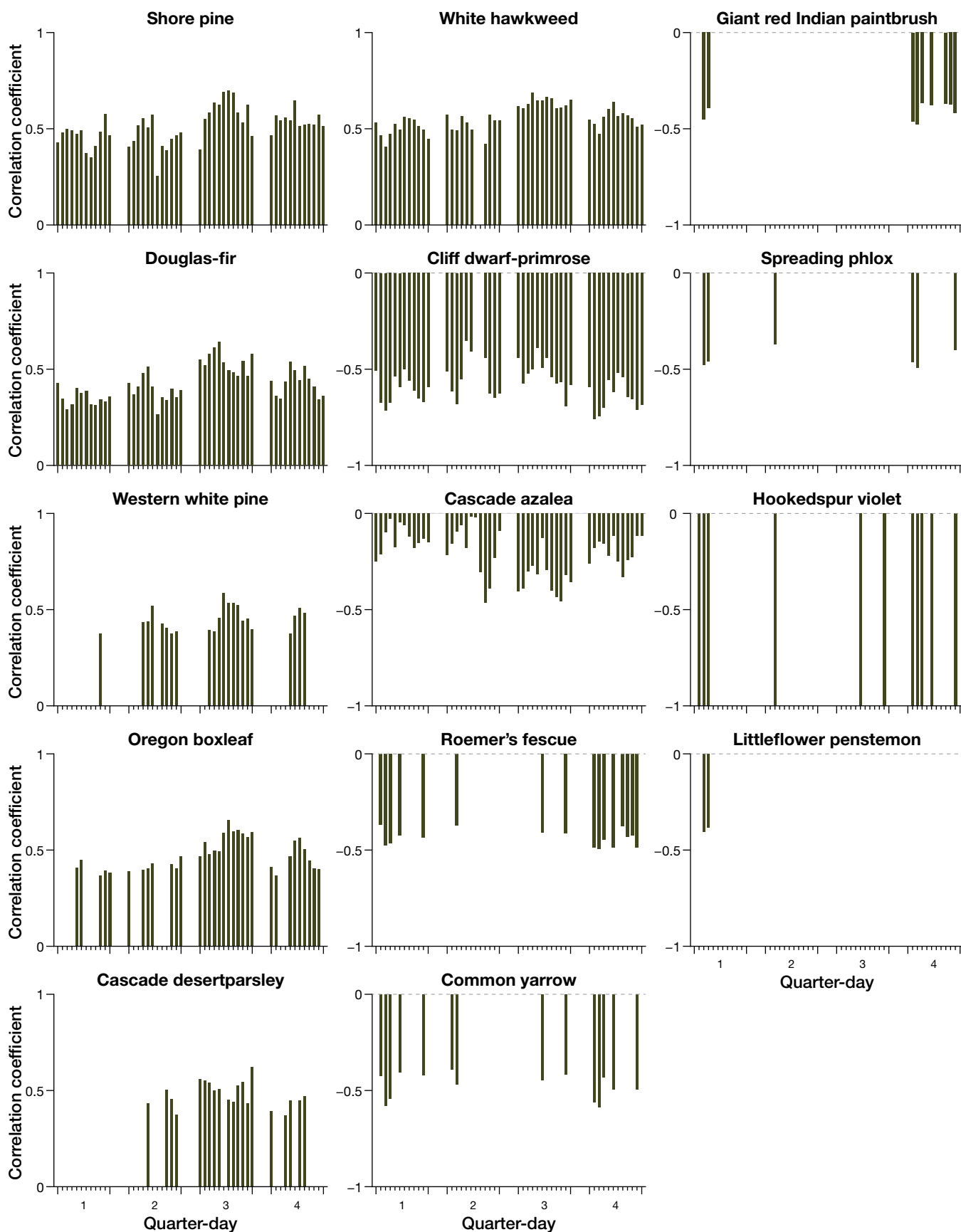


Figure 27—Coefficients for significant Spearman correlations between percentage of canopy cover and mean air temperatures, monthly and by quarter-day, for 14 species in the Olympic Mountain whitebark pine communities study. In each graph, there are four bins along the x axis representing quarter-days (quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, quarter-day 4 = 1800 to 2400). Each bar represents one month (the first bar in each series represents January), so there are up to 12 bars between sets of tick marks (bins). A total of 20 species were investigated.

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND SOIL SURFACE TEMPERATURE—

- Of the 20 species, the canopy covers for 6 species were only negatively correlated with mean monthly soil surface temperatures; 9 species were only positively correlated with mean monthly soil surface temperatures, monthly or by quarter-day, and 5 species (including subalpine fir) had no significant correlations with mean monthly soil surface temperatures.
- Douglas-fir and Oregon boxleaf were positively correlated with mean monthly soil surface temperatures mostly at night, white hawkweed was positively correlated with mean monthly soil surface temperatures mostly during the day, Cascade desertparsley and common juniper were positively correlated with mean monthly soil surface temperatures in the growing-season months during the day and at night, and whitebark pine and orange agoseris were positively correlated with mean monthly soil surface temperatures in winter months and variously during the day and at night.
- Common yarrow, hookedspur violet, and Roemer's fescue were negatively correlated with mean monthly soil surface temperatures at night, and Cascade azalea and broadleaf lupine were negatively correlated with mean monthly soil surface temperatures in the growing-season months and mostly during the day.

Among the tree species, Douglas-fir was the only species with a strong quarter-day correlation signature (fig. 28). Douglas-fir canopy cover was positively correlated with mean monthly soil surface temperatures from spring through fall (May through October) during the night, especially in quarter-day 1 (midnight [0000] to 0600). Oregon boxleaf canopy cover was positively correlated with mean monthly soil surface temperatures during summer months and mostly in the early morning. White hawkweed canopy cover was positively correlated with mean monthly soil surface temperatures in the late summer and fall months and in the morning. Common juniper canopy cover was positively correlated with mean monthly surface temperatures in the afternoon.

Common yarrow and hookedspur violet canopy covers were negatively correlated with mean monthly surface temperatures during summer months in quarter-day 1 (fig. 28). They tended to grow in open areas where radiative heat loss might be expected to be considerable, and thus the low soil surface temperatures in the early morning. The openness of these habitats is likely the important ecological determinant of the locations of common yarrow and hookedspur violet, and these species are simply tolerant of the low morning temperatures. Cascade azalea canopy cover was negatively correlated with mean monthly soil surface temperatures during summer and fall months in the late morning and afternoon.

Other species with more than just an occasional correlation tended not to show any daily pattern. Shore pine canopy cover was positively correlated with mean monthly soil surface temperatures in a few spring, summer, and fall months (fig. 28). Cliff dwarf-primrose canopy cover was negatively correlated with mean monthly soil surface temperatures mostly in fall and winter months. Whitebark pine canopy cover had a moderately strong positive correlation with mean monthly soil surface temperatures in February and March. This interesting pattern is also present in orange agoseris and possibly in Cascade desertparsley. To be clear, warmer soil surfaces in this context are close to 0 °C, and colder soil surfaces are not quite -2 °C, a difference that may be related to snow depth. Broadleaf lupine canopy cover was negatively correlated with mean monthly soil surface temperatures in April and May. Warming of the soil surface at this time of year occurs only after the melting of the snowpack, suggesting a preference by this species for later melting areas.

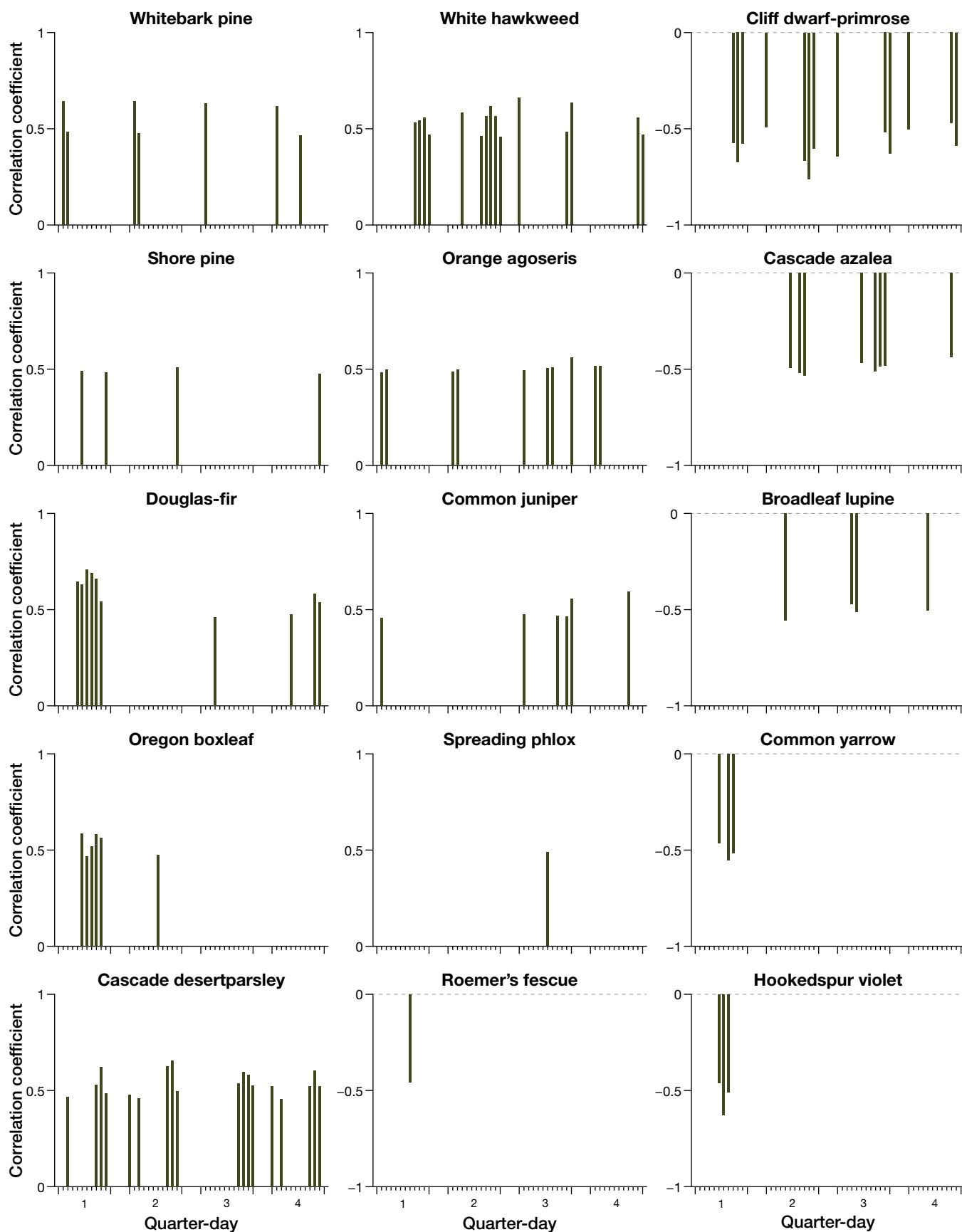


Figure 28—Coefficients for significant Spearman correlations between canopy cover and mean soil surface temperatures, monthly and by quarter-day, for 15 species in the Olympic Mountain whitebark pine communities study. In each graph, there are four bins along the x axis representing quarter-days (quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, quarter-day 4 = 1800 to 2400). Each bar represents one month (the first bar in each bin represents January), so there are up to 12 bars between sets of tick marks (bins). A total of 20 species were investigated.

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND SOIL TEMPERATURE—

- For most species, there was little difference in the seasonal patterns of canopy cover correlations with mean monthly soil temperatures at different times of the day.
- Species with canopy covers that were correlated with mean monthly soil temperatures separated into those with stronger correlations in summer months and those with stronger correlations in fall and early winter months.

Daily patterns of species canopy covers with mean soil temperatures were damped compared to mean monthly air and soil surface temperatures, and this shows in the correlations between canopy covers of species with mean monthly soil temperatures. Generally, the correlations for quarter-day periods resembled the other quarter-day periods for each species (fig. 29).

Among the species with canopy covers that were positively correlated with mean monthly soil temperatures, there were two distinct patterns. Douglas-fir, orange agoseris, whitebark pine, spreading phlox, giant red Indian paintbrush, and common yarrow canopy covers tended to be positively correlated with mean monthly soil temperatures in summer months; and white hawkweed, shore pine, and Cascade deserparsley canopy covers were positively correlated with mean monthly soil temperatures mostly in fall and early winter months. Cascade azalea and subalpine fir were among the species with canopy covers that were negatively correlated with mean monthly soil temperature in summer months. These two species have overlapping ranges; Cascade azalea generally occurs in the understory of subalpine fir growing on cooler aspects. Cliff dwarf-primrose canopy cover was negatively correlated with mean monthly soil temperature in winter and fall months.

Correlations Between Species Canopy Cover and Solar Radiation—

- In general, canopy covers of species were not positively correlated with solar radiation variables in summer months.
- Broadleaf lupine, Cascade deserparsley, cliff dwarf-primrose, orange agoseris, Oregon boxleaf, and whitebark pine were positively correlated with solar radiation variables.
- Spreading phlox, western white pine, thinleaf huckleberry, and Cascade azalea were negatively correlated with solar radiation variables.

Of the 20 species we investigated with correlation analysis, Cascade azalea and thinleaf huckleberry canopy covers for each plot were negatively correlated with one or more of the annual potential solar radiation variables calculated for each plot (fig. 30). The canopy covers of these same species were also negatively correlated with monthly direct solar radiation in most months of the year (fig. 31). Both Cascade azalea and thinleaf huckleberry canopy covers were also negatively correlated with monthly duration of direct solar radiation in winter months, and thinleaf huckleberry canopy cover was negatively correlated with mean monthly diffuse solar radiation in all months of the year (fig. 31). Western white pine was the only other species with a significant negative correlation with direct solar radiation (fig. 31). Its canopy cover was negatively correlated with monthly direct solar radiation in March, May, August, and September.

Only orange agoseris canopy cover was positively correlated with an annual solar radiation variable (annual duration of direct solar radiation) (fig. 30). Cascade deserparsley and Oregon boxleaf canopy covers were positively correlated with monthly direct solar radiation (fig. 31). All three had similar positive correlations with monthly duration of solar direct

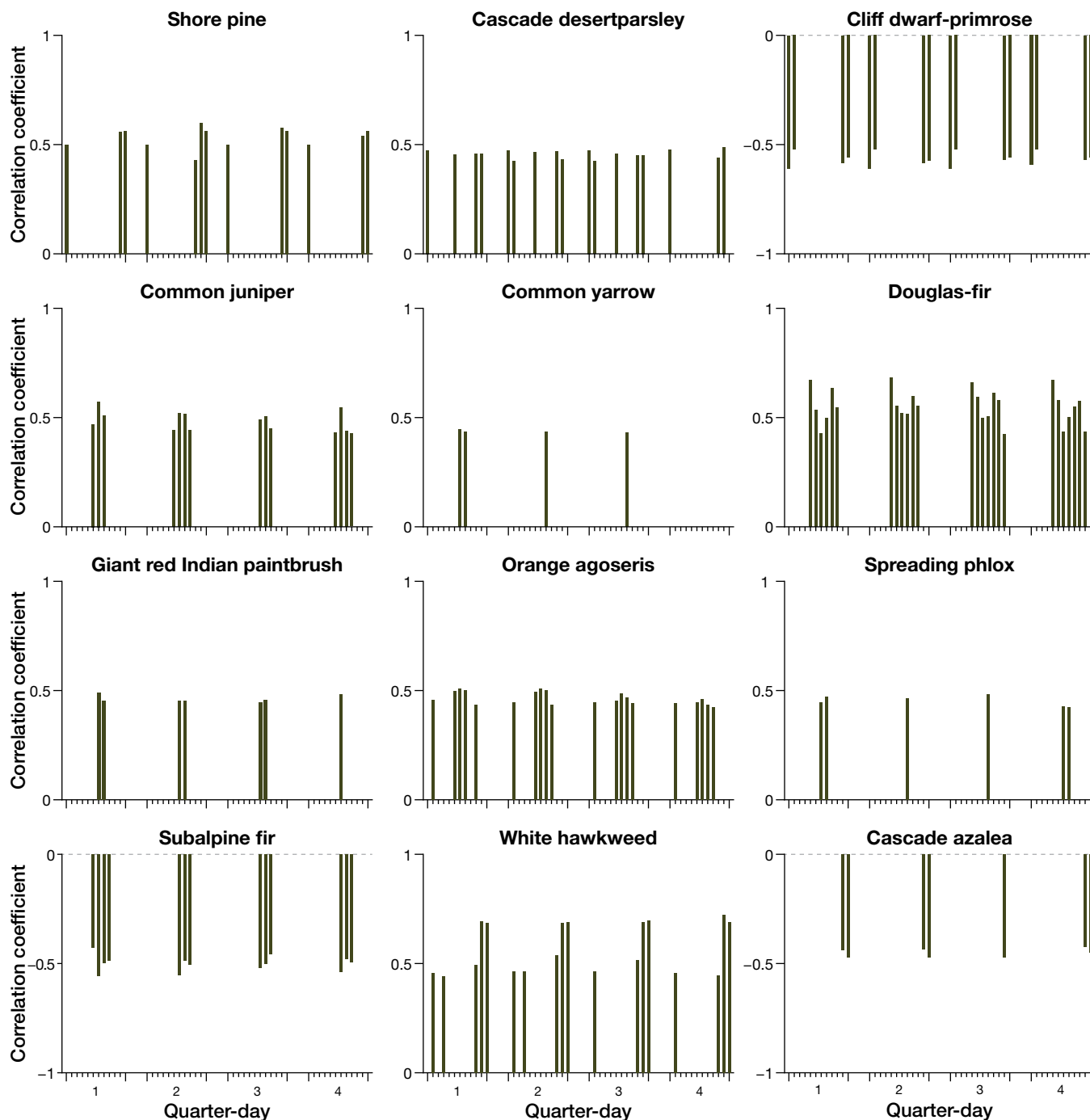


Figure 29—Coefficients for significant Spearman correlations between canopy cover and mean soil temperatures, monthly and by quarter-day, for 12 species in the Olympic Mountain whitebark pine communities study. In each graph, there are four bins along the x axis representing quarter-days (quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, quarter-day 4 = 1800 to 2400). Each bar represents one month (the first bar in each series represents January), so there are up to 12 bars between sets of tick marks (bins). A total of 20 species were investigated.

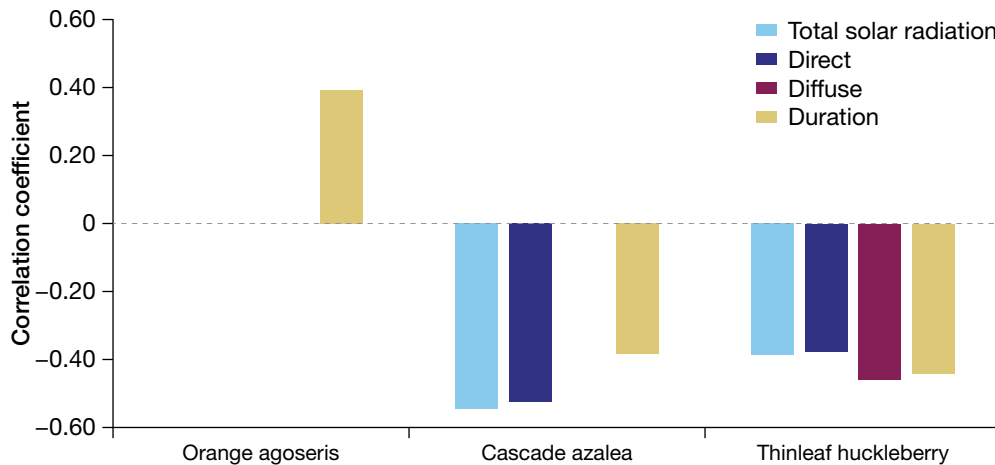


Figure 30—Coefficients for significant Spearman correlations between species canopy cover and annual total solar radiation (direct + diffuse), annual direct solar radiation, annual diffuse solar radiation, and the annual duration of direct solar radiation for three species in the Olympic Mountain whitebark pine communities study. Only these 3 species (of 20) had significant correlations.

radiation in winter months. Broadleaf lupine and cliff dwarf-primrose were the only species with significant positive correlations with monthly diffuse solar radiation, and thinleaf huckleberry was the only species with negative correlations to monthly diffuse solar radiation. Broadleaf lupine was positively correlated with monthly diffuse solar radiation in all months except July through September, while cliff dwarf-primrose was positively correlated only with monthly diffuse radiation in fall and winter months (fig. 31).

Correlations between the canopy covers of species and monthly duration of direct solar radiation were similar to those with monthly direct solar radiation. However, spreading phlox canopy cover was negatively correlated with monthly duration of direct solar radiation in July and August, and whitebark pine canopy cover was positively correlated with monthly duration of direct solar radiation in February and March.

Effects of Snowpack

- The snowpack melted from the end of March through June but mostly in May.
- Significantly more Douglas-fir grew where melting was complete in April; more Cascade desertparsley, Oregon boxleaf, and white hawkweed grew where melting was complete in April or May; and more orange agoseris grew where melting was complete in May.
- Species associated with later melting included subalpine fir and Cascade azalea.

Snowmelt in our study area took place from the end of March through June, although most of the area melted out in May. In figure 32, 20 species are arrayed by their mean Julian day of snowmelt. As is evident from their standard deviations, there is little statistical significance among their positions; however, the arrangement is in general agreement with indications obtained from temperature, solar radiation, and summer soil moisture analyses.

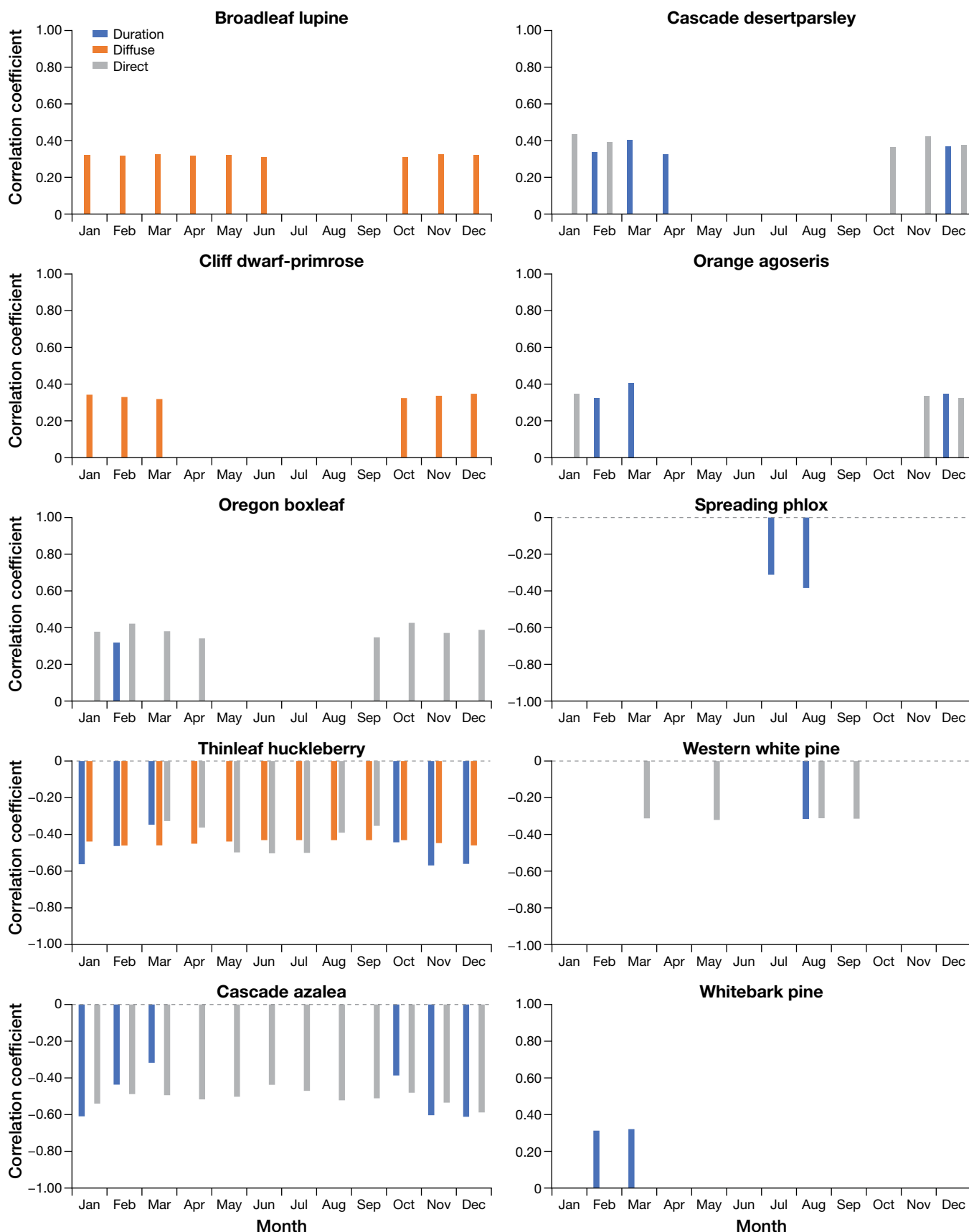


Figure 31—Coefficients for significant Spearman correlations between canopy cover and calculated potential monthly solar radiation by plot, including monthly diffuse solar radiation, monthly direct solar radiation, and monthly duration of direct solar radiation for 10 species in the Olympic Mountain whitebark pine communities study. All the species shown had a significant correlation in at least one month with at least one of these solar radiation variables (out of 20 species investigated).

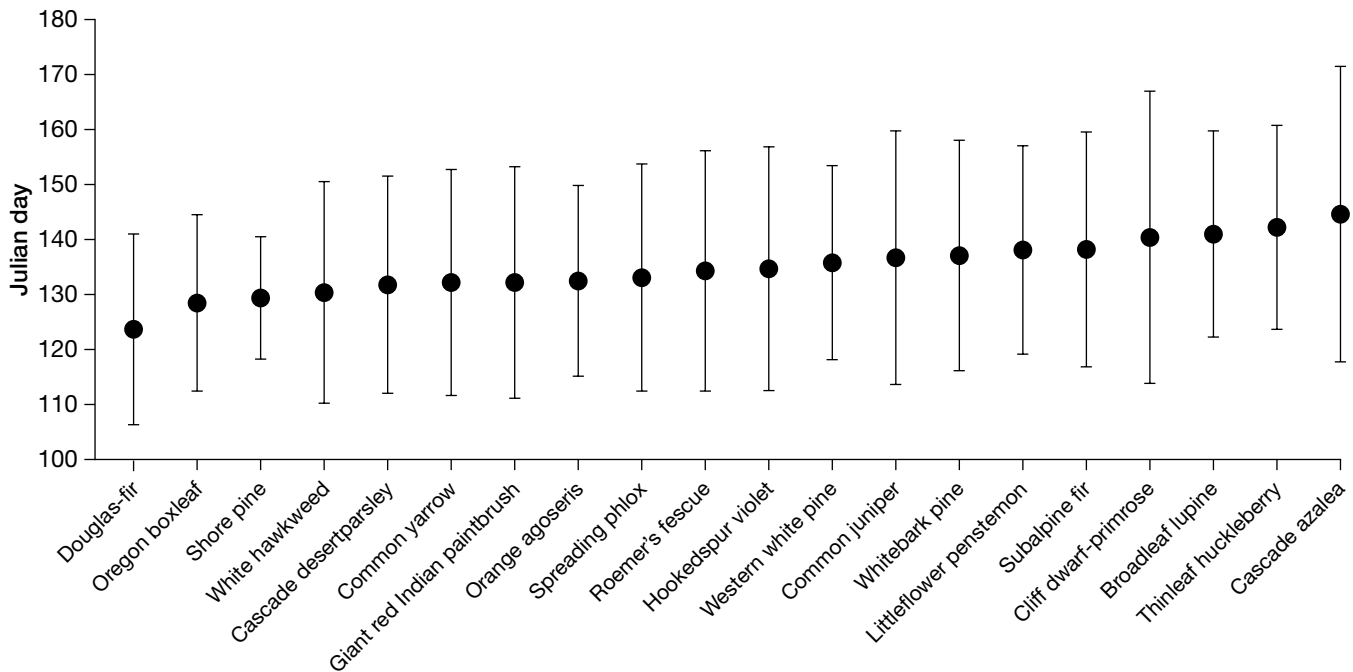


Figure 32—Mean Julian day of snowmelt for Olympic Mountain whitebark pine communities study plots with each of 20 species. Error bars are standard deviations. Reference Julian days: April 1 = 91, May 1 = 121, and June 1 = 152; based on sensor snowmelt dates over 3 years for 36 plots.

When we examined the mean canopy cover of each species by the month in which snowmelt occurred, there were significant differences. Five species differed significantly in canopy cover by snowmelt month (table 24). More Douglas-fir grew where snowmelt occurred in April. More Cascade desertparsley, Oregon boxleaf, and white hawkweed grew in places where the snowpack melted in April or May. More orange agoseris grew where snowmelt occurred in May. Although other species did not have significant differences by month, the months where more canopy cover occurred seem consistent with other findings. For example, subalpine fir, which is found more abundantly on northern aspects than whitebark pine, appeared to grow in areas where the snowpack melts later, on average, than areas where whitebark pine grew. Also, shore pine, which grew primarily in warmer areas, appeared to grow in areas with earlier snowmelt than areas occupied by most other species.

Relationships Between Species Canopy Cover and Summer Soil Moisture and Temperature

- Cascade desertparsley, Oregon boxleaf, and common juniper had significant negative correlations with summer soil moisture in summer months, but although no species had a significant positive correlation with summer soil moisture, total plant canopy cover did.
- The age of the oldest whitebark pine tree on each plot was negatively correlated with summer soil moisture.
- Based on correlations between species canopy cover and plot summer soil moisture and soil temperature, whitebark pine and seven other species grew in relatively warm, dry areas, while subalpine fir and four other species grew in cold, mesic areas.

Table 24—Species presence and mean canopy cover for Olympic Mountain whitebark pine communities study plots where the snowpack melted in April, May, or June and the probability (*P*) that the canopy covers differed by month

Species	Presence ^a	April	May	June	<i>P</i> ^b
	NUMBER OF PLOTS	PERCENT CANOPY COVER			
Douglas-fir	16	16.0	2.7	0.0	0.01
Cascade desertparsley	24	0.7	1.4	0.0	0.01
Oregon boxleaf	21	0.4	0.3	0.1	0.02
White hawkweed	21	0.1	0.1	0.0	0.02
Orange agoseris	21	0.0	0.1	0.0	0.03
Littleflower penstemon	21	0.1	0.9	1.7	0.07
Whitebark pine	30	4.0	9.8	5.9	0.10
Cliff dwarf-primrose	10	0.1	0.1	0.3	0.11
Cascade azalea	5	0.0	1.4	13.4	0.13
Shore pine	8	1.9	1.5	0.0	0.18
Broadleaf lupine	27	2.7	3.8	3.8	0.23
Subalpine fir	28	7.5	25.8	23.7	0.23
Western white pine	14	1.2	2.4	0.1	0.49
Thinleaf huckleberry	8	0.0	0.3	0.7	0.50
Roemer's fescue	27	0.5	1.1	5.3	0.51
Spreading phlox	29	3.7	7.9	9.6	0.52
Common juniper	28	4.1	9.1	3.9	0.53
Hookedspur violet	22	0.0	0.1	0.3	0.63
Oregon boxleaf	28	0.5	0.8	0.5	0.84
Giant red Indian paintbrush	25	0.1	0.2	0.5	0.89

Note: Species are sorted in order of increasing probability value (*P*).

^a The number of plots out of a total of 36 where the species was present.

^b *P* is the Kruskal-Wallis analysis of variance probability > chi-square that was used to test the significance of the difference in the canopy cover of each species on plots where the snowpack melted in each of the 3 months.

Cascade desertparsley, Oregon boxleaf, and common juniper canopy covers were significantly and negatively correlated with summer soil moisture in summer months (fig. 33). The canopy covers of four species had marginal negative correlations with summer soil moisture in summer months (fig. 33). No species canopy cover had a significantly positive correlation with summer soil moisture but total plant canopy cover did. The combined canopy cover of alternate hosts for white pine blister rust is nearly in the center of this distribution but was not significantly correlated with summer soil moisture (fig. 33).

Whitebark pine had a marginally significant negative correlation to summer soil moisture; however, a significant stronger negative correlation was found between the age of the oldest whitebark pine trees on the plots and summer soil moisture ($r = -0.45$, $P = 0.02$).

The relationships between species canopy cover with mean soil temperature and mean summer soil moisture in summer months is shown in figure 34. This figure summarizes important aspects of the physical growing environment for species that occurred on at least five plots. This figure also shows the extent of our sampling in relation to these variables.

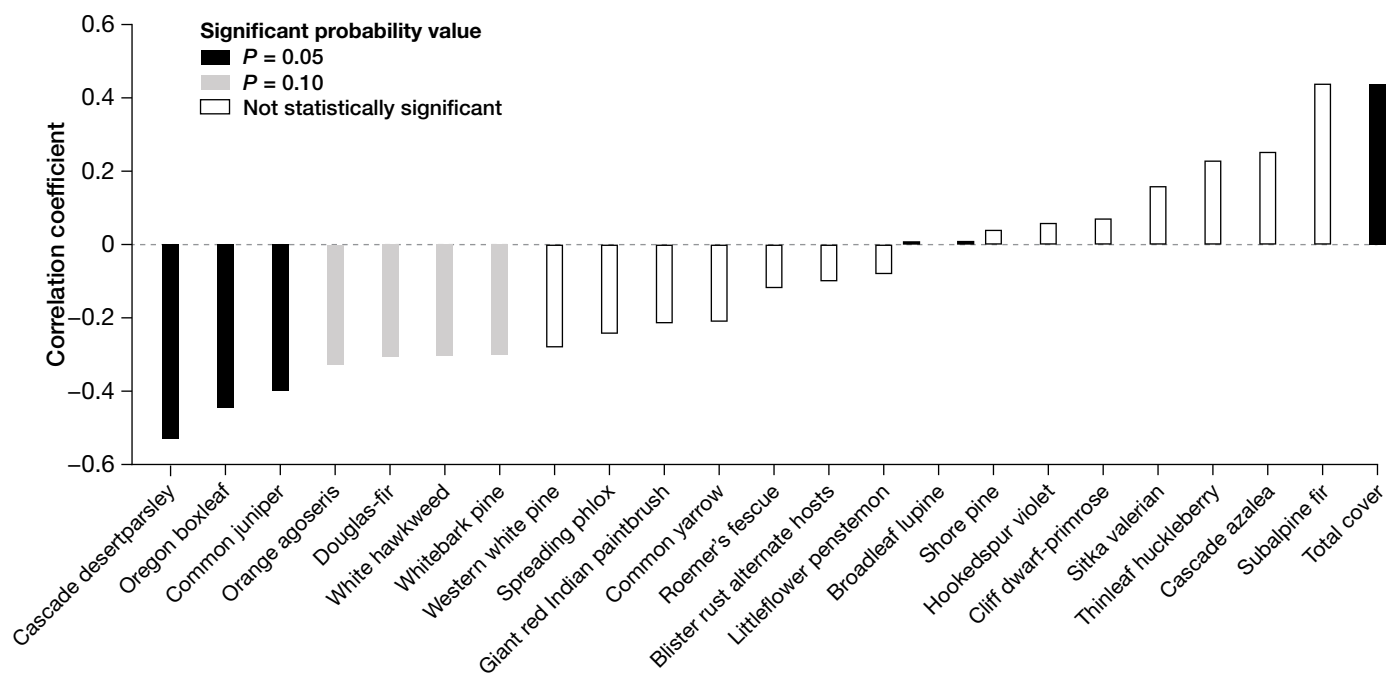


Figure 33—Coefficients for Spearman correlations between species canopy cover and summer soil moisture (measured in July and August) for the Olympic Mountain whitebark pine communities study. Species negatively correlated with summer soil moisture grew in drier habitats, while species with positive correlations with summer soil moisture grew in moister habitats. Also included are correlations between summer soil moisture and the sum of canopy covers of alternate host species for white pine blister rust and the sum of all canopy cover of all species (total canopy cover).

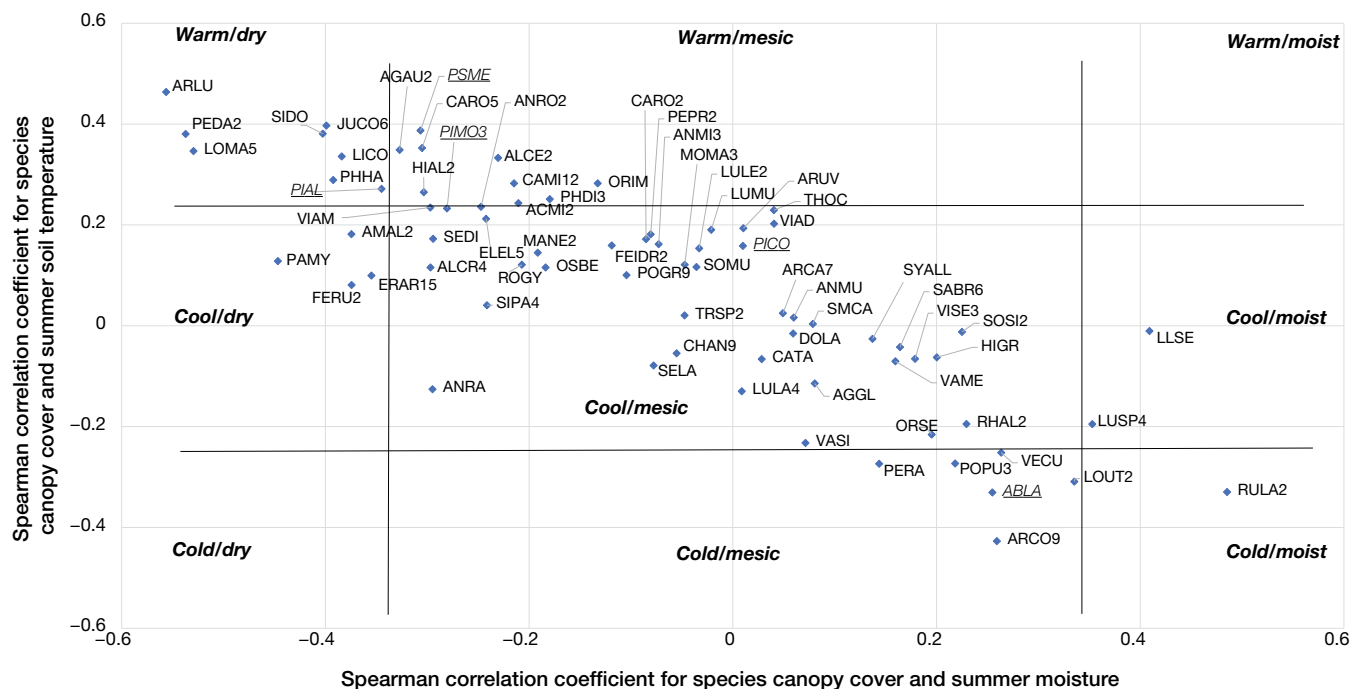


Figure 34—Coefficients for Spearman correlations between each species canopy cover by USDA PLANTS Database symbol (USDA NRCS, n.d.) and mean summer soil moisture (in the top 12 cm of soil) (measured over 5 years in July or August) and mean summer soil temperature (at 20-cm depth) from June through August (measured over 3 years). Lines indicate statistical significance of correlation coefficients. Coefficients between the vertical lines are not significant for summer soil moisture; coefficients outside of the vertical lines are significant ($P = 0.05$) for summer soil moisture. Coefficients between the horizontal lines are not significant for soil temperature; coefficients outside of the horizontal lines are significant for soil temperature. Each species occurred on at least five plots. Statistical significance was used to define the nine environmental categories of warm, cool, or cold combined with dry, mesic, or moist. Tree species are underlined and italicized. Species symbols are defined in table A1.1.

For example, we found no species in what is termed warm/moist or cold/dry environments. Warm/moist in this context would have been represented by seeps, springs, or other riparian areas on south- or west-facing slopes while cold/dry would have been represented by steep, north- or east-facing, upper slopes, which were not present in our sample area.

Plant Association and Community Type Floristic Relations

- The NMDS ordination using a subset of study plots with complete temperature and summer soil moisture data revealed relationships between study plot floristics and several environmental variables.
- Joint plots indicated that overstory canopy closure increased and understory light decreased along ordination axis 1, environments became cooler and subalpine fir increased along ordination axis 2, while warmth and drought increased along ordination axis 3.
- The species and plant associations and community types were arrayed logically and in agreement with other analyses (e.g., subalpine fir/common juniper association was arrayed opposite the subalpine fir/Cascade azalea association and whitebark pine was opposite subalpine fir).

We explored plant association and community type floristic relationships and responses to several site variables with NMDS ordination techniques. The NMDS ordination had a final stress of 9.4 for the three-dimensional solution and a final instability of 0, which was achieved with 137 iterations. To aid the interpretation of these ordinations, mean canopy cover for selected species and mean study plot characteristics for each community taxon are provided in tables A2.14 and A2.18). In addition, we describe each plant association or community type in the section below, and appendix 3 provides a discussion of each plant association or community type. We examined the relationships between temperature and other variables with study plot and species location in three-dimensional ordination hyperspace with the 26 study plots for which we had 3-year temperature data (fig. 35, table 25). In figure 35, we displayed this subset of study plots with joint plots, which showed the five strongest explanatory variables of those that we tested for ordination axes 1 and 2. The study plots are symbol-coded by plant associations and community types that will be further defined in subsequent sections. Ordination axis 1 accounted for 40 percent of variation in the distance matrix, ordination axis 2 accounted for 22 percent of that variation, and ordination axis 3 accounted for 25 percent.

For ordination axis 1, the strongest positive correlation was with overstory canopy closure ($r = 0.74$), followed by the maximum tree diameter at breast height ($r = 0.71$). The next strongest correlation was with PAR at 1.3-m height, which was negative ($r = -0.64$). Following these, there were 18 positive correlations that were all above $r = 0.5$, with mostly air temperatures in winter and spring. There were also negative correlations with elevation ($r = -0.55$) and the duration of the seasonal snowpack ($r = -0.51$).

For ordination axis 2, the strongest positive correlation was with subalpine fir canopy cover ($r = 0.85$). After this, the strongest correlations were with maximum air temperature in December ($r = -0.68$) and maximum September air temperature in quarter-day 2 ($r = -0.67$). Following these, there were 17 negative correlations that were stronger than $r = -0.5$, with mostly mean monthly maximum air, soil surface, and soil temperatures in fall through spring. Also, there was a negative correlation with aspect ($r = -0.60$).

For ordination axis 3, the strongest correlation was with summer soil moisture ($r = -0.46$) followed by the maximum June air temperature in quarter-day 3 ($r = 0.42$). Among the next

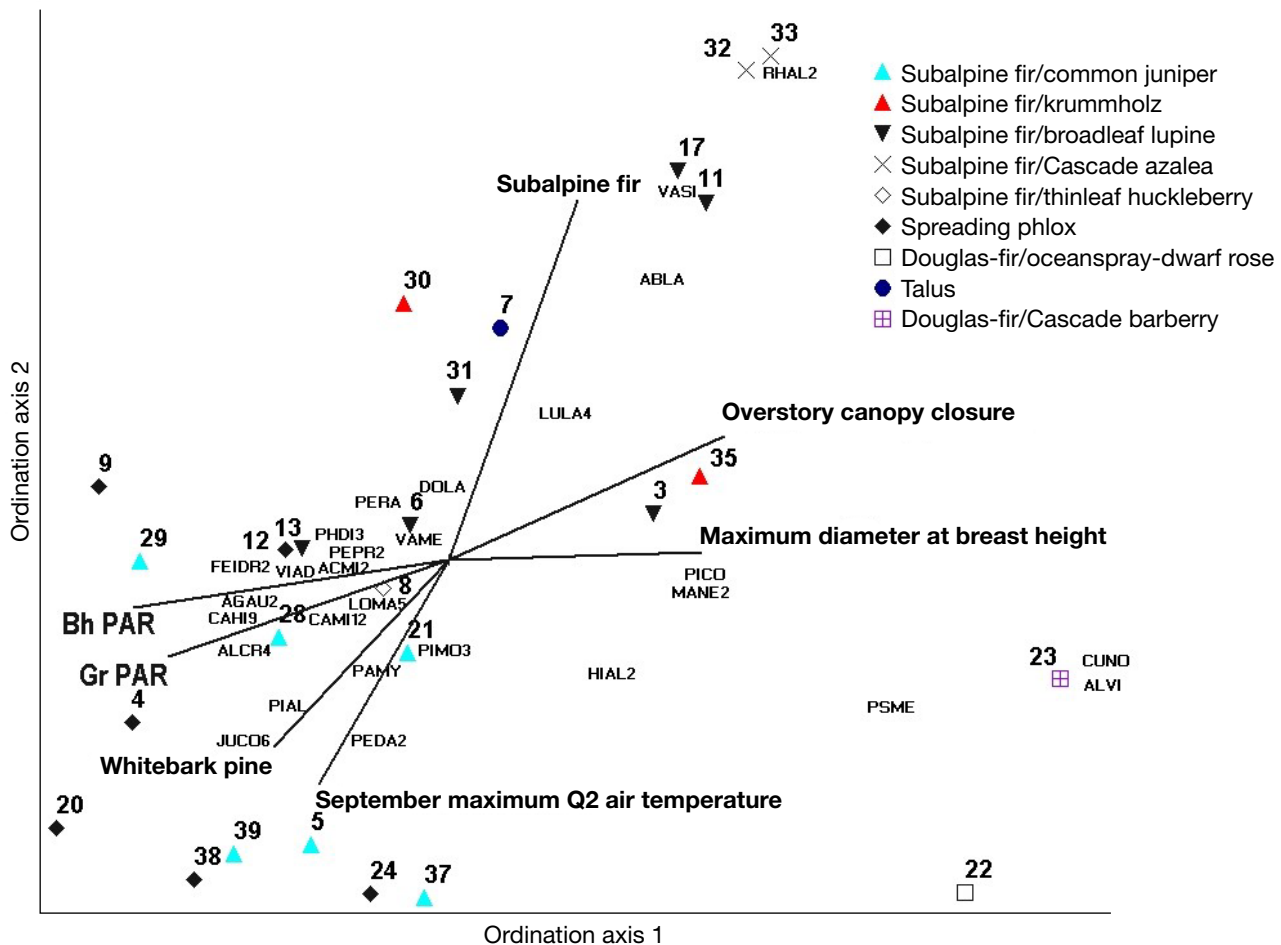


Figure 35—Ordination axes 1 and 2 for the nonmetric multidimensional scaling ordination of 26 study plots where 179 species occurred showing a joint plot of air temperature and several physical site variables as well as subalpine fir and whitebark pine canopy cover data with a cutoff r^2 of 0.5. The joint plot variables are subalpine fir canopy cover, whitebark pine canopy cover, total overstory canopy closure, the maximum September air temperature in quarter-day 2 (Q2, 0600 to 1200), the maximum diameter at breast height (stem diameter of the largest tree on the plot at 1.3-m height), and photosynthetically active radiation (PAR) at ground level (Gr) and at 1.3-m height (Bh). Twenty-six species discussed in the text are shown by their USDA PLANTS Database symbols (USDA NRCS, n.d.), which are defined in table A1.1.

23 correlations, all stronger than $r = 0.30$, were 16 positive correlations with air temperature that were mostly with minimum air temperatures in winter and spring and with maximum air temperatures in summer. There were also positive correlations with overstory canopy closure and total canopy cover and negative correlations with elevation, minimum annual soil temperature, maximum annual soil surface temperature, maximum annual soil temperature, and maximum monthly air temperature in February.

There were seven variables with correlations in two dimensions with an r^2 of at least 0.5 (table 25). The strongest positive correlations with individual axes were subalpine fir canopy cover with ordination axis 2 ($r^2 = 0.72$), overstory canopy closure with ordination axis 1 ($r^2 = 0.55$), and the maximum diameter at breast height (stem diameter of the largest tree at 1.3-m height) on each plot with ordination axis 1 ($r^2 = 0.50$). The strongest negative correlations with individual axes were PAR at 1.3-m height ($r^2 = 0.63$) and at ground-level ($r^2 = 0.56$) with ordination axis 1, the maximum September air temperature in quarter-day 2 (0600 to 1200) with ordination axis 2 ($r^2 = 0.45$), and whitebark pine canopy cover, also with ordination axis 2 ($r^2 = 0.37$).

Table 25—Correlation coefficients for the joint plots with variables that had correlation coefficients in two dimensions of at least $r^2 = 0.5$ and their correlation coefficients with individual axes

Variable	Joint plot scaling (r^2)			Correlation with ordination axis (r^2)		
	Ordination axes 1 + 2	Ordination axes 3 + 1	Ordination axes 3 + 2	1	2	3
Subalpine fir canopy cover	0.76	0.26	0.72	0.26	0.72	0.06
Overstory canopy closure	0.60	0.57	0.28	0.55	0.25	0.13
PAR at 1.3-m height	0.63	0.63	0.10	0.63	0.09	0.03
PAR at ground level	0.59	0.56	0.20	0.56	0.19	0.06
Maximum September air temperature in quarter-day 2	0.52	0.26	0.45	0.26	0.45	0.03
Whitebark pine canopy cover	0.51	0.35	0.37	0.35	0.37	0.00
Maximum tree diameter at breast height	0.50	0.51	0.09	0.50	0.02	0.09

Note: The joint plots are shown in figure 35. The r values for all three ordination axes were positive for subalpine fir canopy cover, overstory canopy closure, and maximum tree diameter at breast height. The r values were negative for maximum September air temperature in quarter-day 2 (0600 to 1200), whitebark pine canopy cover, and both photosynthetically active radiation (PAR) variables.

Plant Association and Community Type Ordination and Descriptions

- The NMDS ordination including all 40 plots and 219 species produced similar study plot groupings as the previous subset of study plots with more complete environmental data suggesting the relationships between the joint plot variables and species and study plot groups from the subset ordination hold for this ordination as well.
- The nonforested, spreading phlox community type and the densely forested, subalpine fir/Cascade azalea plant association formed opposite poles with the other plant associations/communities spread out between them in proportion to subalpine fir abundance, signifying an environmentally driven gradient.
- Tree species, especially subalpine fir, were highly influential in the arrangement of the study plots in the ordination, with other shrub and herb species increasing in importance in the absence of overstory.
- Detailed descriptions of each plant association or community type follow the ordination explanation.

Having examined the correlations between physical and vegetation variables and the three principal ordination axes using a subset of plots and species, we repeated the ordination procedure with all 40 study plots and 219 species. Study plots included in this ordination that were not in the joint plot ordination did not have temperature data, which precluded doing a similar joint plot exercise with this dataset. The NMDS ordination had a final stress of 12.6 for the three-dimensional solution and a final instability of 0, which was achieved with 104 iterations. Ordination axes 1 and 2 are presented in figure 36.

As this ordination produced similar study plot groupings along the three axes, we believe that the relationships between the joint plot variables and species and study plot groups generally hold for this ordination as well. The 23 forest plots that were identified to plant association by using Henderson et al. (1989) mostly grouped into three distinct or slightly overlapping clusters in a three-dimensional ordination (fig. 36). These plant associations were subalpine fir/broadleaf lupine (plots 1, 3, 6, 11, 13, 17, 26, and 31), subalpine fir/common juniper (plots 5, 14, 15, 21, 28, 29, 37, and 39), and subalpine fir/Cascade azalea (plots 27, 32, 33,

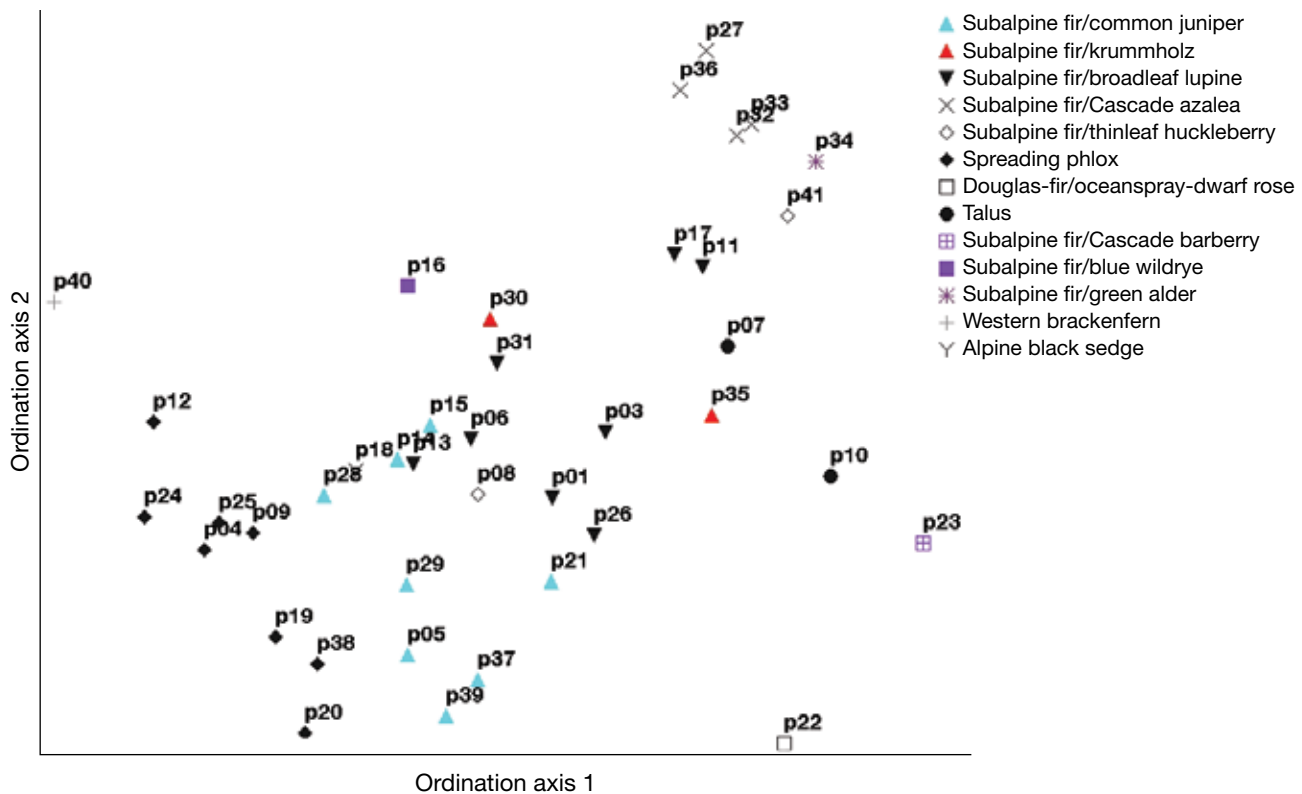


Figure 36—Ordination axes 1 and 2 for the nonmetric multidimensional scaling ordination of all study plots and species (40 plots and 219 species) in the Olympic Mountain whitebark pine communities study. Four principal plant associations/communities account for 28 of the 40 plots. An additional 12 plots range from unique to varying degrees of similarity with one or more of the four principal plant associations/communities.

and 36). There were also two study plots of the subalpine fir/thinleaf huckleberry plant association (plots 8 and 41), and one study plot (plot 22) of the Douglas-fir/oceanspray (*Holodiscus discolor*)–dwarf rose (*Rosa gymnocarpa*) plant association (Henderson et al. 1989).

We also sampled a subalpine fir-dominated forest site that partially overlapped an active seep that was dominated by green alder (*Alnus viridis*), which we refer to as the subalpine fir/green alder community type (plot 34), and one open study plot with 15 percent subalpine fir canopy cover and a diverse understory of grasses and herbs that was dominated by blue wildrye (*Elymus glaucus*) (25 percent) and Roemer's fescue (10 percent), which we refer to as the subalpine fir/blue wildrye community type (plot 16). We sampled two sites within the subalpine fir zone (Henderson et al. 1989) that straddled the ecotone between barren coarse rock talus and seral colonizing vegetation along the edge, which we refer to as the talus plots (plots 7 and 10). There were also two study plots that straddled the ecotone between subalpine fir krummholz and cushion plant communities (plots 30 and 35).

We measured eight clustered study plots (fig. 36) that were dominated by a combination of spreading phlox and whitebark pine, which we refer to as the spreading phlox community type (plots 4, 9, 12, 19, 20, 24, 25, and 38). This community had little or no subalpine fir, and all the study plots had less than 26 percent whitebark pine canopy cover, so we consider this to be a nonforest plant association with alpine affinities.

Other unique but distinct plant communities included one late-melting, snowbank meadow plot that was dominated by a combination of Parry's rush (*Juncus parryi*), woolly pussytoes (*Antennaria lanata*), and black alpine sedge, which we refer to as the black alpine

sedge community type (plot 18). There was one study plot that was heavily dominated by western brackenfern (*Pteridium aquilinum*) (45 percent) and little else, which we refer to as the western brackenfern community type (plot 40).

The amount of subalpine fir canopy cover is a strong determinant in the arrangement of study plot groupings in figure 36. The order of plant association groupings on ordination axis 2 strongly approximates the abundance of subalpine fir as it did in figure 35. In figure 37, the order of the five plant associations that is shown based on stem density of subalpine fir closely approximates the order on ordination axis 2 in figures 35 and 36. The nonforested spreading phlox community type and the densely forested subalpine fir/Cascade azalea plant association form opposite poles with the other plant associations spread out between them in proportion to subalpine fir abundance, signifying an environmentally driven gradient.

Other tree species are also important drivers in the ordination but not as much as subalpine fir. For example, the presence of much more whitebark pine on plot 8 than on plot 41, both in the subalpine fir/thinleaf huckleberry plant association, appears to be the main reason the two plots do not cluster together. Relatively large amounts of Douglas-fir appear to be responsible for the separation of plots 22 and 23 from the rest of the ordination groups, and these two plots are separated from each other based on large amounts of Alaska cedar on plot 23. The latter species was associated with a spring just off from the plot.

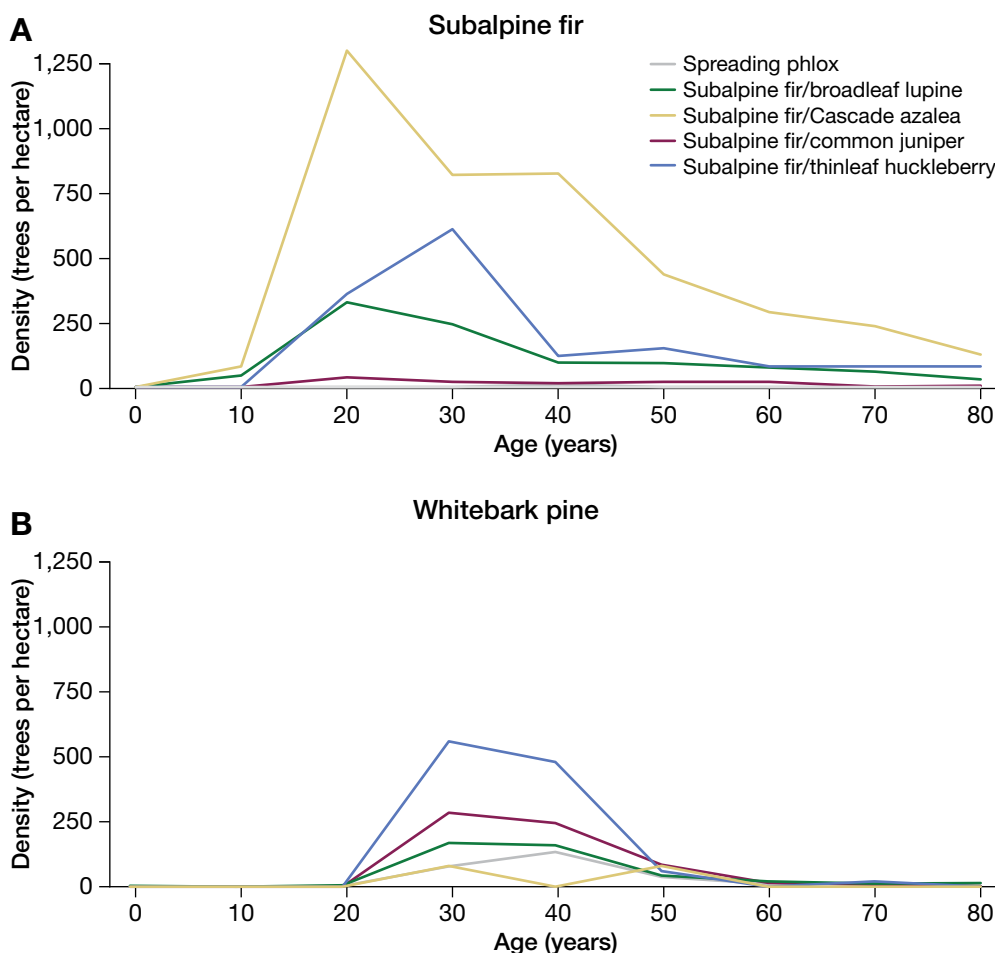


Figure 37—Comparison of the age structure of (A) subalpine fir and (B) whitebark pine for five plant associations/communities in the Olympic Mountain whitebark pine communities study. Older trees exist but only in small numbers. Several plant associations/communities have small numbers of other tree species present.

Other species generally had less effect on the ordination; however, they became important in the absence of overstory. Thus, spreading phlox and common juniper were especially important to the grouping of the spreading phlox community type where tree cover was minimal. Both species were also quite important in the subalpine fir/common juniper plant association and were responsible for the closeness of these two plant associations/communities in the ordination. Also, spreading phlox, but not common juniper, was an important species in the subalpine fir/broadleaf lupine plant association. The lack of common juniper in subalpine fir/broadleaf lupine plots tended to separate this plant association from the subalpine fir/common juniper plant association, but the presence of spreading phlox in both groups tended to pull them closer together, while separating them from the subalpine fir/Cascade azalea plant association where neither spreading phlox nor common juniper was found. The cover of the key understory species in the subalpine fir/Cascade azalea plant association varied greatly depending on the successional condition of the plot (largely because of overstory canopy density). For this reason, Cascade azalea was not as influential in the ordination as some of the above-mentioned species. It was also for this reason, that one of the subalpine fir/thinleaf huckleberry plots, which also had a depauperate understory due to a dense overstory, grouped closely with some of the subalpine fir/Cascade azalea depauperate plots.

SUBALPINE FIR/BROADLEAF LUPINE PLANT ASSOCIATION—

- Plots in this plant association were generally in a successional young condition, including expanding tree islands and areas with infilling scattered trees.
- This plant association had the second most subalpine fir seedlings per hectare (7,916) and the most whitebark pine seedlings per hectare (558) of any plant association or community type.
- In the ordination, this plant association fell between the cool, moist subalpine fir/Cascade azalea and the warm, dry subalpine fir/common juniper plant associations to which it was closer.
- Complete overstory canopy closure may be limited by low soil temperature.

Plots 1, 3, 6, 11, 13, 17, 26, and 31 were in the subalpine fir/broadleaf lupine plant association. Elevations of these plots ranged from 1529 to 1845 m, aspects ranged from 213 to 314°, and slope steepness ranged from 30 to 72 percent. The mean summer soil moistures ranged from 2.8 to 5.8 percent, and the mean summer (June through August) soil temperatures ranged from 7.2 to 15.7 °C.

Using a combination of core sample ages and diameter-age modeling, we determined that trees in these eight plots ranged in age from 8 to 221 years (fig. 38). There were few trees >100 years old, and most trees were <40 years old. Trees >100 years old were mostly subalpine firs; at lower elevations, a few were shore pines, Douglas-firs, western white pines, and whitebark pines. The reverse, J-shaped distribution of subalpine fir tree ages in figure 38 is derived by larger numbers of young trees growing at the edge of expanding tree islands or infilling stands of scattered older trees or large canopy gaps. This plant association had the second highest number of seedlings of any community type or plant association, with 8,474 seedlings per hectare, mostly subalpine fir (table 26). Many of the subalpine fir seedlings recorded for plot 17 appeared to be horizontal layered stems. This plant association had 558 whitebark pine seedlings per hectare, which was more than any other community type or plant association. There were 133 standing dead whitebark pine seedlings per hectare, which

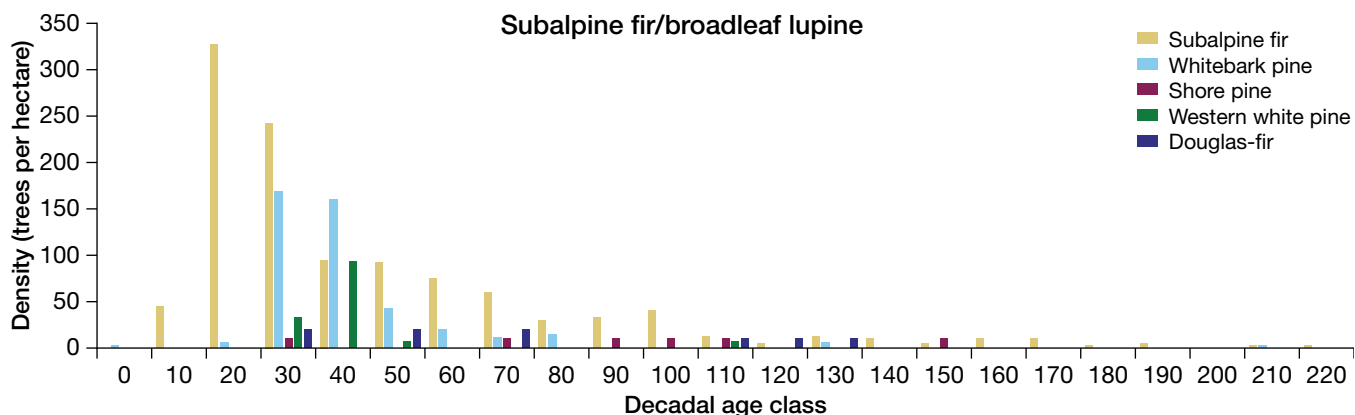


Figure 38—Mean age structure of trees ≥ 1.3 m tall in the subalpine fir/broadleaf lupine plant association of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

Table 26—The mean density of live and dead seedlings (<1.3 m tall) by plant association or community type for the Olympic Mountain whitebark pine communities study

	n	Subalpine fir density	Whitebark pine density	Shore pine density	Western white pine density	Douglas-fir density
TREES PER HECTARE (STANDARD DEVIATION)						
Live trees:						
Subalpine fir/broadleaf lupine	8	7,253 (7,390)	558 (813)	199 (563)	66 (188)	398 (112)
Subalpine fir/common juniper	8	93 (115)	47 (81)	7 (19)	0	0
Subalpine fir/Cascade azalea	4	10,616 (7,516)	66 (133)	0	0	0
Subalpine fir/thinleaf huckleberry	2	626 (134)	133 (187)	0	0	0
Subalpine fir/krummholz	2	160 (226)	67 (94)	0	0	0
Subalpine fir/green alder	1	3,185	0	0	0	0
Black alpine sedge	1	692	292	0	0	0
Spreading phlox	8	33 (94)	264 (645)	0	4 (9)	7 (1)
Dead trees:						
Subalpine fir/broadleaf lupine	8	0	133 (375)	0	0	0
Subalpine fir/common juniper	8	0	13 (38)	0	0	0
Subalpine fir/Cascade azalea	4	0	0	0	0	0
Subalpine fir/thinleaf huckleberry	2	67 (94)	0	0	0	0
Subalpine fir/krummholz	2	0	0	0	0	0
Subalpine fir/green alder	1	0	0	0	0	0
Black alpine sedge	1	27	0	0	0	0
Spreading phlox	8	0	14 (38)	0	0	0

Note: Only plant associations or community types where we found seedlings are shown. Only germinants were found in subalpine fir/green alder, and no seedlings were found in subalpine fir/blue wildrye, subalpine fir/Cascade barberry, Douglas-fir/oceanspray, western brackenfern, and talus plant associations or community types.

was both more standing dead whitebark pine seedlings and more standing dead seedlings of any species than in any other community type or plant association. There were 255 standing dead trees (≥ 1.3 m tall) per hectare from four species, including 138 standing dead whitebark pine trees per hectare, mostly < 20 -cm d.b.h. but with a few 30- to 40-cm d.b.h. There were also 88 standing dead subalpine fir trees per hectare, with a similar diameter distribution but with a few between 40- to 50-cm d.b.h. There were a few standing dead western white pine and shore pine trees and a few that were not identified but that were almost certainly one of these species. The largest standing dead tree was a shore pine that was close to 65-cm d.b.h. There was an average of 22.3 t (SD = 31.9) per hectare of CWD on the ground in this plant association, with roughly a third each from subalpine fir, western white pine, or not identified. This was the second highest amount of CWD found in any community type. Only the subalpine fir/green alder community type had a greater density of CWD on its single plot. Most of the CWD was 25 to 45 cm in diameter and in decay classes 3 or 4. There was no whitebark pine CWD identified in this plant association.

In the ordination (fig. 36), this plant association was positioned between the cooler, moister subalpine fir/Cascade azalea plant association and the warmer, drier subalpine fir/common juniper plant association to which it was closer. Over all the plots, the overstory had 10 to 80 percent subalpine fir canopy cover and 0.2 to 30 percent whitebark pine canopy cover. There was 8 to 30 percent broadleaf lupine canopy cover and 0 to 12 percent spreading phlox canopy cover. On these plots, broadleaf lupine was associated with open areas and canopy gaps, while spreading phlox was in even more open or rockier areas than broadleaf lupine. Most of the species growing in this plant association were obligate heliophytes—plants that grow best in direct sunlight—and were also present in the spreading phlox community type. Several alternate host species for white pine blister rust were present on these plots. Sickletop lousewort was on all the plots, and giant red Indian paintbrush was on all but one plot. Also present on a few plots were harsh Indian paintbrush and prickly currant. The species richness was 15 species per plot.

Complete (100 percent) overstory canopy closure had not been attained. Overstory canopy closure on these plots ranged from 29 to 80 percent. The plot with 80 percent overstory canopy closure (plot 17) contained an expanding tree island that filled almost the entire plot. Places where dense shade developed had few understory plants of any species. If the overstory canopy closure reached 100 percent, plots 6, 13, and 17 would likely fall into the general range of soil temperatures suggested by Körner and Paulsen (2004) as limiting for root growth.

SUBALPINE FIR/COMMON JUNIPER PLANT ASSOCIATION—

- Plots in this plant association were successional young.
- Subalpine fir was generally the youngest tree species present, and of only 146 seedlings per hectare, two-thirds of the seedlings were subalpine fir, and one-third of the seedlings were whitebark pine.
- In the ordination, this plant association fell between the subalpine fir/broadleaf lupine plant association and the spreading phlox community type but with greater affinity to the latter.
- Complete overstory canopy closure would likely be inhibited by low soil temperatures on only two of eight plots.

Plots 5, 14, 15, 21, 28, 29, 37, and 39 were in the subalpine fir/common juniper plant association. Elevations of these plots ranged from 1571 to 1857 m, aspects ranged from 233 to 264°, and slope steepness ranged from 41 to 69 percent. The mean summer soil moistures ranged from 3 to 7.2 percent, and the mean June through August soil temperatures ranged from 10.5 to 13.7 °C.

By using a combination of core sample ages and diameter-age modeling, we determined that trees in these eight plots ranged in age from 25 to 155 years (fig. 39). There were few trees >100 years old, and most were <50 years old. Trees >100 years old were whitebark pines and Douglas-firs in plots on west-southwestern aspects at various elevations. Whitebark pines ranged in age from 35 to 155 years. Subalpine firs ranged in age from 25 to 94 years. There were 146 seedlings per hectare in this plant association; about two-thirds of the seedlings were subalpine fir, and one-third of the seedlings were whitebark pine (table 26). Standing dead seedlings were represented only by 13 whitebark pine trees per hectare. There were 255 standing dead trees (≥ 1.3 m tall) per hectare. Almost all were small, whitebark pine trees <20-cm d.b.h. and mostly <10-cm d.b.h. There were also a few standing dead subalpine fir and western white pine trees of similar size. There was an average of 9.2 t (SD = 11.5) per hectare of CWD on the ground in this plant association, with two-thirds of it from whitebark pine, and most of the remainder was not identified. No subalpine fir CWD was identified. Most of the CWD was 15 to 25 cm in diameter and in decay classes 2 to 4.

In the ordination (fig. 36), this plant association fell between the subalpine fir/broadleaf lupine plant association and the spreading phlox community type on ordination axis 2. However, although it is distinguishable from the subalpine fir/broadleaf lupine plant association on all axes, it cannot be distinguished from the spreading phlox community type on ordination axes 1 and 3. This shows a close relationship between the spreading phlox community type and the subalpine fir/common juniper plant association. The biggest distinction was the presence of more and larger trees as well as more common juniper in the subalpine fir/common juniper plant association than was found in the spreading phlox community type.

The overstory canopy closure ranged from 14 to 44 percent, with whitebark pine accounting for 2 to 25 percent and subalpine fir accounting for 1 to 15 percent. The ground cover tended to be sparse (10 to 75 percent), and it was dominated by common juniper and spreading phlox. The species richness was 11 species per plot. If the overstory canopy closure reached 100 percent, only plots 14 and 29 would likely fall into the general range of soil temperatures suggested by Körner and Paulsen (2004) as limiting for root growth.

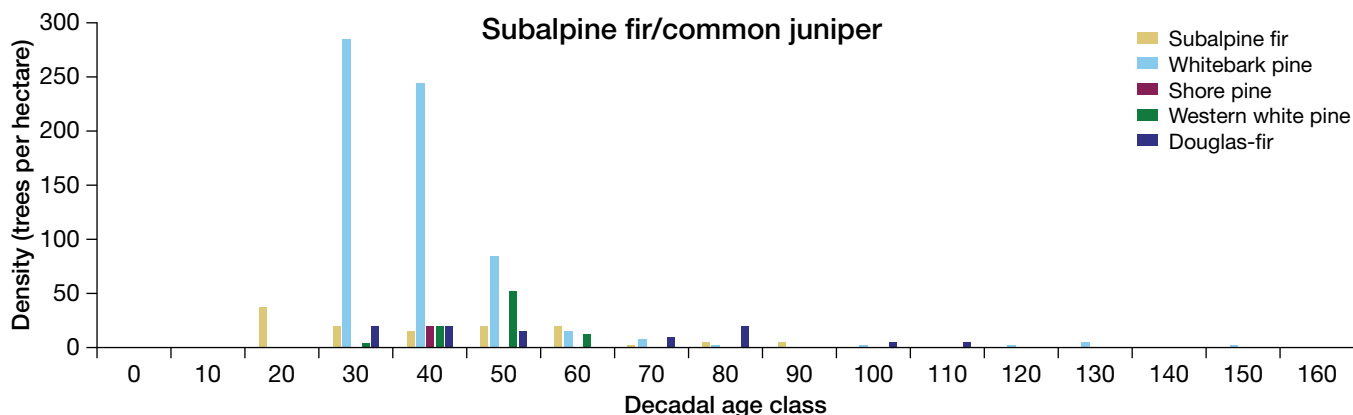


Figure 39—Mean age structure for trees ≥ 1.3 m tall in the subalpine fir/common juniper plant association of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

SUBALPINE FIR/CASCADE AZALEA PLANT ASSOCIATION—

- Although most trees were <40 years old and few were >100 years old, this plant association was the most successional advanced, with a reverse, J-shaped age distribution, suggesting subalpine fir overstory trees will be replaced as mortality occurs.
- Seedlings were denser in this plant association than any other and included 10,616 subalpine fir and 66 whitebark pine trees per hectare.
- In the ordination, this plant association was well separated from all others and was in a position suggesting cool, moist conditions.
- Root-limiting, cold soil temperatures were suggested in two of three plots for which soil temperature data were collected; however, these plots already had 50 to 80 percent overstory canopy closure.

Plots 27, 32, 33, and 36 were in the subalpine fir/Cascade azalea plant association. Elevations of these plots ranged from 1513 to 1619 m, aspects ranged from 311 to 360°, and slope steepness ranged from 40 to 69 percent. The mean summer soil moistures ranged from 5.3 to 6.5 percent, and the mean June through August temperatures ranged from 7.5 to 8.9 °C.

Using a combination of core sample ages and diameter-age modeling, we determined that trees in these four plots ranged in age from 18 to 261 years (fig. 40). Subalpine fir age structure has a notably reverse, J-shaped distribution, suggesting the stand has achieved a stable state where younger trees replace older trees as they die. Few trees were >100 years old, and most were <40 years old. All 16 of the trees >100 years old were subalpine firs, and 7 of these came from the lowest elevation plot, including the only 2 trees >200 years old. There were 10,682 seedlings per hectare in this plant association, nearly all of which were subalpine fir. This was more seedlings per hectare than in any other plant association or community type. The only other species present were 66 seedlings per hectare of whitebark pine. No mortality was observed among the seedlings. There were 345 standing dead trees (≥ 1.3 m tall) per hectare. All were subalpine fir, with 240 trees per hectare <10-cm d.b.h. and none >30-cm d.b.h. There was an average of 10.4 t (SD = 14.4) per hectare of CWD on the ground in this plant association, almost all from subalpine fir. No whitebark pine CWD was identified. All CWD was 15 to 25 cm in diameter, mostly in decay classes 2 and 3.

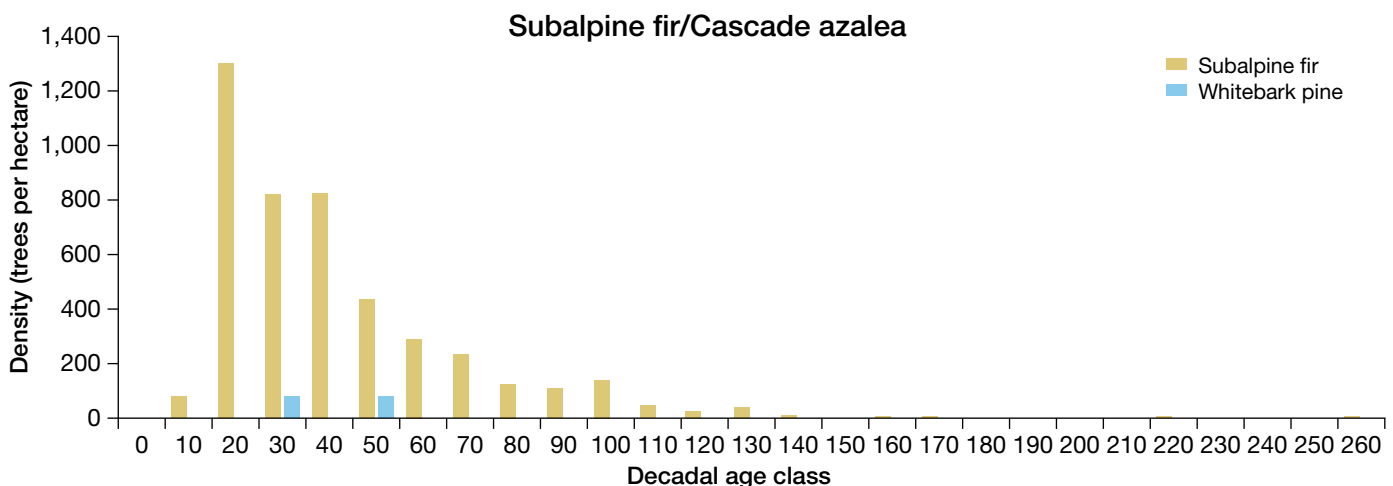


Figure 40—Mean age structure of trees ≥ 1.3 m tall in the subalpine fir/Cascade azalea plant association of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

The understory was dominated by Cascade azalea (25 to 95 percent). The high dominance of subalpine fir and Cascade azalea makes this plant association distinct from the others in the ordination (fig. 36). The four plots were closely clustered and mostly well separated from the other plant associations. It is closest to the subalpine fir/broadleaf lupine plant association in the ordination (fig. 36). The species richness was eight species per plot.

The overstory canopy closure ranged from 50 to 85 percent and was almost exclusively subalpine fir. The understory canopy closure ranged from 25 to 98 percent and was inversely proportional to the overstory canopy closure. If the overstory canopy closure reached 100 percent, two of the three plots in this plant association for which we had soil temperature data may fall into the general range of temperatures that can limit root growth (Körner and Paulsen 2004). However, these two plots already had 50 to 80 percent overstory canopy closure as well as a shrubby understory in more open areas.

SUBALPINE FIR/THINLEAF HUCKLEBERRY PLANT ASSOCIATION—

- This was a successional young plant association with young trees infilling between scattered older trees.
- Of 758 seedlings per hectare recorded in this plant association, 82 percent were subalpine fir, and the remainder were whitebark pine.
- Of just two plots, one clustered in the ordination with the subalpine fir/broadleaf lupine plant association and one (which had a highly depauperate understory) with the subalpine fir/Cascade azalea plant association.
- The overstory canopy of the depauperate plot would likely not entirely close because of cold soil conditions.

Plots 8 and 41 were in the subalpine fir/thinleaf huckleberry plant association. Elevations of these plots ranged from 1497 to 1597 m, aspects ranged from 220 to 230°, and slope steepness ranged from 25 to 60 percent. The mean summer soil moistures ranged from 3 to 6.7 percent, and the mean June through August soil temperatures ranged from 8 to 14 °C.

Using a combination of core sample ages and diameter-age modeling, we determined that trees in these two plots ranged in age from 23 to 258 years (fig. 41). Few trees were >100 years old, and most were <40 years old. Nine of the twelve trees >100 years old were subalpine fir, one was shore pine, and two, including the oldest tree and the third-oldest tree, were whitebark pines. There were 758 seedlings per hectare recorded for this plant association; 82 percent were subalpine fir, and the remainder were whitebark pine. The only seedling mortality observed were 67 seedlings per hectare of whitebark pine. There were 500 standing dead trees (≥ 1.3 m tall) per hectare, of which 270 were subalpine firs, 70 were western white pines, 60 were whitebark pines, and 20 were shore pines. There was an average of 71.6 t (SD = 45.9) per hectare of CWD on the ground in this plant association. About two-thirds of CWD was not identified, one-third of CWD was shore pine, and there were small amounts of subalpine fir and whitebark pine. Most CWD was 25 to 35 cm in diameter, mostly in decay class 3.

In the ordination (fig. 36), one of these plots clustered with the subalpine fir/broadleaf lupine plant association and one with the subalpine fir/Cascade azalea plant association. In the latter case (plot 41), the overstory was so dense it suppressed nearly all the understory. Similar depauperate understories were also found in stem exclusion phases of the subalpine fir/Cascade azalea plant association, so an association with this group in the ordination was not surprising. The depauperate plot understory did not permit classification into a plant association. However, we classified plot 41 in the subalpine fir/thinleaf huckleberry plant

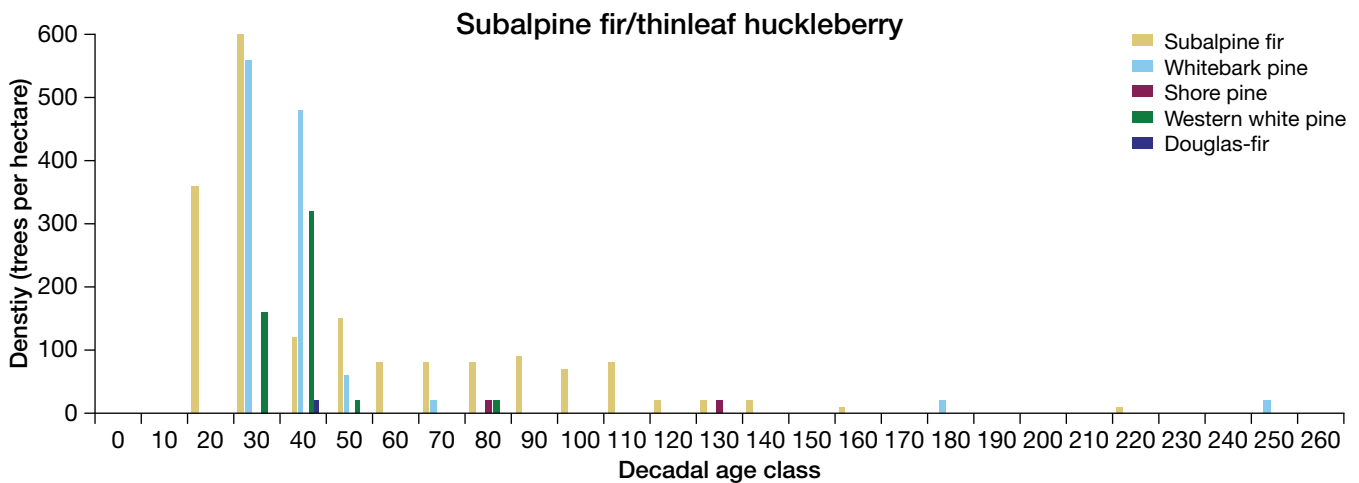


Figure 41—Mean age structure of trees ≥ 1.3 m tall in the subalpine fir/thinleaf huckleberry plant association of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

association based on observations we made outside of the plot where thinleaf huckleberry grew more abundantly, but there were no apparent physical differences. Both plots had small amounts of thinleaf huckleberry (<4 percent), only trace amounts of broadleaf lupine, and no Cascade azalea. The species richness was 24 species per plot.

If overstory canopy closure reached 100 percent, only plot 41 would likely have cold enough soils to limit root growth, although this plot already had 85-percent overstory canopy closure. Thus, it may be that the depauperate understory was due as much to cold soil as to dim light.

DOUGLAS-FIR/CASCADE BARBERRY (*MAHONIA NERVOSA*) COMMUNITY TYPE—

- This lowest elevation plot was one of the oldest and most successional advanced, although several alpine heliophytes were present in a canopy gap, suggesting a colder, more open past.
- No seedlings were found on this plot.
- In the ordination, this plot was separate from all others and in a position suggestive of a relatively warm environment.
- Complete overstory canopy closure would not result in root-limiting soil temperatures.

Plot 23, the lowest elevation plot, was in the Douglas-fir/Cascade barberry community type. It was at an elevation of 1420 m, with an aspect of 228° and a slope steepness of 52 percent. The summer soil moisture averaged 4.6 percent, and the mean June through August soil temperature was 9.3 °C.

Using a combination of core sample ages and diameter-age modeling, we determined that trees ≥ 1.3 m tall ranged in age from 26 to 220 years (fig. 42). About 13 percent of trees ≥ 1.3 m tall were >100 years old, and most were <50 years old. Ninety percent of the trees >100 years old were Douglas-fir, and the remainder were subalpine fir. The oldest tree on the plot that we were able to core sample was a 123-year-old Douglas-fir that germinated in about 1887. However, it was 60-cm d.b.h., and one other that was not successfully bored was 93-cm d.b.h. Modeling tree ages based on diameters suggested that this larger Douglas-fir tree began growing around 1815. The model also suggested that one subalpine fir on the plot may date to around 1785. We did not find any seedlings on this plot. There were only two standing dead trees (≥ 1.3 m tall)—a subalpine fir that was 18.4-cm d.b.h. and a Douglas-fir that was

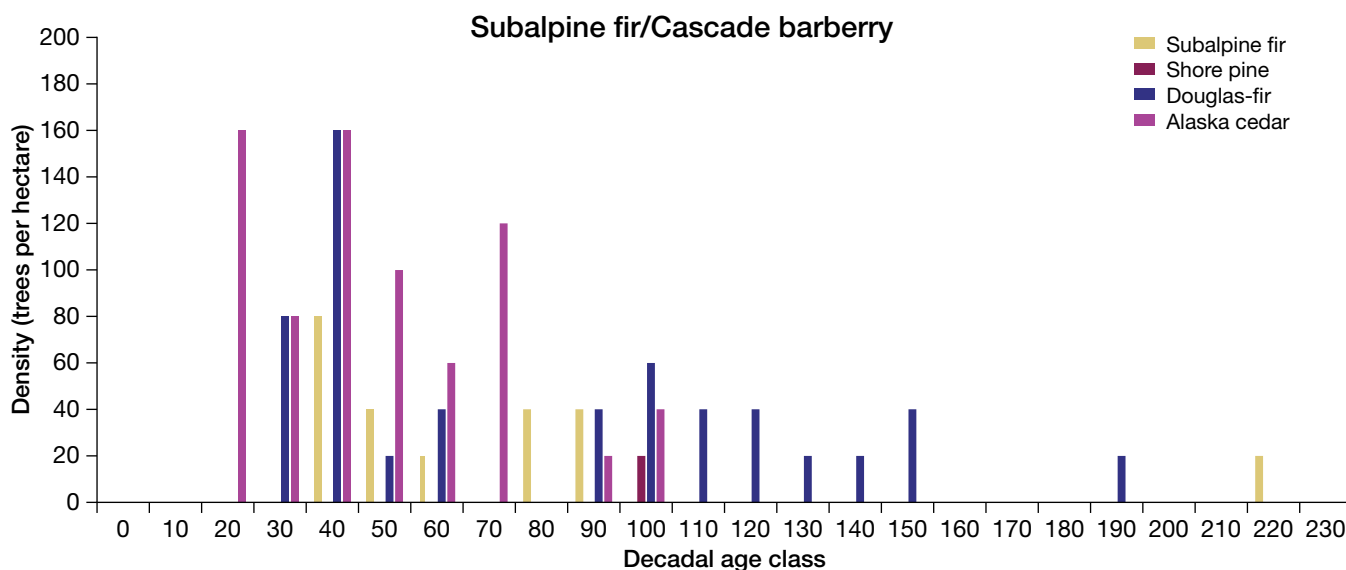


Figure 42—Mean age structure of trees ≥ 1.3 m tall in the Douglas-fir/Cascade barberry plant community type of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

76.4-cm d.b.h. Both represented 20 trees per hectare. There were 6.5 t per hectare of CWD on the ground. All CWD was Douglas-fir, 10 to 20 cm in diameter, and in decay class 3.

In the ordination (fig. 36), plot 23 was separate from all other plots. The combination of 85 percent canopy cover of Douglas-fir with 40 percent canopy cover of Alaska cedar and 22 percent canopy cover of subalpine fir in the overstory was unique, but the combination in the understory of Cascade barberry, dwarf rose, common snowberry (*Symphoricarpos albus*), and kinnikinnick (*Arctostaphylos uva-ursi*), with sweetcicely (*Osmorhiza berteroi*), American trailplant (*Adenocaulon bicolor*), and several alpine and other heliophytic herbs and shrubs was also unique. Some of the alpine heliophytes were common juniper, Cascade desertparsley, bluebell bellflower (*Campanula rotundifolia*), and white hawkweed, all of which survived in a shrinking canopy gap. These species were common in higher, more open areas but were absent in the forest below, except for white hawkweed, which was common in forest canopy gaps. The species richness was 34 species per plot. No evidence of fire was found on this plot.

The overstory canopy closure was 90 percent, and understory canopy closure was 55 percent, but under the heaviest shade, the forest floor was depauperate. Even if the overstory achieved 100 percent canopy closure, the soil temperature would likely remain high enough for growing-season root growth (Körner and Paulsen 2004).

SUBALPINE FIR/GREEN ALDER COMMUNITY TYPE—

- This low-elevation plot was in an early successional stage following a nearly complete late-successional overstory of subalpine fir die-off—the cause is not known.
- There were 3,185 subalpine fir germinants per hectare on the plot but no older seedlings.
- This was a complex plot consisting of an upland subalpine fir community and a green alder seep.
- Although it was closest to the subalpine fir/Cascade azalea plant association in the ordination, it was separated from all groups by its high position on all three axes, suggesting a cool, moist site with low light and high subalpine fir canopy cover (the latter reflecting its recent past).

Plot 34, one of the lowest elevation plots, was in the subalpine fir/green alder community type. It was at an elevation of 1528 m, with an aspect of 321° and a slope steepness of 41 percent. We did not monitor this plot for temperature or summer soil moisture; however, the presence of an almost 10-cm-deep, dense, humic organic surficial layer as well as a spring on the plot suggested a moist soil that was unique among our plots.

Trees we sampled on this plot ranged in age from 110 to 185 years. Using a combination of core sample ages and diameter-age modeling, we determined that trees ≥ 1.3 m tall ranged in age from 30 to 230 years (fig. 43), although many of the largest trees on the plot were dead. About 43 percent of the live trees ≥ 1.3 m tall were >100 years old, but most trees were <80 years old. All the trees on the plot were subalpine fir. Modeling tree ages based on diameters suggested that the oldest remaining live tree on the plot germinated around 1780. No seedlings older than germinants were recorded in the plot, but we recorded 3,185 subalpine fir germinants per hectare. This plot had by far more standing dead trees (≥ 1.3 m tall) than any other plot. All of them were subalpine fir, and most were in decay class 2. The density of standing dead trees was 2,140 trees per hectare, of which 1,040 were <10 -cm d.b.h. However, decreasing numbers of standing dead trees were present in each 10-cm d.b.h. size class up to the 70- to 80-cm d.b.h. size class, which had 40 standing dead trees per hectare. Thus, there were more standing dead than live trees on this plot. The cause of death of so many trees could not be determined, but the surrounding stand was mostly healthy. There were 143.5 t per hectare of CWD on the ground, which is more than on any other plot. All of it was from subalpine fir, about 15 to 35 cm in diameter, and in decay classes 2 or 3. This plot had the largest subalpine fir trees that we found (up to 62-cm d.b.h. for live trees and 75-cm d.b.h. for standing dead trees). Most of the trees had apparently died relatively recently over a short period as all were in a similar state of decay. Of 104 measured stems, only 26 were alive. Thus, there was only 35 percent overstory canopy closure for the plot. Core samples taken from the largest live trees on the plot suggested an origin date of around 1825. The largest of these trees was 62-cm d.b.h., so throughout its life, this tree averaged about three rings per centimeter of diameter growth. If this tree is representative of the largest standing dead tree, which was 13 cm larger in diameter, the dead tree would be 39 years older ($13 \text{ cm} \times 3$), with an origination date around 1786.

In the ordination (fig. 36), this plot clustered closest to the subalpine fir/Cascade azalea plant association but was separated from this and all other groups by its high position on all three ordination axes. This position suggested low understory light and high subalpine fir canopy cover, both of which reflect its recent past with formerly high subalpine fir canopy cover. This position also indicated an environment with low temperatures and moist soils. This is a complex plot with more than one plant association; however, no part of it keys to any plant association in Henderson et al. (1989). Within the plot there was a spring, which caused a canopy gap dominated by green alder with 20 percent canopy cover. But the remainder of the plot was still unique. Cascade azalea was present (1 percent), so perhaps a portion of the plot had affinities to the subalpine fir/Cascade azalea plant association. This seems plausible, but most of the plot was dominated by herbs, including Sitka valerian (*Valeriana sitchensis*) (25 percent), Siberian springbeauty (*Claytonia sibirica*) (35 percent), and largeleaf sandwort (*Moehringia macrophylla*) (20 percent). Thus, it also resembled the subalpine fir/Sitka valerian plant association described for the Mount Baker-Snoqualmie National Forest (Henderson et al. 1992), although that plant association lacked Siberian springbeauty and largeleaf sandwort. Although there was much light at ground level, we did not find any tree regeneration older than germinants. The species richness for the plot was 45.

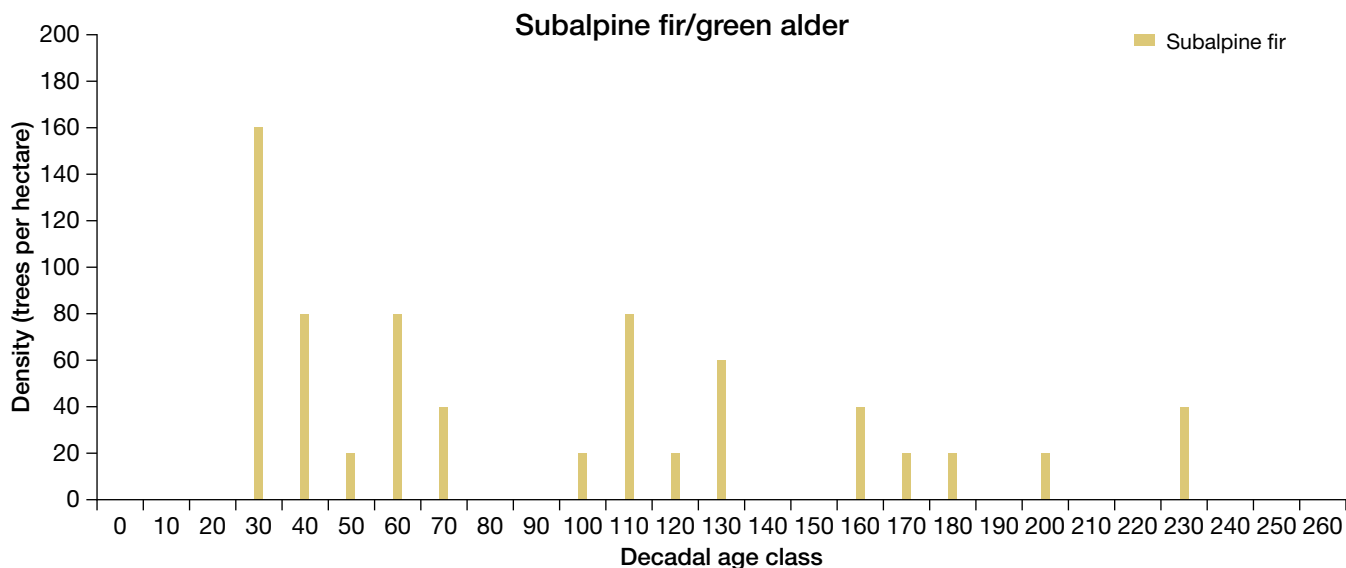


Figure 43—Mean age structure of trees ≥ 1.3 m tall in the subalpine fir/green alder community type of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

SUBALPINE FIR/BLUE WILDRIE COMMUNITY TYPE—

- This plot was fundamentally a grass and herb meadow with a scattering of trees about equally divided by trees >50 years old and <50 years old, but we did not find any seedlings on the plot.
- Of 39 measured tree stems, 29 were standing dead whitebark pine, which died of white pine blister rust.
- In the ordination, this plot was generally near both the subalpine fir/common juniper and subalpine fir/broadleaf lupine plant associations.
- If the overstory canopy closure approached 100 percent, the soils would likely become too cold for root growth.

Plot 16 was in the subalpine fir/blue wildrye community type. It was at an elevation of 1632 m, with an aspect of 274° and a slope steepness of 66 percent. The summer soil moisture averaged 4.8 percent, and the mean June through August soil temperature was 10.5°C .

By using a combination of core sample ages and diameter-age modeling, we estimated that trees ≥ 1.3 m tall ranged in age from 21 to 192 years (fig. 44). There were similar numbers of trees >50 years old and <50 years old. Only two trees were >100 years old, with the oldest a subalpine fir tree estimated at 190 years that germinated around 1820. The oldest tree on the plot that we core sampled was a 97-year-old subalpine fir that germinated around 1913. There was also a 96-year-old western white pine, a 67-year-old Douglas-fir, and several whitebark pines between 50 and 70 years old. Although the modeled ages of all measured trees on the plot suggested that the first trees in the area were subalpine fir, which entered around 1820, they also suggested that most trees entered after 1900, including all the whitebark pine. Of 39 measured tree stems, 29 were dead whitebark pine; most or all died of white pine blister rust. No seedlings were recorded in this plot. There were 840 standing dead trees (≥ 1.3 m tall) per hectare of whitebark pine. Of these, 560 trees per hectare were <10 -cm d.b.h., 260 trees per hectare were 10- to 20-cm d.b.h., and the remainder were 20- to 30-cm d.b.h. We found no pieces of CWD, suggesting that all the mortality was recent.

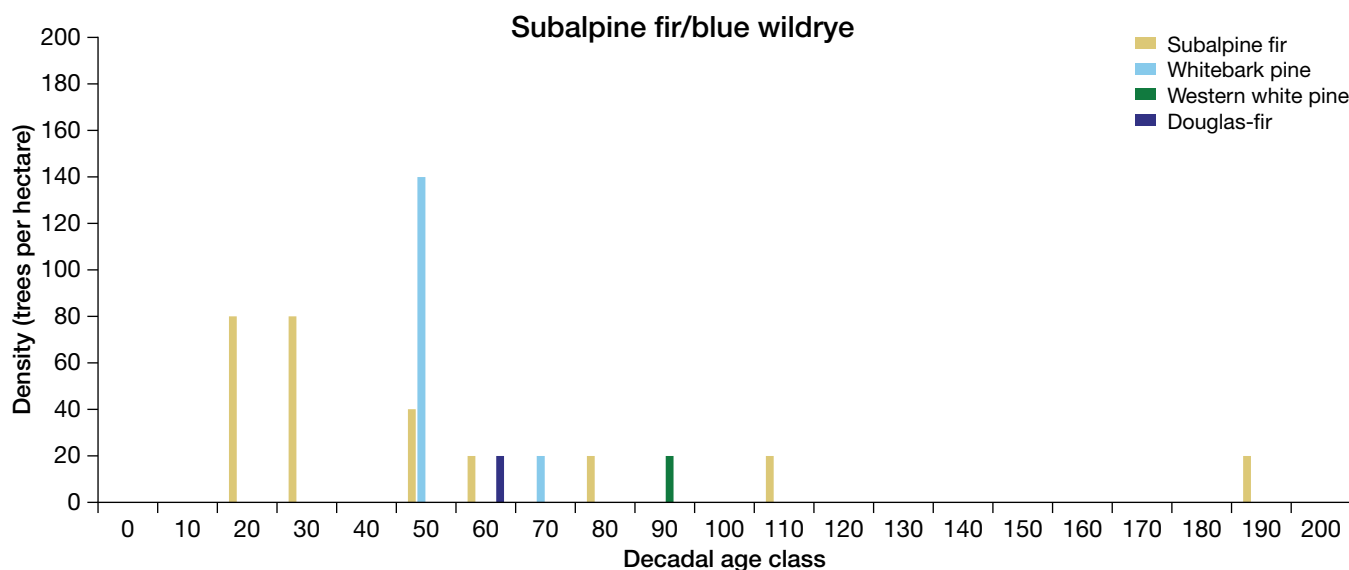


Figure 44—Mean age structure of trees ≥ 1.3 m tall in the subalpine fir/blue wildrye community type of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

In the ordination (fig. 36), this plot stood out as unique but was generally near both the subalpine fir/common juniper and subalpine fir/broadleaf lupine plant associations. This site had 25 percent blue wildrye canopy cover and 10 percent Roemer's fescue canopy cover. The species richness for the plot was 48.

At the present time, there is only 25 percent overstory canopy closure contributed to by four species of conifers, so this community is still fundamentally a meadow. If the overstory canopy closure approached 100 percent, the soils would likely become too cold for root growth (Körner and Paulsen 2004).

SUBALPINE FIR/KRUMMHOLZ COMMUNITY TYPE—

- These two plots were likely in a late-successional stage, with the trees likely all >50 years old and many >200 years old.
- There were 227 seedlings per hectare; 160 were subalpine fir (some appeared to be layered branch sprouts), and 167 were whitebark pine (we did not find any whitebark pine older than seedlings).
- These complex plots were closest to the subalpine fir/broadleaf lupine plant association in the ordination, but both also overlapped areas with the spreading phlox community type.
- These plots would likely not develop root-limiting low temperatures with a complete overstory canopy closure.

Plots 30 and 35 were in the subalpine fir/krumholz community type based on the krumholz structure of subalpine fir, although there were also some floristic similarities. Elevations of these plots ranged from 1742 to 1893 m, aspects ranged from 265 to 266°, and slope steepness ranged from 33 to 55 percent. The mean summer soil moisture ranged from 3.6 to 5.4 percent, and the mean June through August soil temperature ranged from 10.4 to 14.1 °C.

In both plots, the tree stems turned vertically from lengthy prostrate (lying stretched out on the ground) stems that had layered during their lives. Thus, ages of trees in these stands taken from upright stems have little meaning, except possibly to indicate when a

change in growth form occurred (fig. 45). Plot 30 was a krummholz stand of subalpine fir, with some trees as tall as 7.5 m; however, most or all turned up from prostrate stems on the ground or sprouted from layered stems or branches. The tallest trees in plot 35 were 3.1 m tall from where they turned up from the ground. One subalpine fir core sample from a prostrate portion of the stem on plot 35 was 210 years old, but this was still at an undetermined distance from its point of germination. Two trees cored at breast height on vertical stems on plot 30 were 50 and 122 years old. We recorded 227 seedlings per hectare in this community type, of which 160 were subalpine fir, and the remainder were whitebark pine (table 26). Some of the subalpine fir seedlings appeared to be layered sprouts. No mortality was recorded among seedlings. There were 1,720 live, upright subalpine fir stems per hectare and 140 live, upright Douglas-fir stems per hectare in this community. All the Douglas-fir was on the lower elevation plot 35 and because of snow breakage, its form resembled krummholz. There were 180 dead standing trees per hectare on this plot ≥ 1.3 m tall. Of these, 140 dead standing trees per hectare were subalpine fir, and 40 dead standing trees per hectare were Douglas-fir. Nearly all the dead standing trees were <10 -cm d.b.h., but 10 trees per hectare of subalpine fir were between 10- and 20-cm d.b.h. There was an average of 11.5 t (SD = 5.9) per hectare of CWD on the ground in these plots. About two-thirds of the CWD was from subalpine fir, and one-third was from whitebark pine. CWD pieces were 15 to 25 cm in diameter and in decay classes 2 or 3.

In the ordination (fig. 36), plot 30 clustered with the subalpine fir/broadleaf lupine plant association because of its 5 percent broadleaf lupine canopy cover and 30 percent subalpine fir canopy cover. The open portion of the plot was vegetated with the spreading phlox community type, which makes this a complex plot. However, the highest canopy cover of any understory species was broadleaf lupine at 5 percent. This species was closely associated with the lee edge of the subalpine fir stand, which provided some shade, wind protection, and snow

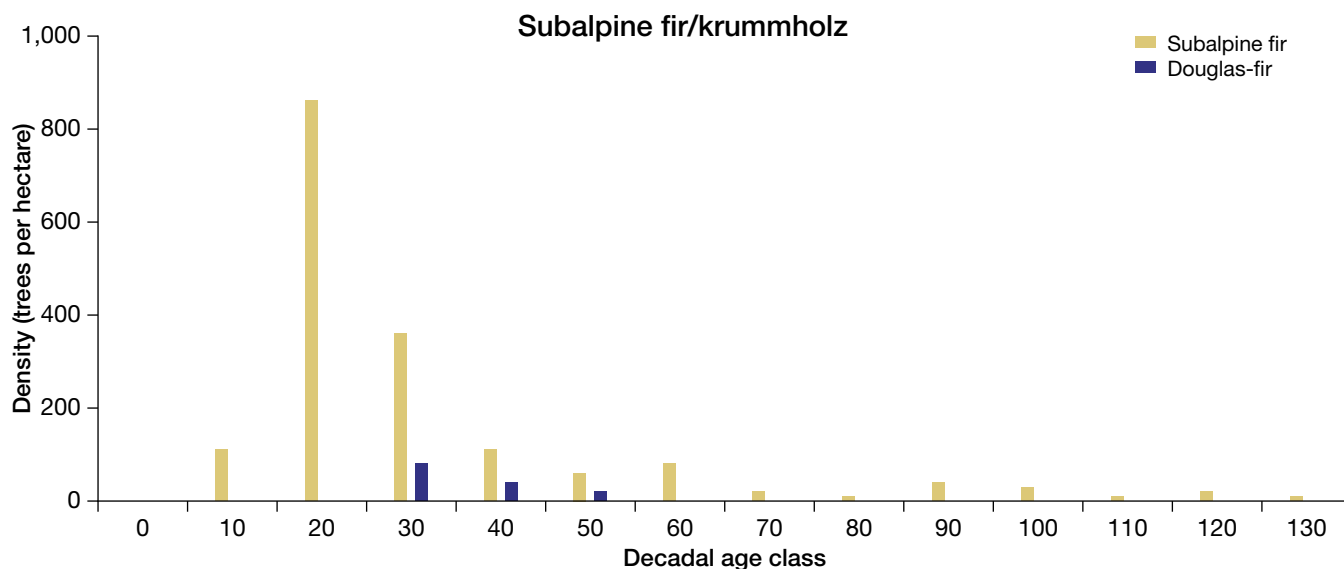


Figure 45—Mean age structure of the upright portion of stems in the subalpine fir/krummholz community type of the Olympic Mountain whitebark pine communities study. Substantial portions of the stems were prostrate on the ground. Those stem portions were not included in the ages that we present, meaning that these trees were considerably older than the ages presented for the upright, live stem portions. These tree ages were for trees that were ≥ 1.3 m tall above the point where they turned up from the ground. The age structure suggested that most vertical growth has occurred in the last 40 years and that Douglas fir has entered only in the last 60 years. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

capture. Plot 35 was also a complex plot in that it included a rocky and sparse tundra type on the windward side of the narrow ridge that it was on, as well as a dense, low stand of krummholz subalpine fir, with a depauperate understory on the ridgeline itself. To the lee side of the ridge, there was some Cascade azalea growing without a tree overstory where snow accumulated, but that was not within the plot. Plot 35 clustered most closely with the subalpine fir/broadleaf lupine plant association because of a small (0.2 percent) amount of broadleaf lupine. The relative importance of this small coverage was inflated by the even smaller amounts of canopy cover of the other species. However, this clustering is less than perfect, and there was also a tendency for this plot to cluster loosely with the spreading phlox community type because of that community's presence in the open part of the plot. The windward tundra community most closely resembled the spreading phlox community type, and it was in this community where the Douglas-fir was found. The species richness was 28 species per plot.

The overstory canopy closure in plot 30 was 30 percent and consisted entirely of subalpine fir. The overstory canopy closure in plot 35 was 28 percent (consisting of about 20 percent subalpine fir and 8 percent Douglas-fir). The Douglas-fir growing on this plot was clearly struggling, both with slow growth and stem and limb snow breakage. Our soil temperature modeling suggested that these plots would not develop root-limiting, low soil temperatures if the overstory canopy closed over (Körner and Paulsen 2004). This may have been different in the Little Ice Age, and perhaps warming soils have permitted more vigorous tree top growth. There is currently no indication that wind or snow abrasion is limiting their top growth on plot 30, but some was observed in plot 35. Nevertheless, both stands appear to be developing into upright tree islands.

DOUGLAS-FIR/OCEANSPRAY-DWARF ROSE PLANT ASSOCIATION—

- This formerly more open woodland plot appeared to be slowly filling with trees, but no seedlings were recorded.
- This plot was among the warmest and driest, and most of the understory vegetation was under tree shade, while openings were barren.
- In the ordination, it was closest to the subalpine fir/broadleaf lupine plant association on axes 1 and 2 but distant on ordination axis 3, with a location suggesting a warm site.
- Complete overstory canopy closure would not result in root-limiting soil temperatures.

Plot 22 was in the Douglas-fir/oceanspray-dwarf rose plant association (Henderson et al. 1989). It was at an elevation of 1543 m, with an aspect of 206° azimuth, and a slope steepness of 58 percent. The summer soil moisture averaged 4.4 percent, and the mean June through August soil temperature was 15.7 °C.

Using a combination of core sample ages and diameter-age modeling, we estimated that trees ≥ 1.3 m tall ranged in age from 25 to 180 years (fig. 46). Although trees ≥ 1.3 m tall were sparse on this plot ($n = 12$), half of them were 100 years old or older, the oldest being a Douglas-fir that germinated around 1830. All other trees in this open woodland plot entered the stand after 1885 and mostly in the 1900s. No seedling trees were recorded on this plot. There was only one standing dead tree on the plot (a western white pine) that was 36.2-cm d.b.h., representing 20 trees per hectare. We found no CWD in our survey, and litter was sparse and discontinuous.

In the ordination (fig. 36), this plot clustered closest to the subalpine fir/broadleaf lupine plant association on axes 1 and 2, but it was far removed from this plant association on ordination axis 3. In Henderson et al. (1989), this plot keys to the Douglas-fir/oceanspray-dwarf

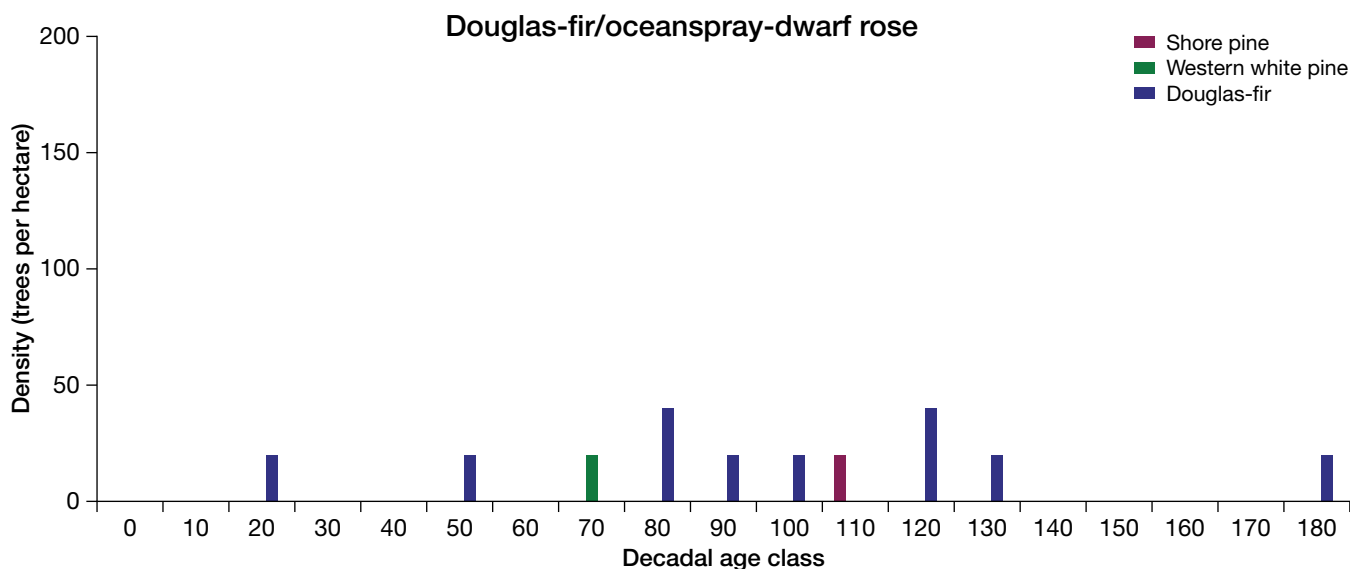


Figure 46—Mean age structure of trees ≥ 1.3 m tall in the Douglas-fir/oceanspray-dwarf rose plant association of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

rose plant association. The sparse understory was dominated by dwarf rose (5 percent), kinnikinnick, and American vetch (*Vicia americana*) (3 percent each). Nearly all the understory vegetation (25 percent understory canopy closure) was associated with tree shade—openings were relatively barren mineral soil. The species richness for the plot was 31.

The overstory canopy closure was 35 percent and consisted mostly of Douglas-fir with some shore pine and white pine. Complete canopy closure would not result in root-limiting temperatures.

SPREADING PHLOX COMMUNITY TYPE—

- This was a nonforest community type with alpine affinities, although a tree invasion appeared to be starting, as there were 297 seedlings per hectare, of which 264 were whitebark pine, making this the only community type with more whitebark pine seedlings than subalpine fir seedlings.
- Whitebark pine was represented in various age classes up to more than 100 years old but with considerable mortality.
- In the ordination, it was closest to the subalpine fir/broadleaf lupine plant association on axes 1 and 3 but was generally lower on axes 1 and 2 than that plant association, suggesting a warmer, more open community than that plant association.
- Three of eight plots would likely have root-limiting, low soil temperatures if complete overstory canopy closure occurred.

Plots 4, 9, 12, 19, 20, 24, 25, and 38 were in the spreading phlox community type. The elevations of these plots ranged from 1630 to 1803 m, aspects ranged from 192 to 273°, and slope steepness ranged from 50 to 82 percent. The mean summer soil moisture ranged from 3.7 to 5.9 percent, and the mean June through August soil temperature ranged from 12.8 to 14.8 °C.

Because this community type had sporadic whitebark pine canopy cover (up to 25 percent); Douglas-fir, subalpine fir, and western white pine in small amounts; and little or no canopy cover from other tree species, we considered it a nonforest community type with

alpine affinities. By using a combination of core sample ages and diameter-age modeling, we determined that trees in these plots ranged in age from 24 to 164 years (fig. 47). Few trees were >100 years old, and most were <50 years old. Trees >100 years old included only two whitebark pines. The only subalpine fir tree that we encountered was 40 years old. We recorded 297 seedlings per hectare in this community type, of which 264 were whitebark pine. The only seedling mortality recorded was 14 trees per hectare of whitebark pine. This was the only community type or association in which we found more whitebark pine seedlings than subalpine fir seedlings. There were 46 standing dead trees (≥ 1.3 m tall) per hectare of whitebark pine. Nearly all were <20-cm d.b.h., but with a few between 20- and 40-cm d.b.h. No other species was represented, and most mortality was due to white pine blister rust. There was an average of 5.8 t (SD = 12.6) per hectare of CWD on the ground in these plots. About three-quarters of it was from whitebark pine, and one-quarter was not identified. Most of the CWD was about 45 cm in diameter and in decay classes 3 or 4. Most of the unidentified CWD may well have been from whitebark pine, and we observed white pine blister rust on some whitebark pines in this community, suggesting a cause of the high proportion of CWD from this species. The average white pine blister rust infection severity code was 1.8.

In the ordination (fig. 36), these plots tended to be close to the subalpine fir/broadleaf lupine plant association on axes 1 and 3 but widely separated from most other plots on ordination axis 2. The resemblance to the subalpine fir/broadleaf lupine plant association is because all the major species in the spreading phlox community type were present and often well represented in that plant association; however, the reverse is not true. On average, the dominant species were spreading phlox (13 percent), common juniper (10 percent), whitebark pine (9 percent), and white sagebrush (*Artemisia ludoviciana*) (2 percent). Belsky and del Moral (1982) described a similar community in the Deer Park area of the Olympic Mountains, which they considered to be an alpine community. Kuramoto and Bliss (1970) described a cushion plant community from the northeastern Olympic Mountains that was also similar. The species richness was 13 species per plot.

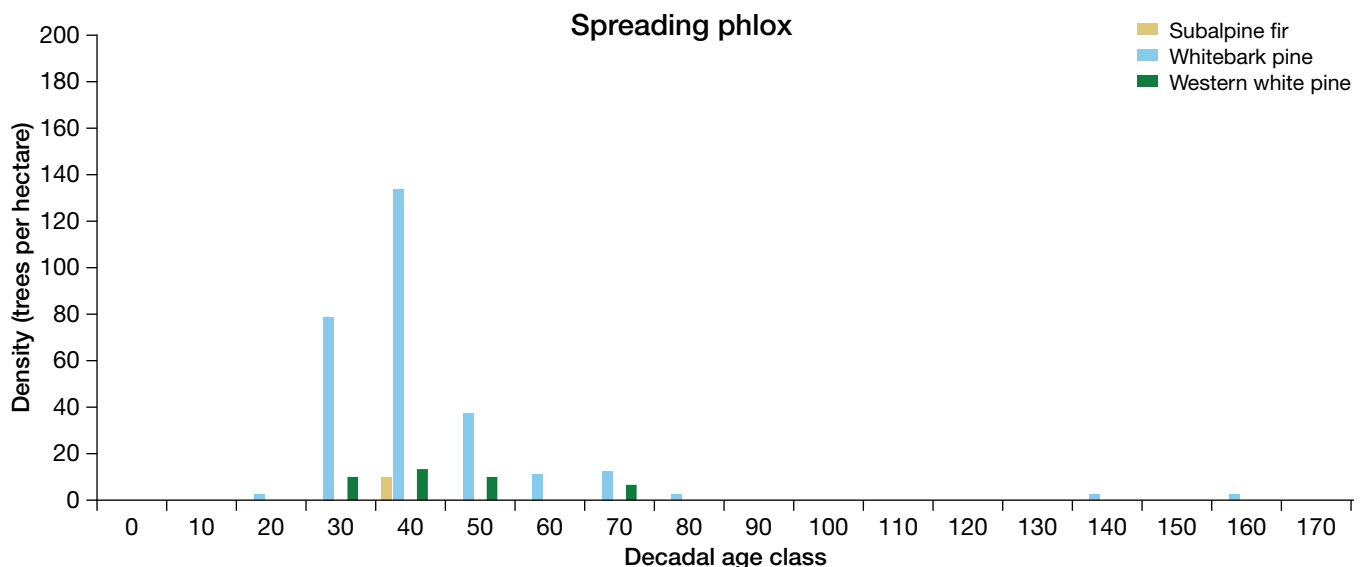


Figure 47—Mean age structure of trees ≥ 1.3 m tall in the spreading phlox community type of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

WESTERN BRACKENFERN COMMUNITY TYPE—

- This was a nonforested community type on a warm, dry, highly unstable scree slope, with only one small whitebark pine, which was a seedling, on the entire plot.
- The dominant species was western brackenfern, which did not occur on any other plot.
- This plot was low on ordination axis 1 because of its lack of overstory canopy cover, but although nearly unique, it was closest to the spreading phlox community type in the ordination because of the presence of common juniper, spreading phlox, and white sagebrush.
- Its soils were too warm to be root limiting even if a complete overstory canopy closure were possible.

Plot 40 was in the western brackenfern community type. It was at an elevation of 1693 m, with an aspect of 216° and a slope steepness of 63 percent. The summer soil moisture averaged 3.9 percent, and the mean June through August soil temperature was 15.3 °C.

This mid-elevation plot was on an open, scree slope, with loose, sandy, gravelly, cobbly soil with scattered boulders. There were no trees other than a single whitebark pine seedling in this plot. There was only one unidentified standing dead tree on the plot; it was 5.9-cm d.b.h. We found no CWD in our survey, litter was sparse and discontinuous, and we found no evidence of fire.

In the ordination (fig. 36), this plot clustered closest to the spreading phlox community type on axes 1 and 2 but was distant from this and all other groups on ordination axis 3. The dominant species was western brackenfern (45 percent), which was evenly distributed. Common juniper (5 percent) and white sagebrush (4 percent) were also present. Eight other species had lesser canopy covers (≥ 1 percent), and the remainder had no more than a fraction of a percentage of canopy cover. Western brackenfern did not occur on any other plot in the study area. The association of this community with the spreading phlox community type in the ordination was due to the presence of small amounts of common juniper, spreading phlox, and white sagebrush on the plot, which were all present in the spreading phlox community type. The species richness was 29.

Although soil temperatures would not inhibit an overstory canopy from forming, the soils are so unstable that trees cannot establish.

BLACK ALPINE SEDGE COMMUNITY TYPE—

- This unique plot, with the latest melting snowpack of all plots and cool, moist soil, was in a late-successional stage, although tree invasion may be taking place.
- There were 984 seedlings per hectare (692 subalpine fir and 292 whitebark pine), but the presence of few taller trees suggested seedling success may be low.
- This plot was separate from all others on all ordination axes in a position suggesting a warm, dry, open site, which was an artifact of having so few species in common with any other plot.
- This plot had cool soil temperatures that would restrict complete overstory canopy closure from occurring.

Plot 18 was in the black alpine sedge community type. It was at an elevation of 1741 m, with an aspect of 275° and a slope steepness of 10 percent. The summer soil moisture averaged 12.7 percent, and the mean June through August temperature was 9.1 °C. This plot was on a gently sloping, west-facing bench that accumulated a heavy snowpack that melted in July, making this the latest plot to melt out in our sample. The mineral component of the soil was sandy loam, but humic organic material was high in the upper 10 cm, making the soil water retentive.

There were only a few scattered trees ≥ 1.3 m tall. All were subalpine fir or whitebark pine in the range of 19 to 30 years old (fig. 48). However, there were 984 seedlings per hectare, of which 692 were subalpine fir, and the remainder were whitebark pine. Most of the seedlings growing on the plot had estimated ages of <25 years. All of the 67 standing dead seedlings per hectare were subalpine fir. We found no standing dead trees (≥ 1.3 m tall) and no CWD on the plot.

In the ordination (fig. 36), this plot was separate from all others on all axes. This was to be expected, as it shared few species in common with any of the other plots and was dominated by species that were not present elsewhere. Subalpine fir and whitebark pine had about 3 percent combined canopy cover. The five species that dominated this plot were Parry's rush (35 percent), woolly pussytoes (20 percent), black alpine sedge (15 percent), Cusick's speedwell (*Veronica cusickii*) (10 percent), and Rocky Mountain goldenrod (*Solidago multi-radiata*) (5 percent). Nearby lower areas of the bench were dominated more heavily by black alpine sedge, but it disappeared on slightly higher ground than this plot location. Thus, this plot was transitional between an even snowier community dominated heavily by black alpine sedge and less snow-affected communities with none of the sedge. The species richness on this plot was 16.

Low soil temperatures would likely restrict complete overstory canopy closure.

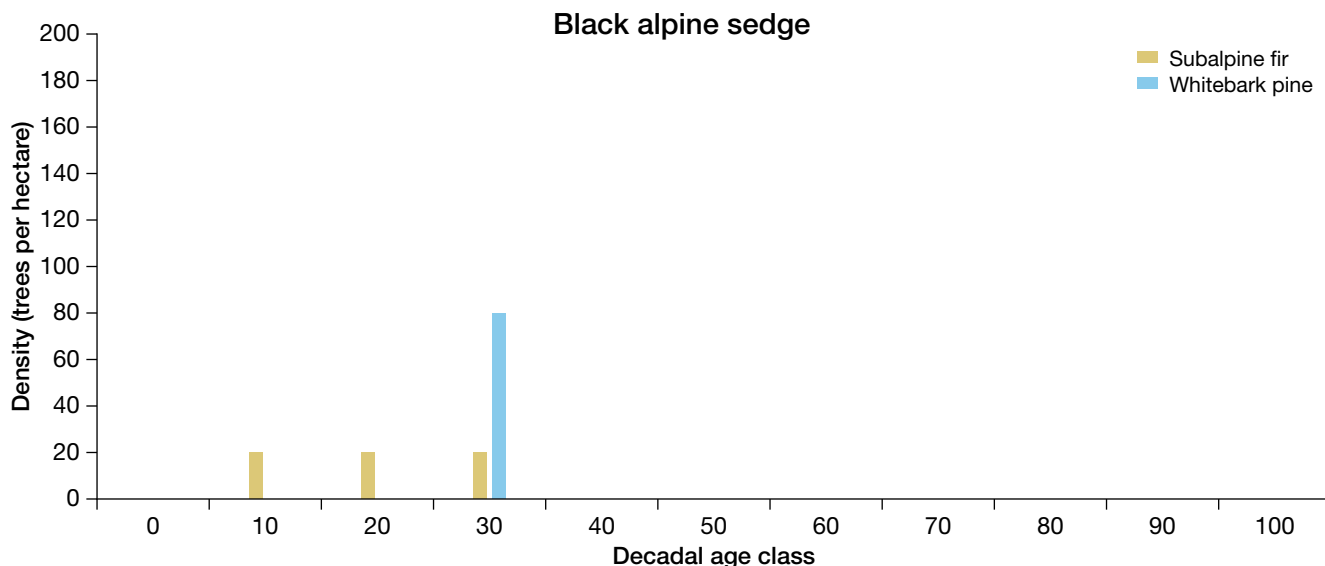


Figure 48—Mean age structure of trees ≥ 1.3 m tall in the black alpine sedge community type of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

TALUS PLOTS—

- Plants only grew where finer soil materials had accumulated along the margins of these unstable boulder fields.
- Few trees were >100 years old, and most were <40 years old.
- Whitebark pine did not occur on these plots.
- In the ordination, these two plots were loosely associated with each other but not with any other type.

Plots 7 and 10 were talus plots. The elevations of these plots ranged from 1591 to 1685 m, aspects ranged from 262 to 270°, and slope steepness ranged from 49 to 57 percent. These plots were located along the same margin of the same talus slope, with plot 10 being 94 m higher in elevation. The soil moisture was unmeasurable because of lack of soil, so we assumed it was close to 0 percent for most of the plot. The mean June through August soil temperature was 8.8 °C on plot 7 in a small pocket of soil between boulders. Both plots were on a steep, coarse, talus slope consisting of boulders and cobbles with little vegetation. All vegetation was confined to a narrow strip along the south side of each plot. These plots were in a topographic low with high ridges to the south and east, meaning that they were topographically shaded for much of winter and in the morning hours all year. Because of cold-air drainage from the ridges, these plots were also frost pockets. This area is likely in an avalanche chute; however, the age of the trees along the margins suggested stand-replacing snow avalanches may not be common on the margins. Some of the trees had bark scars on their upslope sides from being struck by rocks.

Using a combination of core sample ages and diameter-age modeling, we determined that trees in these plots ranged in age from 26 to 179 years (fig. 49). Few trees were >100 years old, and most were <40 years old. The oldest tree on plot 10 was a 179-year-old subalpine fir that germinated around 1831, and the oldest tree on plot 7 was a 116-year-old subalpine fir that germinated around 1894. No seedling trees were recorded on these plots. We found no standing dead trees and no CWD on either plot.

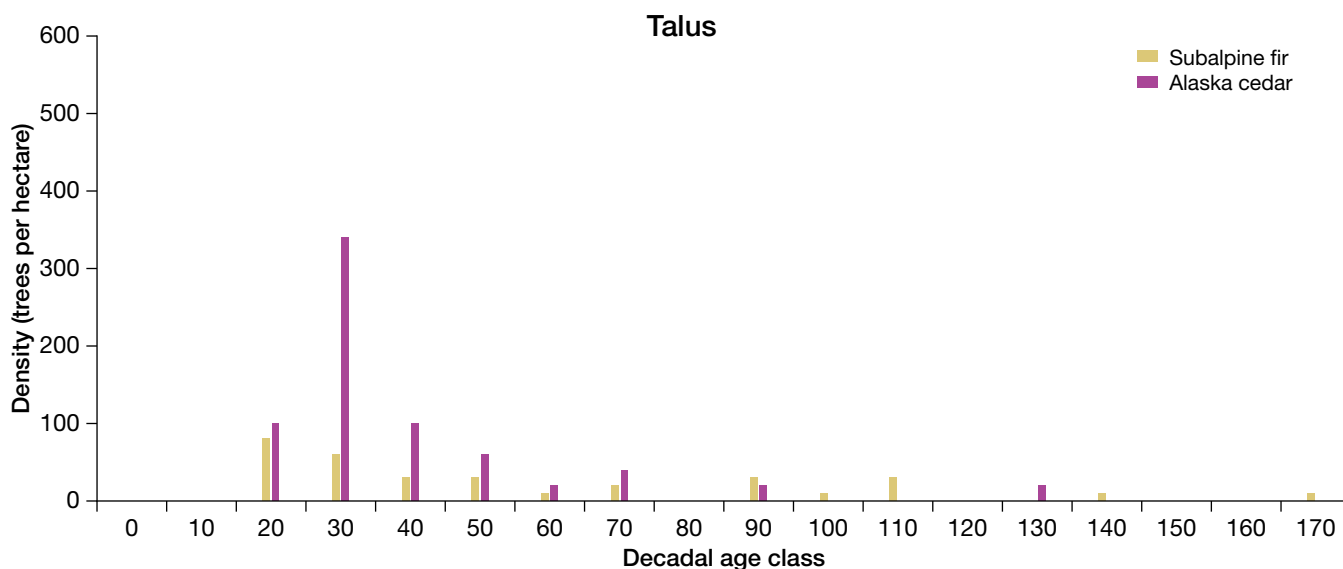


Figure 49—Mean age structure of trees ≥ 1.3 m tall in the talus plots of the Olympic Mountain whitebark pine communities study. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

In the ordination (fig. 36), these two plots tended to be loosely associated with each other on all three axes, but they had no clear affinity to other groups. The two plots in this group were floristically dissimilar and were placed here simply because of their similar association with a talus slope margin. On plot 7, the understory consisted of western mountain ash (2 percent) (*Sorbus sitchensis*), Oregon boxleaf (1 percent), and trace amounts of 10 other species. The dominant understory species on plot 10 included green alder (15 percent), American rockbrake (7 percent) (*Cryptogramma acrostichoides*), and 4 percent each of western columbine (*Aquilegia formosa*) and heartleaf arnica (*Arnica cordifolia*). The species richness was 14 species per plot.

On plot 7, overstory canopy closure was 10 percent from subalpine fir, and on plot 10, overstory canopy closure was 10 percent from equal amounts of subalpine fir and Alaska cedar.

Species Richness

- Species richness increased with coarse fragment content, slope steepness, warmer aspects, variation in and the amount of light (PAR at ground-level and 1.3-m), maximum monthly air temperatures from fall through winter, monthly soil temperatures (especially summer maximums), minimum monthly soil surface temperatures in summer, and amount and severity of white pine blister rust.
- Species richness decreased with summer soil moisture, overstory canopy closure, minimum air temperatures (especially spring through summer), amount and age of subalpine fir, and amount of CWD.

Four of seven physical site variables had significant correlations with species richness, including coarse fragment content ($r = 0.51$), summer soil moisture ($r = -0.46$), slope steepness ($r = 0.38$), and aspect ($r = 0.36$).

Four of seven measured light or canopy cover variables had significant correlations with species richness, including standard deviation of ground-level PAR ($r = 0.53$), PAR at 1.3-m height ($r = 0.49$), overstory canopy closure ($r = -0.44$), and ground-level PAR ($r = 0.38$). None of the 40 potential solar radiation variables (direct, diffuse, duration) were significantly correlated with species richness.

There were 43 of 560 temperature variables that were significantly correlated with species richness. Seventeen of these significant correlations were with air temperatures. All significant correlations between air temperatures and species richness were either maximum or minimum monthly temperatures. All seven of the maximum monthly air temperature correlations were positive and occurred from September through January, and the strongest had an $r = 0.53$ (maximum January air temperature in quarter-day 3). All 10 of the significant minimum air temperature correlations were negative. Seven were in the months of May through September, two were in December, and one was annual. The strongest correlation had an $r = -0.50$ (minimum December air temperature in quarter-day 2). There were 20 significant correlations between soil temperature variables and species richness. All were positive correlations with mean maximum soil temperatures. All but two of these occurred from June through August. The two that did not were mean maximum annual soil temperatures. The strongest correlation was with the maximum June soil temperature in quarter-day 1 ($r = 0.56$). There were six significant soil surface temperature correlations with species richness. Five of these were in July, and one was the maximum annual soil surface temperature for each plot. All were positive correlations. The strongest correlation ($r = 0.61$) was with the minimum July soil surface temperature in quarter-day 3, and the other four July correlations were also with minimum soil surface temperatures.

Of 20 tree-related variables, only 5 were significantly correlated with species richness. All were negative correlations. Four were with subalpine fir, and one was with total CWD. The strongest correlation was with subalpine fir canopy cover ($r = -0.64$). The remaining correlations were with subalpine fir stem diameter at breast height, subalpine fir age, and subalpine fir foliar carbon.

Five plot-level white pine blister rust indicators were positively correlated with species richness (mean white pine blister rust infection severity code, mean diameter at breast height of infected trees, mean percentage of dying crowns, mean percentage of dead crowns, and summed percentage of canopy cover of alternate host species for white pine blister rust). Of these, the strongest correlation was with the mean white pine blister rust infection severity code ($r = 0.54$).

Tree Growth and Age

- Subalpine fir and whitebark pine seedlings grew in height at similar rates in open-canopy plots, reaching 1.3-m height in 43 to 44 years, but subalpine fir seedlings in closed-canopy plots grew slowly, reaching 1.3-m height in 92 years.
- Subalpine fir ≥ 1.3 m tall grew in diameter at a similar or slightly slower rate than whitebark pine.
- Whitebark pines < 90 years old and Douglas-fir grew in diameter at similar rates. Whitebark pines ≥ 90 years old are growing in diameter faster now than in the past.

Subalpine fir seedlings (up to 1.3 m tall) in open-canopy plots grew in height at a nearly identical rate as whitebark pine seedlings (fig. 50). All the whitebark pine seedlings grew in open-canopy plots. However, subalpine fir seedlings in closed-canopy plots grew in height much more slowly. These relationships predict that in open-canopy areas, whitebark pines would attain a stem height of 1.3 m in 44 years, and subalpine fir would attain a stem height of 1.3 m in 43 years. In closed-canopy areas, subalpine fir would attain a stem height of 1.3 m in 92 years.

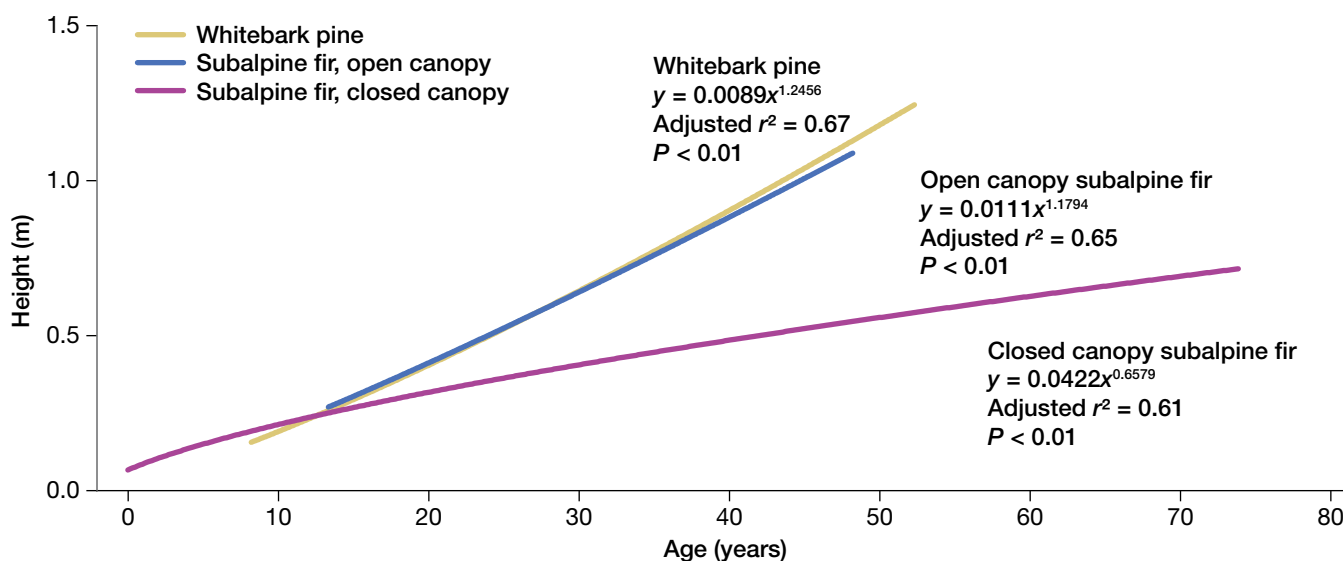


Figure 50—Estimated growth in height of subalpine fir seedlings (< 1.3 -m height) in closed- and open-canopy plots for the Olympic Mountain whitebark pine communities study, and whitebark pine seedlings, all of which were in open-canopy plots.

Larger (≥ 1.3 m tall) whitebark pine trees that were <90 years old and Douglas-fir trees grew in diameter at similar rates (fig. 51). However, older (≥ 90 years old) whitebark pine trees grew in diameter faster even though they were similar in size to the younger trees. The power curve describing their growth suggests much slower growth in the past, but the small sample size warrants a cautious interpretation (fig. 51). Subalpine fir ≥ 1.3 m tall grew in diameter at a similar or slightly slower rate than whitebark pine.

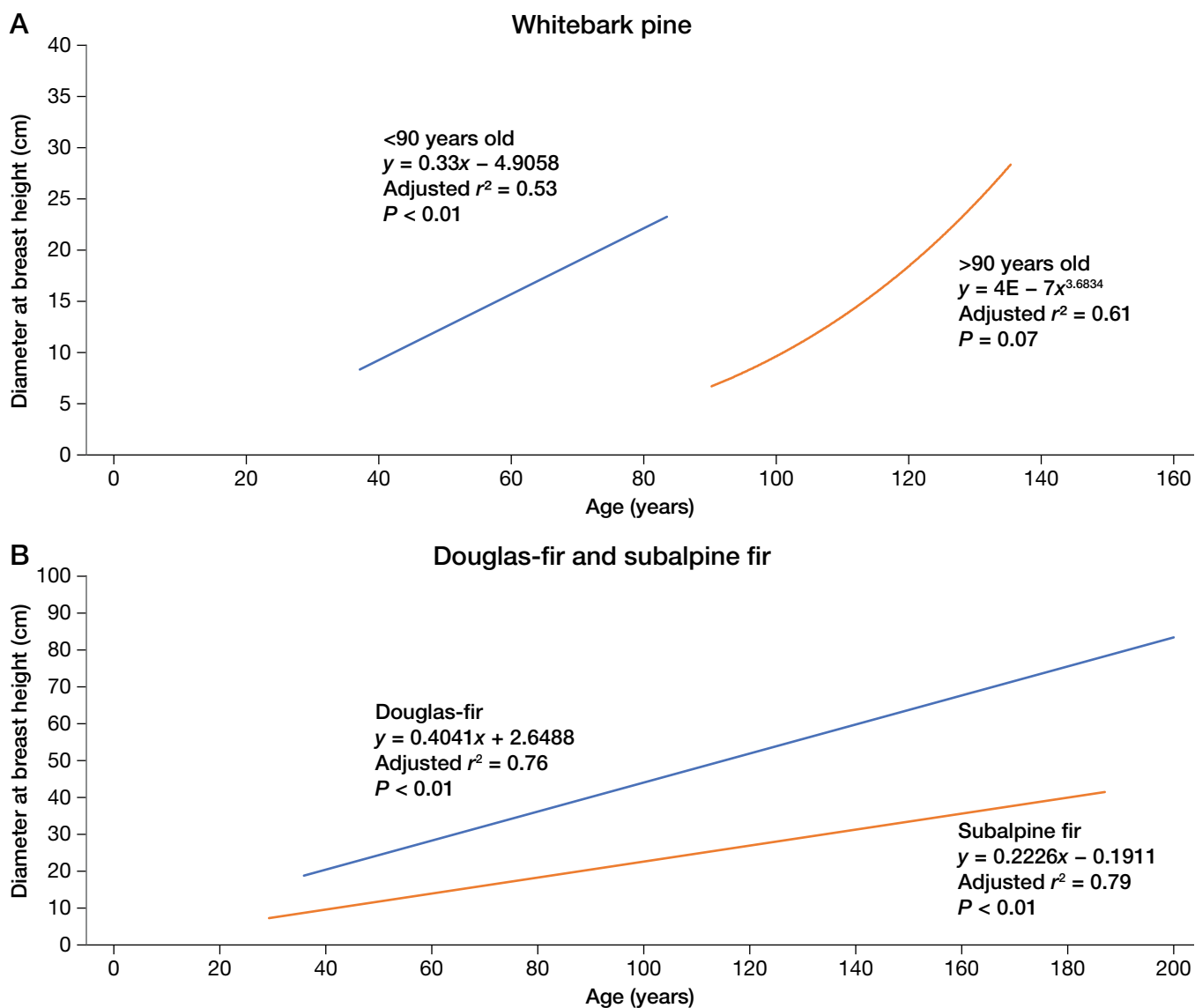


Figure 51—Estimated rates of growth in diameter at breast height for (A) whitebark pine and (B) Douglas-fir and subalpine fir trees (≥ 1.3 m tall) for the Olympic Mountain whitebark pine communities study. The Douglas-fir and subalpine fir relationships were significant.

Basal Area Relationships

- Basal area per hectare increased with overstory canopy closure, age of the oldest tree on the plot, and number of frost-free days but decreased with mean growing-season air temperature, mean monthly soil temperature in July, and elevation.
- An overall multiple linear regression model including mean monthly soil temperature in July and elevation accounted for 68 percent of plot basal area per hectare variation.
- A linear regression model including mean monthly soil temperature in July accounted for 51 percent of subalpine fir basal area per hectare variation.
- The strongest correlations for whitebark pine basal area per hectare were with slope steepness ($r = 0.33$) and summer soil moisture ($r = -0.33$).

Overall, basal area per hectare had a highly significant and strong correlation with percentage of overstory canopy closure ($r = 0.90$). Aside from this correlation, the five strongest correlations with total plot basal area per hectare were with mean growing-season soil temperature ($r = -0.63$), elevation ($r = -0.62$), age of the oldest tree on the plot ($r = 0.61$), mean monthly soil temperature in July ($r = -0.60$), and the number of frost-free days ($r = 0.58$). Correlations between basal area per hectare and the mean monthly soil temperature in August (negative) and the mean annual air temperature (positive) were significant but weaker. Variables tested but not significantly correlated with basal area per hectare included mean monthly soil temperature in June, slope steepness, mean monthly soil temperature in September, mean annual soil temperature at either 3- or 5-years duration, aspect, and summer soil moisture over 5 years. The best linear regression model to explain total basal area in square meters per hectare included mean monthly soil temperature in July and elevation (adjusted $r^2 = 0.68$, $P < 0.01$, $n = 22$):

Total basal area per hectare = $296.4418 - 4.18034 \times \text{mean monthly soil temperature in July} - 0.13047 \times \text{elevation}$

For subalpine fir basal area per hectare, the five strongest correlations were with mean monthly soil temperature in July ($r = -0.73$), mean growing-season soil temperature ($r = -0.69$), mean monthly soil temperature in August ($r = -0.66$), age of the oldest tree on the plot ($r = 0.64$), and mean monthly soil temperature in June ($r = -0.51$). Correlations (all negative) between subalpine fir basal area per hectare and mean annual soil temperature calculated from 3- or 5-year datasets, mean monthly soil temperature in September, elevation, aspect, and slope steepness were significant but weaker. Variables tested but not significantly correlated with subalpine fir basal area per hectare included mean summer soil moisture measured over 5 years, the number of frost-free days, and the mean annual air temperature. In terms of an explanatory linear regression model, mean monthly soil temperature in July accounted for more variation than any other variable or combination of variables (adjusted $r^2 = 0.51$, $P < 0.01$, $n = 22$):

Subalpine fir basal area per hectare = $71.20419 - 4.32408 \times \text{mean monthly soil temperature in July}$

For whitebark pine basal area per hectare, the strongest and significant correlations were with slope steepness ($r = 0.33$) and mean summer soil moisture measured over 5 years ($r = -0.33$). Other variables that were not significantly correlated with whitebark pine basal area per hectare included mean growing-season soil temperature; mean monthly soil temperature in June; elevation; aspect; mean monthly soil temperatures in July, August, or September; mean annual soil temperature calculated from either 3- or 5-year data; age of the oldest tree on the plot; mean annual air temperature; and number of frost-free days. We found no significant linear regression models to explain the variation in the basal area per hectare of whitebark pine with any of these variables or any combination of these variables.

Stand Structure by Age Class, Elevation, and Aspect for Trees

- Subalpine fir was the most common tree ≥ 1.3 m tall (947 trees per hectare) followed by whitebark pine (310 trees per hectare), western white pine and Douglas-fir (39 trees per hectare), Alaska cedar (37 trees per hectare), and shore pine (5.6 trees per hectare).
- Subalpine fir was more common on northern exposures; whitebark pine was more common on southern exposures; Alaska cedar was more common in moist, low-elevation sites; and Douglas-fir was more common at the low elevations on southwestern aspects.
- Whitebark pine codominated with subalpine fir in mid-elevation southwestern aspects and was reproducing faster than subalpine fir only in this situation.
- Age and density of subalpine fir and Douglas-fir were negatively correlated with elevation, but whitebark pine was not correlated with elevation.
- Fifty-five percent of trees at lower elevations, eighty-three percent of trees at mid-elevations, and eighty-two percent of trees at higher elevations established 20 to 60 years ago; respectively, 5, 0.3, and 1 percent of trees at these elevations dated to or before 1850.

Subalpine fir was the most common tree ≥ 1.3 m tall in the study area with a mean density of 947 trees per hectare. Next was whitebark pine with a mean density of 310 trees per hectare, western white pine and Douglas-fir both with a mean density of 39 trees per hectare, Alaska cedar with a mean density of 37 trees per hectare, and shore pine with a mean density of 5.6 trees per hectare. However, none of the species was evenly distributed, and usually either subalpine fir or whitebark pine strongly dominated in different areas. Subalpine fir was especially common on northern exposures and whitebark pine on southern exposures. Alaska cedar was concentrated on portions of just two plots in low-elevation, moist areas, and Douglas-fir was mostly at the lowest elevations.

Most trees were <100 years old, and this was true regardless of species (fig. 52). Three species had significant negative correlations between age and elevation: subalpine fir ($r = -0.34$), Douglas-fir ($r = -0.54$), and Alaska cedar ($r = -0.46$). Of the trees >100 years of

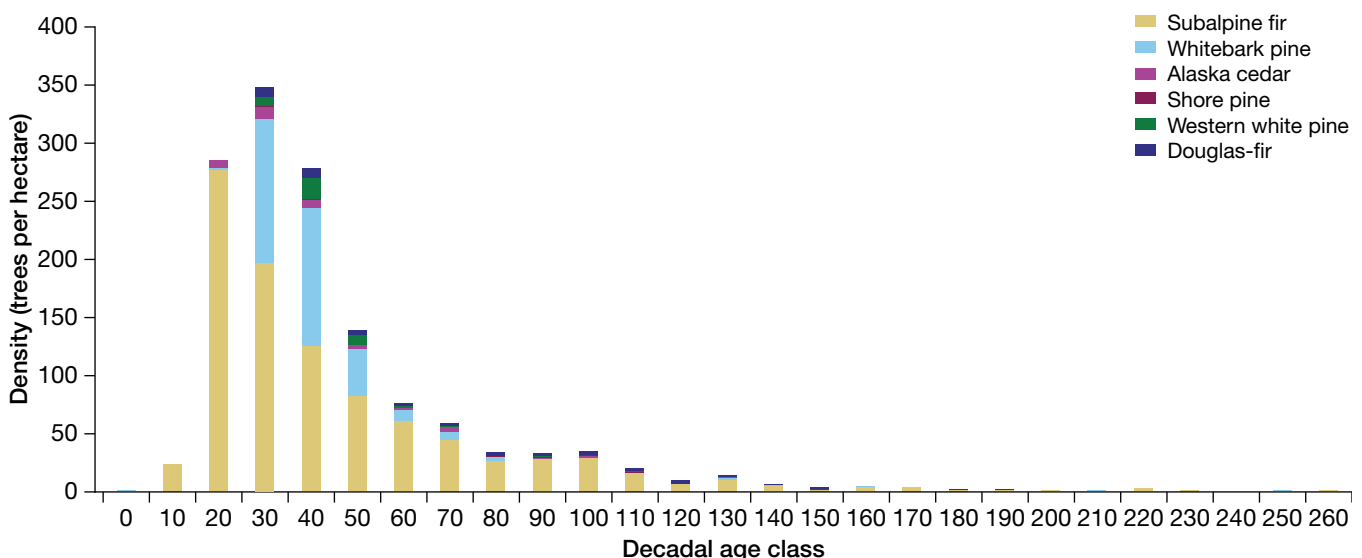


Figure 52—Age-class distribution of trees ≥ 1.3 m tall for the Olympic Mountain whitebark pine communities study. The year 1850 (approximate end of the Little Ice Age) occurred in the 160-year age class. Trees <1.3 m tall ranged in age up to about 50 years old. Therefore, the age classes of 0 to 40 years show fewer trees than that which occurred on the landscape. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

age, we found 57 percent at <1578-m elevation (lower third of our study area), and only 19 percent came from elevations >1735 m (upper third of our study area).

There were differences in age class distributions of trees by both elevation and aspect (figs. 53 and 54). Subalpine fir was the sole dominant tree species on northern aspects. Other species may have been present and sometimes important on west-northwestern aspects, but subalpine fir generally dominated there as well. Subalpine fir was also an important species on southwestern aspects, but it was dominant there only at high elevations. Douglas-fir was the dominant species on southwestern aspects at low elevations, although it was not reproducing there as fast as subalpine fir or whitebark pine. Whitebark pine shared dominance with subalpine fir in mid-elevation southwestern aspects and appeared to be reproducing faster than subalpine fir only in this situation.

At low elevations, trees around age 100 years dominated and appeared to suppress younger trees (figs. 53 and 54). At mid- and high elevations, trees that were only age 40 to 100 years dominated but not sufficiently to suppress reproduction (figs. 53 and 54). Recruitment has been especially high for subalpine fir in mid-elevations on northwestern to west-northwestern aspects. Recruitment increased more recently at high elevations on west-northwestern and southwestern aspects where subalpine fir density is increasing faster than whitebark pine. Only at mid-elevations on southwestern-aspect slopes did whitebark pine become more dominant than subalpine fir.

More than half (55 percent) of all trees at low elevations established between 20 and 60 years ago, but in the same period, 83 and 82 percent of trees were established at mid- and high elevations, respectively. Only 5 percent of low-elevation trees, 0.3 percent of mid-elevation trees, and 1 percent of high-elevation trees date to or before 1850.

At low elevations, 56 percent of the current forest basal area was established in a 60-year period between 100 and 160 years ago (after the Little Ice Age). During a 60-year period between 40 and 100 years ago, 77 percent of the current forest basal area at mid-elevations and 60 percent at high elevations was established. Although 28 percent of the current forest basal area established before 1850 at low elevations, only 12 percent at mid-elevations and 17 percent at high elevations established before 1850.

There were significant negative correlations between subalpine fir and Douglas-fir densities and elevation (table 27). The correlation between shore pine density and elevation was also negative but not significant, and the correlations between whitebark pine and western white pine densities and elevation were both low and not significant. The correlation between Alaska cedar density and elevation should be disregarded as the trees for this species came from only two plots.

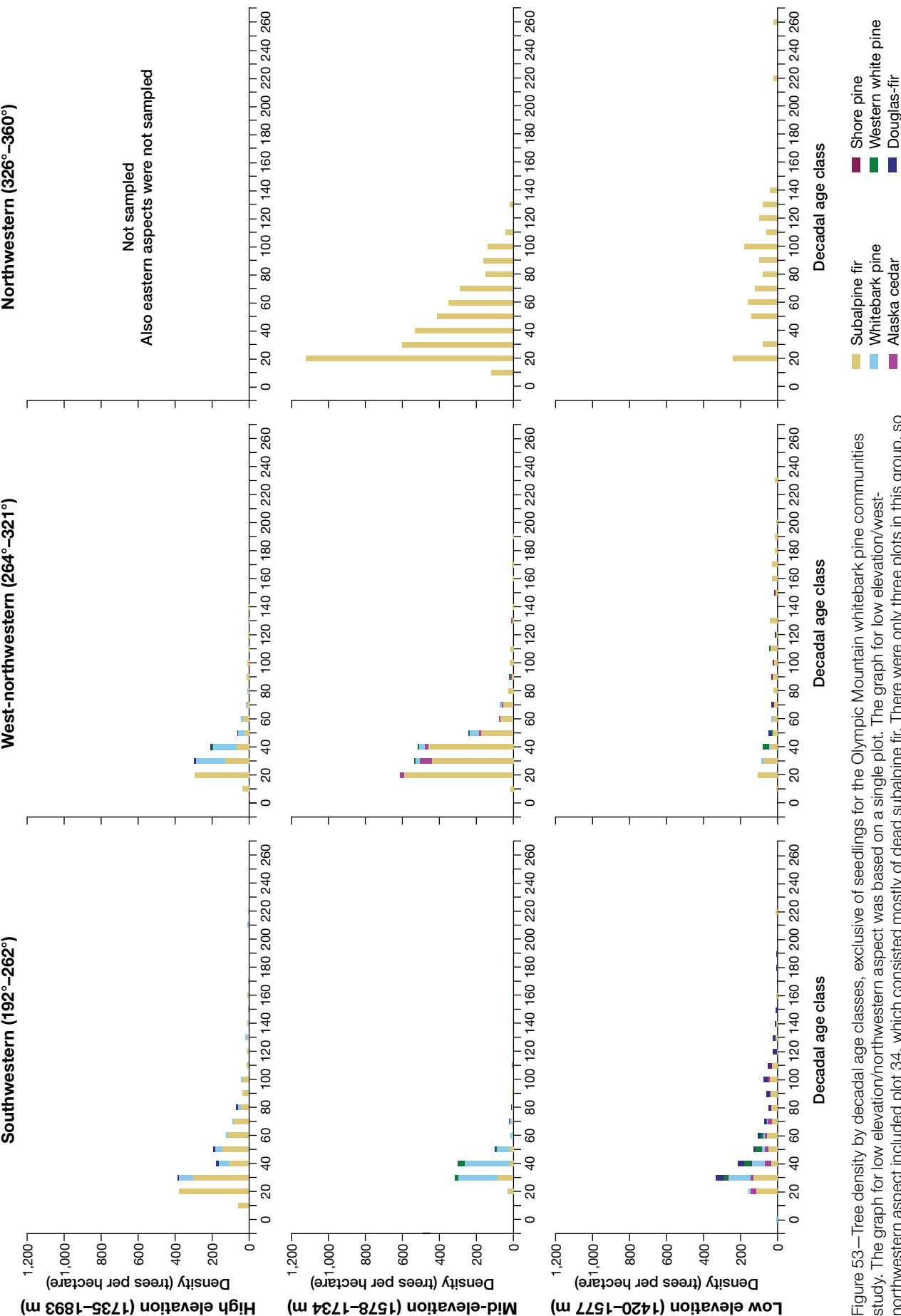


Figure 53—Tree density by decadal age classes, exclusive of seedlings for the Olympic Mountain whitebark pine communities study. The graph for low elevation/northwestern aspect was based on a single plot. The graph for low elevation/west-northwestern aspect included plot 34, which consisted mostly of dead subalpine fir. There were only three plots in this group, so this outlier plot tended to reduce the density of live subalpine fir more than it should because so many of the trees on this plot were dead. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

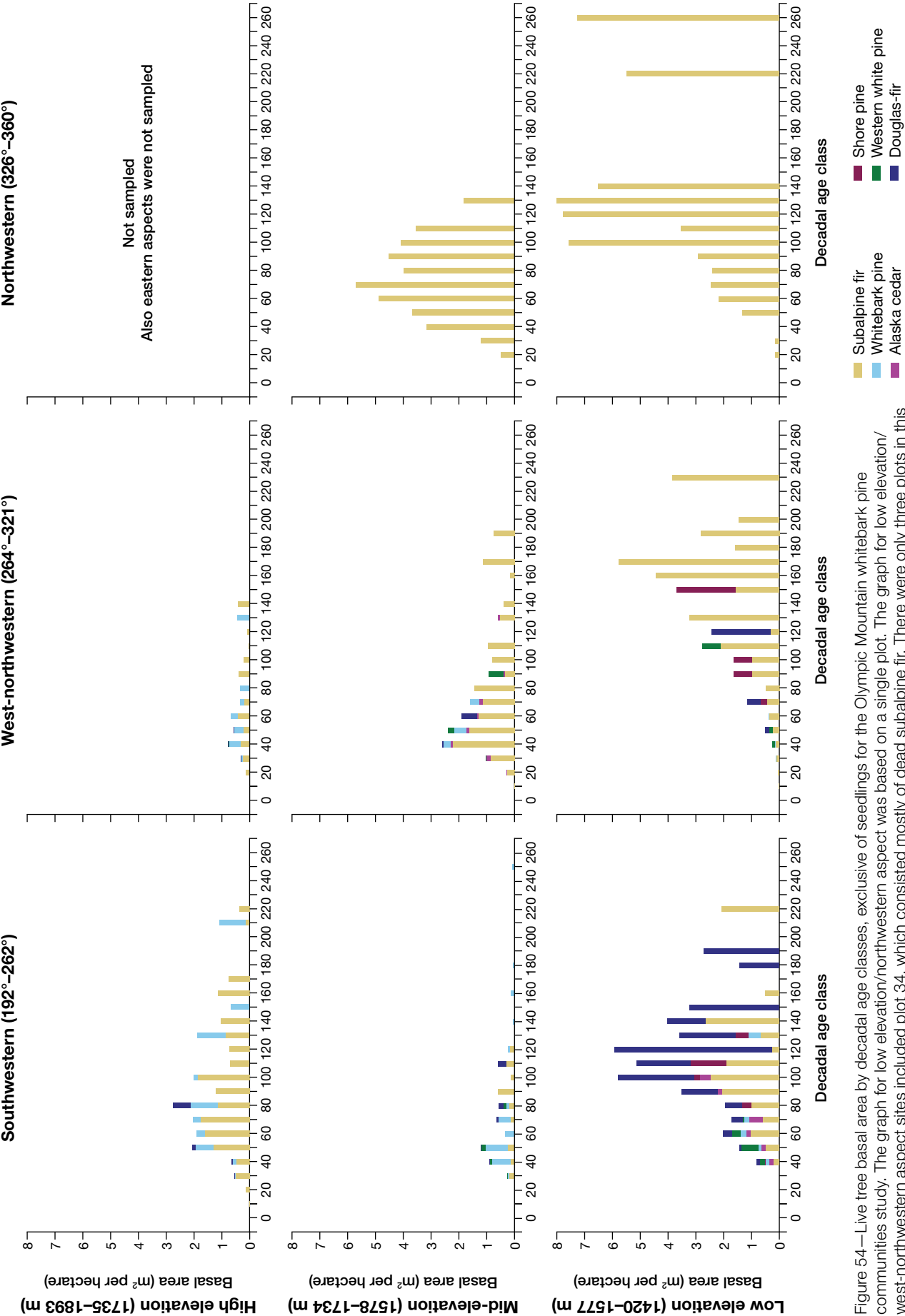


Figure 54—Live tree basal area by decadal age classes, exclusive of seedlings for the Olympic Mountain whitebark pine communities study. The graph for low elevation/northwestern aspect was based on a single plot. The graph for low elevation/west-northwestern aspect sites included plot 34, which consisted mostly of dead subalpine fir. There were only three plots in this group, so this outlier plot tended to reduce the basal area of live subalpine fir more than it should because so many of the trees on this plot were dead. Note that the lowest value for each age class is used as the label (0 = 0 to 10 years, etc.).

Table 27—Spearman correlation coefficients (*r*) and probability values (*P*) for correlations between density of trees (≥ 1.3 m tall) and elevation by species for the Olympic Mountain whitebark pine communities study

	Douglas-fir	Subalpine fir	Shore pine	Whitebark pine	Western white pine	Alaska cedar
Spearman <i>r</i>	−0.54	−0.39	−0.33	0.04	0.09	0.46
<i>P</i>	<0.01	<0.01	0.38	0.38	0.50	<0.01
Number of plots	10	31	5	27	13	2
Mean elevation (m)	1574	1673	1530	1690	1591	1592
Mean age (years)	77	60	33	47	50	50

Habitat Relationships for Seedlings (Reproduction)

- There were more subalpine fir seedlings (trees <1.3 m tall) than for any other species on all aspects, but most occurred in the understory of established stands in low light with low air and soil temperatures.
- There were more dead whitebark pine seedlings than dead subalpine fir seedlings.
- Whitebark pine reproduction increased with summer soil and air temperatures, suggesting an affinity for warm, extended growing seasons.
- We found little reproduction of other species.

There were significantly more live subalpine fir seedlings than live whitebark pine seedlings ($P < 0.01$). However, there were significantly more dead whitebark pine seedlings than dead subalpine fir seedlings ($P < 0.01$).

Subalpine fir seedlings were more numerous on all aspects in our study area than that of any other species (fig. 55). We found no difference in the number of live seedlings by aspect for whitebark pine ($P = 0.93$), but the difference by aspect was significant for subalpine fir seedlings ($P = 0.02$) (fig. 55).

Although all species appeared to decrease in density with increasing elevation, the differences were not significant (fig. 56). However, there was significantly more mortality in whitebark pine seedlings than in subalpine fir seedlings, most of which occurred at lower elevations ($P < 0.01$).

Whitebark pine seedling density was significantly and positively correlated with several summer soil and air temperatures (table 28). Its highest correlation was with mean monthly air temperature in September ($r = 0.46$), suggesting an affinity to locations providing extended growing-season temperatures in fall. Subalpine fir seedling density was positively correlated with three measures of overstory site occupancy (overstory canopy density, tree density, and basal area), indicating that most of the seedlings occurred in the understory of established stands; a negative correlation with ground-level PAR provides further support. These shady, subcanopy positions also tend to have low soil and air temperatures during summer, so subalpine fir seedling density was negatively correlated with air and soil temperatures as well.

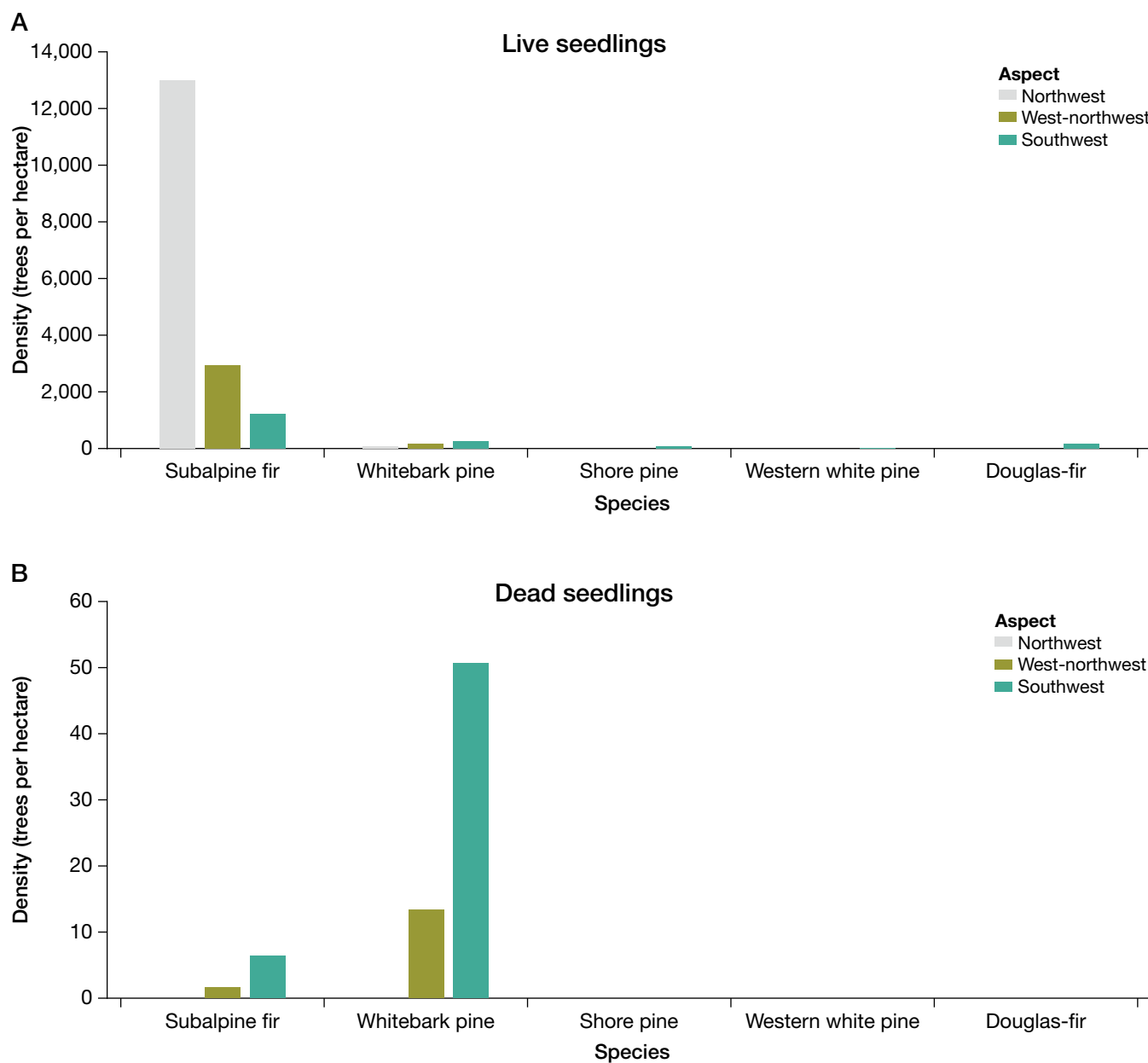


Figure 55—(A) Live and (B) dead seedling (<1.3 m tall) densities by aspect for the Olympic Mountain whitebark pine communities study. Subalpine fir was reproducing faster than any other species on all aspects in the study area. However, seedling mortality appeared to be greater for whitebark pine than for any other species.

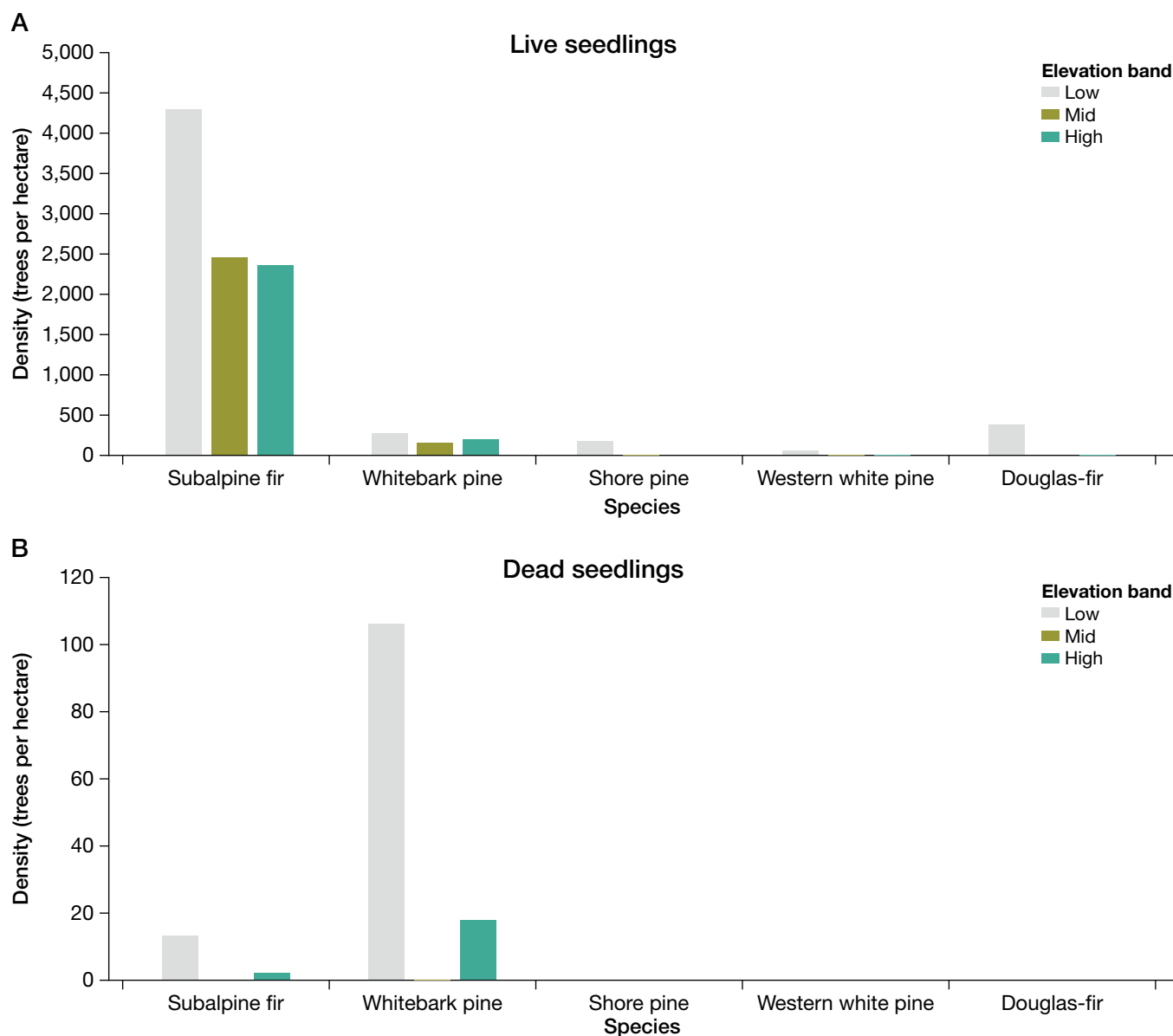


Figure 56—(A) Live and (B) dead seedling (<1.3 m tall) densities by elevation band for the Olympic Mountain whitebark pine communities study. Each band is one-third of the elevation interval between the lowest and highest plots.

Table 28—Pearson product-moment correlation coefficients (*r*) and probability values (*P*) for correlations between the total number of trees ≥ 1.3 m tall by species and light and temperature variables for all Olympic Mountain whitebark pine communities study plots

Species	Statistic	Ground-level PAR ^a	Overstory canopy closure ^b	Tree density ^c	Basal area ^d	Annual soil temp ^e	Growing season soil temp ^f	JJA air temp ^g	July air temp ^h	August air temp ^h	September air temp ^h
		PERCENT		TREES PER HECTARE	M ² PER HECTARE	DEGREES CELSIUS					
	<i>n</i>	36	40	40	40	36	35	36	22	22	22
Whitebark pine	<i>r</i>	-0.02	0.08	0.08	-0.06	0.32	0.42	0.36	0.39	0.45	0.46
	<i>P</i>	0.90	0.64	0.62	0.73	0.05	0.01	0.03	0.07	0.04	0.03
Subalpine fir	<i>r</i>	-0.58	0.55	0.45	0.39	-0.35	-0.42	-0.47	-0.49	-0.42	-0.29
	<i>P</i>	<0.01	<0.01	<0.01	0.01	0.04	0.01	<0.01	0.02	0.05	0.20

^a Ground-level PAR is the percentage of full-sun photosynthetically active radiation measured just above the ground.

^b Overstory canopy closure is the total percentage of canopy closure of all trees.

^c Tree density is the number of trees per hectare for trees ≥ 1.3 m tall.

^d Basal area is the basal area per hectare of trees ≥ 1.3 m tall.

^e Annual soil temp is the mean annual soil temperature.

^f Growing season soil temp is the mean soil temperature from when the soil first rose above 3.2° C in spring until it fell below 3.2° C in fall.

^g JJA air temp is the mean air temperature over the months of June, July, and August.

^h July air temp, August air temp, and September air temp are mean monthly air temperatures for these months.

Standing Dead Trees (Snags ≥ 1.3 m Tall)

- Where determinable, the cause of death for whitebark pines was always white pine blister rust, but there were no epidemic diseases affecting other species, and there was little bark beetle activity.
- Half the whitebark pine stems in the 10- to 40-cm-d.b.h. size class were dead, and whitebark pines appeared to die at more than twice the rate of subalpine fir.
- Although subalpine fir was currently (at the time of field data collection) dominant, the sum of live and standing dead whitebark pine trees in mid-elevation, west-northwestern aspects was second only to mid-elevation, southwestern aspects, meaning this was formerly an important area for whitebark pines.

When we were able to determine the cause of death for whitebark pines, the cause was always white pine blister rust (recorded for 7 percent of the standing dead trees). Similarly, we noted that 11 percent of western white pine had died of white pine blister rust. This determination can only be made for recently dead trees, and it is nearly certain that many, if not most, of the remaining standing dead trees of these species were also killed by white pine blister rust.

There were no epidemic diseases affecting any of the other species, and there was only scant evidence of bark beetle activity. In most cases, competition with larger trees appeared to cause mortality of other species. The only exception was on plot 34 where subalpine fir mortality was high in all diameter at breast height size classes. Subalpine fir was the only tree species on the plot, and most were dead. These trees appeared to have grown rapidly to large size before dying. The only reproduction recorded on the plot were subalpine fir germinants, suggesting that this species was not successfully growing to larger sizes. This dead patch was quite local and did not extend far beyond the plot. We were not able to determine the cause of mortality, but the site had wet soils, and we speculate that a hydrologic change may have killed these trees. There were many seeps and springs in the area including one at the edge of the plot. Another possible cause of mortality is the balsam wooly adelgid (*Adelges piceae*). One study suggests that subalpine fir in the Olympic Mountains is more susceptible to severe damage from this insect species than almost anywhere else in North America (Hrinkevich et al. 2016). However, the highly localized nature of the damage is difficult to explain if this is the cause. In any case, 88 percent of the standing dead subalpine fir trees in our sample that were ≥ 50 -cm d.b.h. came from this plot, and 40 percent of all the standing dead subalpine fir trees in our sample came from this plot.

Whitebark pine trees appeared to be dying at more than twice the rate of subalpine fir (table 29). It seems reasonable that most of this difference can be accounted for by white pine blister rust. Likewise, western white pine trees are also dying much faster than subalpine fir because of white pine blister rust. None of the other species had a large enough sample

Table 29—Number of live and standing dead trees (≥ 1.3 m tall) per hectare and the percentage of stems that were dead by species for the Olympic Mountain whitebark pine communities study

	Subalpine fir	Whitebark pine	Alaska cedar	Shore pine	Western white pine	Douglas-fir	Unknown
Live trees per hectare	903	297	36	5	37	36	0
Dead trees per hectare	127	109	0	3	10	3	6
Percentage of dead stems	12	27	0	38	21	8	100

size to identify trends in mortality (table 29). Shore pine also had a high proportion of dead stems, but the sample size was small for this species. In some areas, this species was over-mature and apparently dying out of the stand.

The overall proportion of live and standing dead trees by diameter at breast height size class was similar (fig. 57). However, what is apparent is the larger proportion of standing dead whitebark pine in the three smallest diameter at breast height size classes when compared to live trees. In each case, half or more of the standing dead trees were whitebark pine, but in each case, much less than half of the live trees were whitebark pine.

There were no whitebark pine trees >50-cm d.b.h., live or dead, in our sample and only a small number that were >40-cm d.b.h. The proportion of dead stems in the smallest diameter at breast height size class was less than half that of the next three larger diameter at breast height size classes (table 30). This observation should be tempered by the fact that smaller

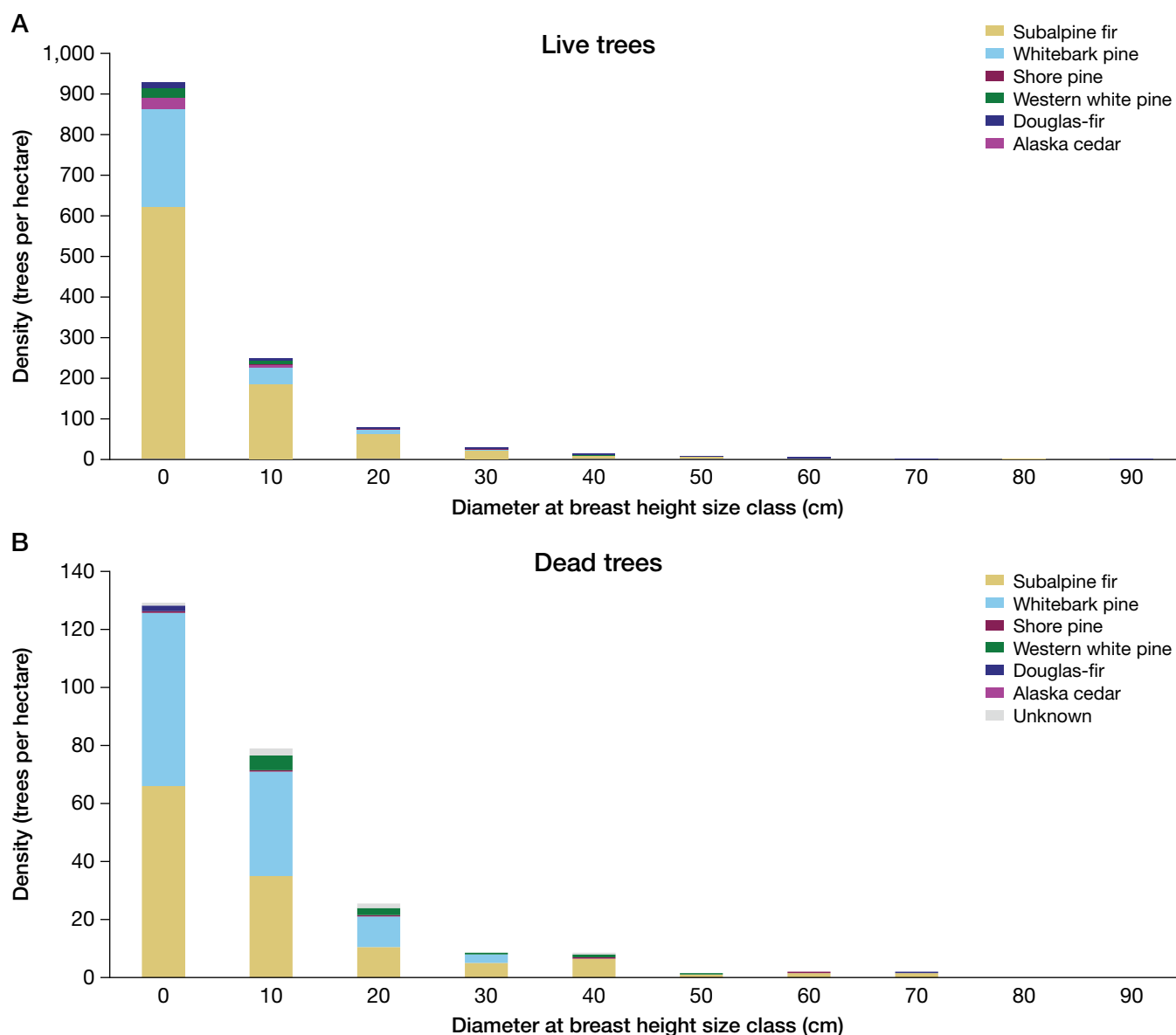


Figure 57—(A) Live and (B) standing dead tree (≥ 1.3 m tall) densities by diameter at breast height size class. It should be noted that 64 percent of the standing dead trees in the “unknown” species category were identified in the field to be of the genus *Pinus*. Note that the lowest value for each diameter at breast height size class is used as a label (0 = 0 to 10 cm, etc.).

Table 30—Mean live and standing dead whitebark pine and subalpine fir tree (≥ 1.3 m tall) densities by diameter at breast height size class for the Olympic Mountain whitebark pine communities study

Diameter at breast height size class	Live whitebark pine	Dead whitebark pine	Total whitebark pine	Live subalpine fir	Dead subalpine fir	Total subalpine fir	Dead whitebark pine	Dead subalpine fir
CM	TREES PER HECTARE						PERCENT	
0 to 10	242	60	302	622	66	688	20	10
10 to 20	41	36	77	184	35	219	47	16
20 to 30	10	11	20	62	11	72	53	15
30 to 40	3	3	6	20	5	25	55	20
40 to 50	2	0	2	7	7	13	0	50
50 to 60	0	0	0	6	1	7	—	14
60 to 70	0	0	0	2	2	4	—	43
70 to 80	0	0	0	0	2	2	—	100
80 to 90	0	0	0	1	0	1	—	0
All	297	109	406	903	127	1,030	27	12

— = undefined.

trees fall and decompose more rapidly than large trees, so we would not expect to find as many as in larger diameter at breast height size classes. Fully half of the stems from the 10- to 40-cm-d.b.h. size classes were dead. Except for the 40-cm-d.b.h. size class where the sample size for both species was quite small, and larger diameter at breast height size classes where whitebark pine was not represented, much higher proportions of whitebark pine were dead compared to subalpine fir.

The overall pattern of mortality across the landscape (fig. 58) resembles the overall pattern of live trees (fig. 53). There are two places where the proportionate equivalence between live and standing dead trees seems to break down. The low-elevation, west-northwestern aspect data consisted of three plots, including plot 34. Plot 34 was an outlier—nearly all the trees on the plot were standing dead subalpine fir. This skews the data to show a disproportionately large amount of standing dead subalpine fir compared to live subalpine fir or compared to other dead species. These standing dead subalpine firs still had bark intact, suggesting they had not been dead for long. Had we sampled the plot a few years earlier, these dead trees would have been alive, and the proportions of live and standing dead trees on this plot would be more like the other subalpine fir plots.

The other, more interesting difference was in the mid-elevation, west-northwestern aspect data where among live trees, subalpine fir was clearly the dominant species (fig. 53), but among dead trees, whitebark pine was far more numerous (fig. 58). This suggests that whitebark pine is being displaced in this area by subalpine fir. There are now more standing dead whitebark pine than live whitebark pine in this area, and it would appear from the numbers of trees that have died, that this was formerly important whitebark pine habitat.

The ratio of live to standing dead whitebark pine trees was not evenly distributed over the study area. The ratios for southwestern aspects were 1.5 for low-elevation, 5 for mid-elevation, and 2.3 for high-elevation areas. For west-northwestern aspects, the ratios were 3.9 for low-elevation, 0.3 for mid-elevation, and 11 for high-elevation areas. Thus, the

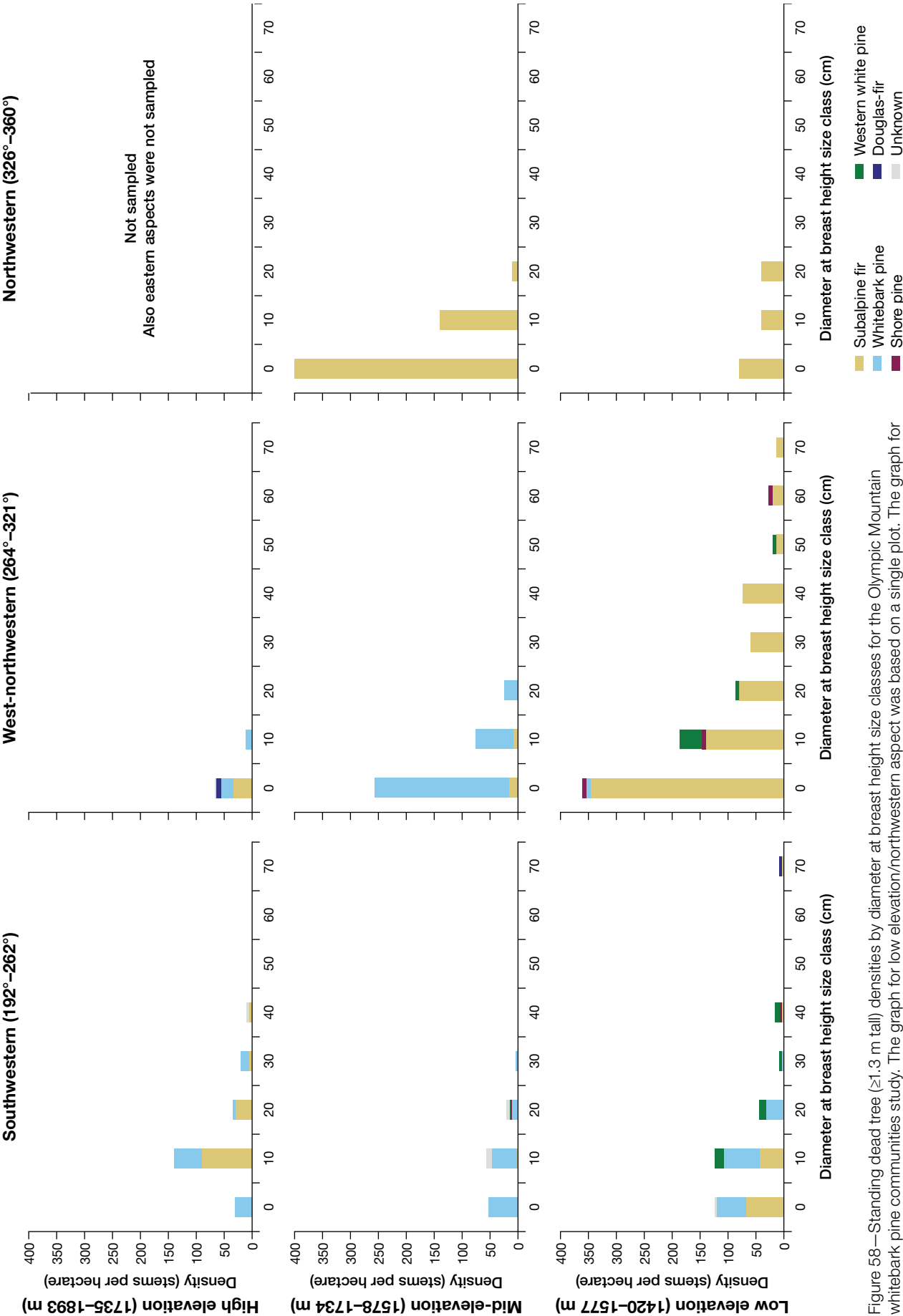


Figure 58—Standing dead tree (≥1.3 m tall) densities by diameter at breast height size classes for the Olympic Mountain whitebark pine communities study. The graph for low elevation/northwestern aspect was based on a single plot. The graph for low elevation/west-northwestern aspect included plot 34, which consisted mostly of standing dead subalpine fir. There were only three plots in this group, so this outlier plot inflated the standing dead subalpine fir compared to other dead species. Note that the lowest value for each diameter at breast height size class is used as a label (0 = 0 to 10 cm, etc.).

ratio was 5 to 22 times higher on other aspects and elevations compared to the mid-elevation, west-northwestern aspects. The density of whitebark pine trees and snags combined in the mid-elevation, west-northwestern aspects was the second highest at 444 trees per hectare (after the mid-elevation, southwestern aspects with 686 trees per hectare), so this was an important portion of the overall population.

Coarse Woody Debris

- CWD was mostly in decay class 3 and between 10 and 30 cm in diameter, mostly at low elevations, and with more from subalpine fir than from other species.
- Most of the identified mid- and high-elevation CWD was subalpine fir or whitebark pine; the largest proportion of whitebark pine CWD was in mid-elevations and on southwestern aspects.
- Plant communities with more CWD, such as the subalpine fir/thinleaf huckleberry plant association, tended to be dominated by older subalpine fir and grew at lower elevations on western aspects.

Most of the CWD that we found was in decay class 3, with the greatest volume between 10 and 30 cm in diameter (fig. 59). There was more subalpine fir CWD than any other species that could be identified; however, the unidentified group was also large (fig. 59).

The mean diameters of CWD pieces that we measured on our plots did not differ significantly by elevation ($P = 0.23$) or aspect ($P = 0.20$) (table 31). The differences between the mean diameters within elevation band or within aspect group were not significant.

There was a significant difference in the total volume of CWD among the combined elevation band and aspect group ($P = 0.02$) (fig. 60). Tukey HSD tests indicated that CWD volume at low-elevation, west-northwestern aspect sites was greater than at mid-elevation, west-northwestern aspect; mid-elevation, southwestern aspect; or high-elevation, west-northwestern aspect sites (fig. 60).

Overall, there was significantly more CWD volume at low-elevation than at mid- or high-elevation sites, which did not differ from each other (ANOVA: $P = 0.02$, Tukey HSD: $P = 0.05$) (fig. 61). CWD in decay classes 2 and 3 was abundant at low-elevation sites but was sparse higher up (figs. 59 and 61). Volumes of CWD in decay class 2 were marginally different among the elevation bands and aspect groups ($P = 0.06$), but there was a significant difference in volumes of CWD in decay class 3 ($P = 0.04$). There was significantly more CWD in decay class 3 at low-elevation, west-northwestern aspect; mid-elevation, southwestern aspect; and high-elevation, southwestern aspect sites. At mid- and high elevations, most of the identified CWD was from subalpine fir and whitebark pine (fig. 61). In mid-elevations, the proportion of whitebark pine was larger than elsewhere, and we found nearly all the whitebark pine CWD on southwestern aspects (fig. 59) at the mid- and high elevations (fig. 61).

The plant associations with more CWD tended to be dominated by older subalpine fir and grew at low elevations on western aspects (fig. 62).

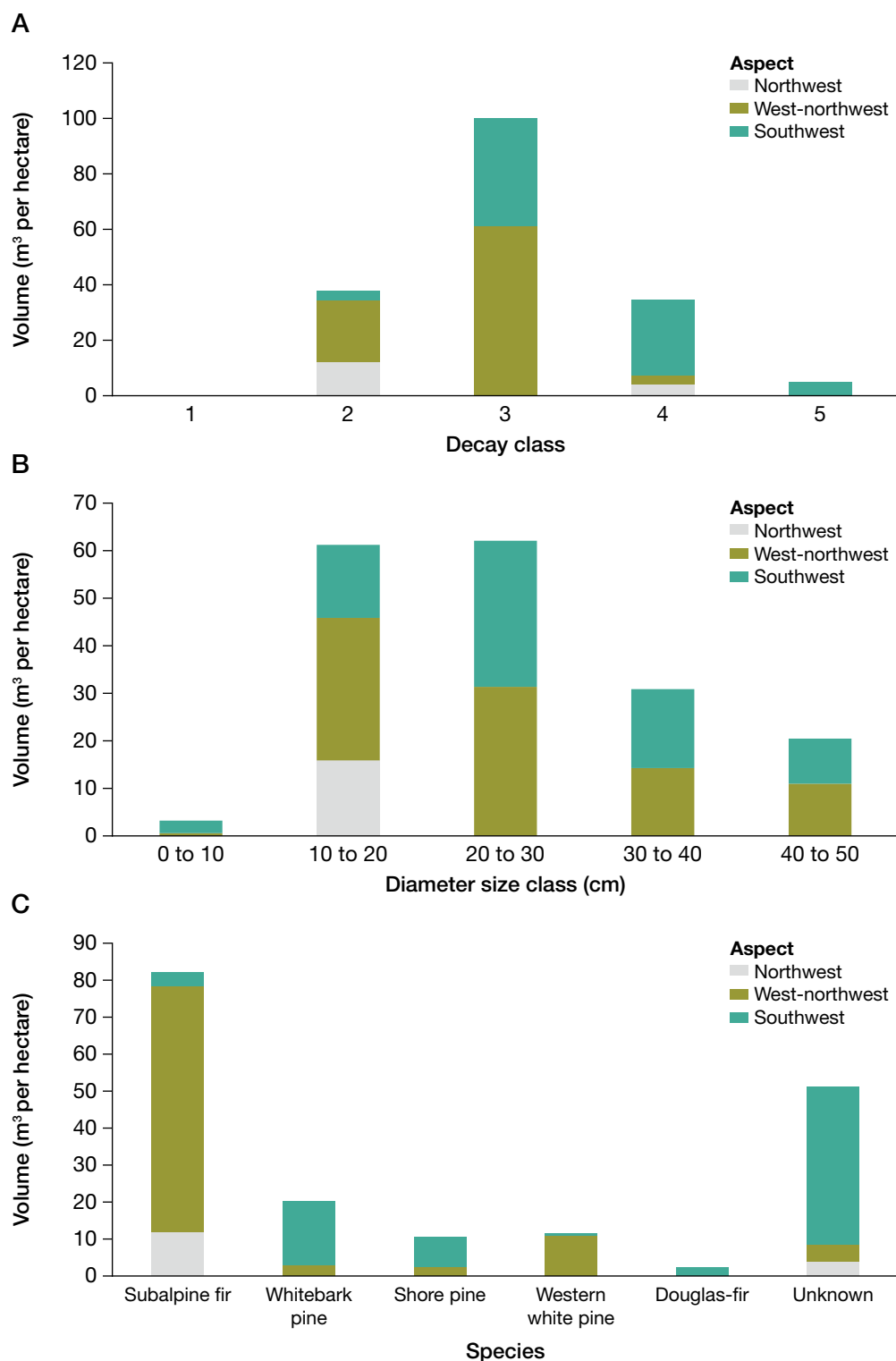


Figure 59—Mean coarse woody debris volume by (A) aspect and decay class, (B) aspect and diameter size class, and (C) aspect and species for the Olympic Mountain whitebark pine communities study.

Table 31—Mean diameter of coarse woody debris by elevation band and aspect group for the Olympic Mountain whitebark pine communities study

Elevation band or aspect group	n	Mean diameter	Standard deviation
CENTIMETERS			
Low elevation	35	19.7	8.4
Mid-elevation	21	16.3	8.8
High elevation	17	16.7	6.4
Northwest	4	11.0	0.8
West-northwest	33	18.8	7.7
Southwest	36	18.1	8.7

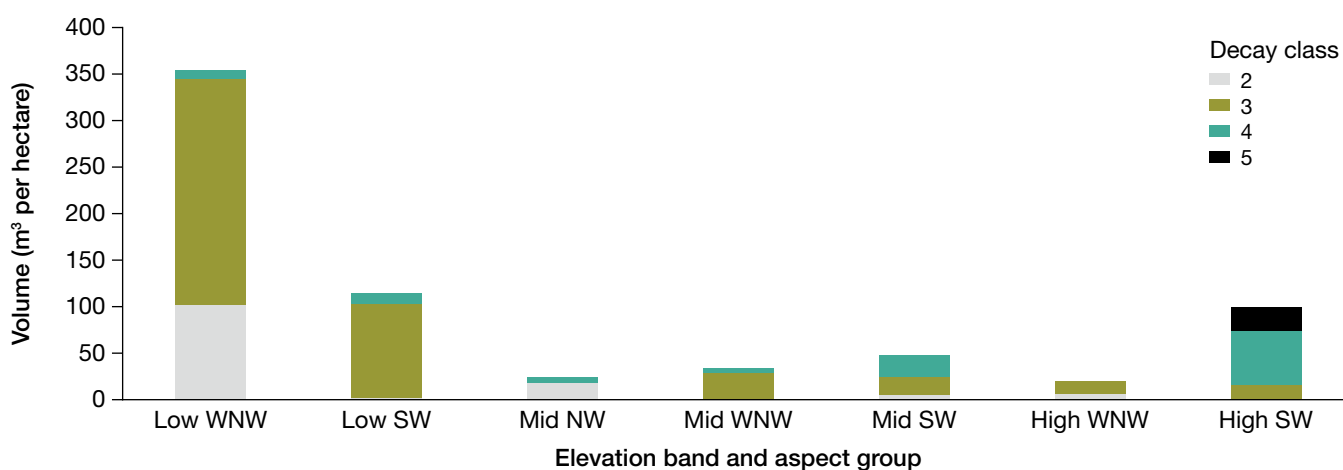


Figure 60—Mean coarse woody debris volume by aspect group and elevation band and decay class for the Olympic Mountain whitebark pine communities study. Coarse woody debris in decay class 1 was not detected. WNW = west-northwest, SW = southwest, NW = northwest.

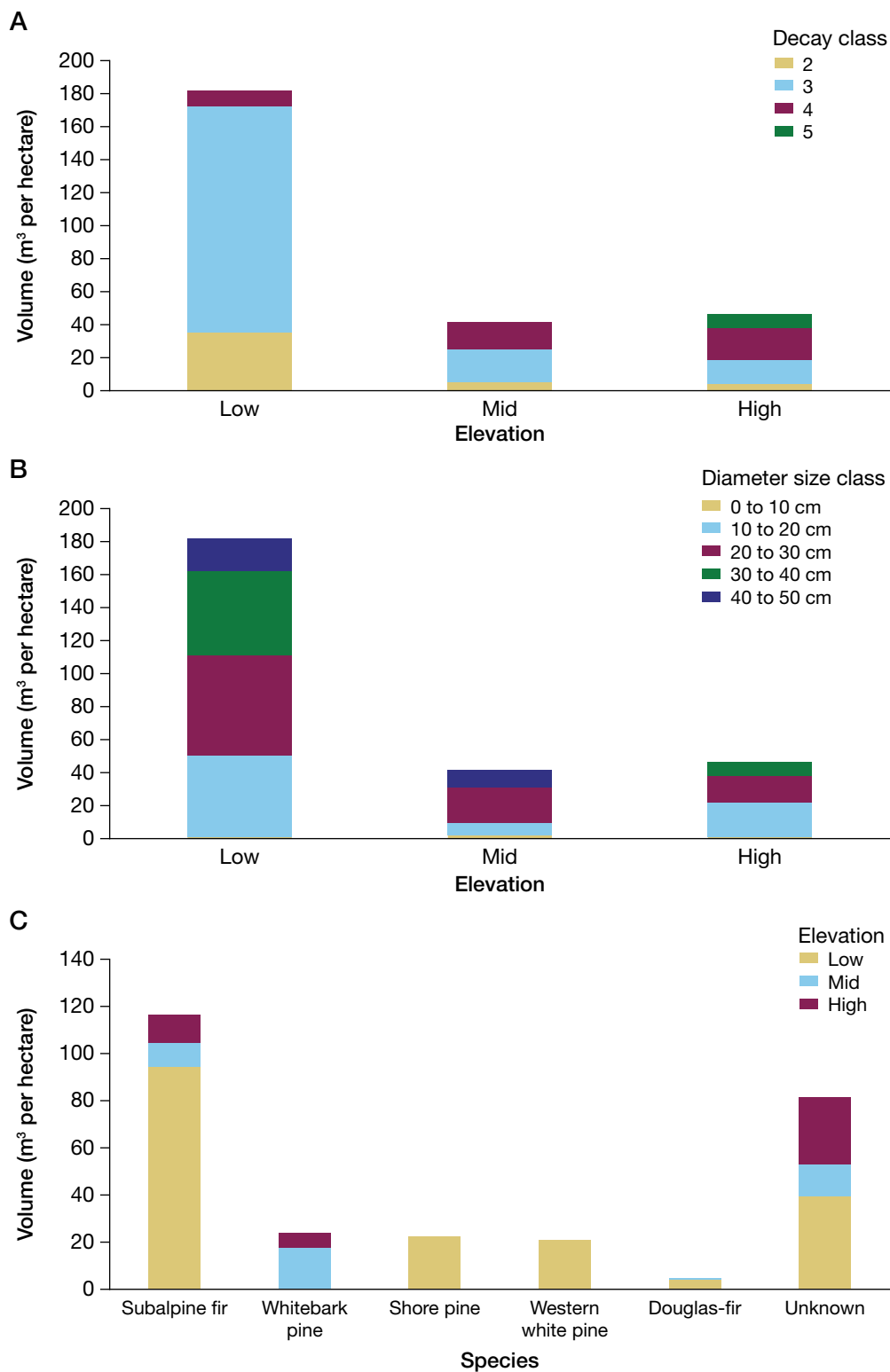


Figure 61—Mean coarse woody debris volume in three elevation bands by (A) decay class, (B) 10-cm diameter size class and (C) species of the Olympic Mountain whitebark pine communities study.

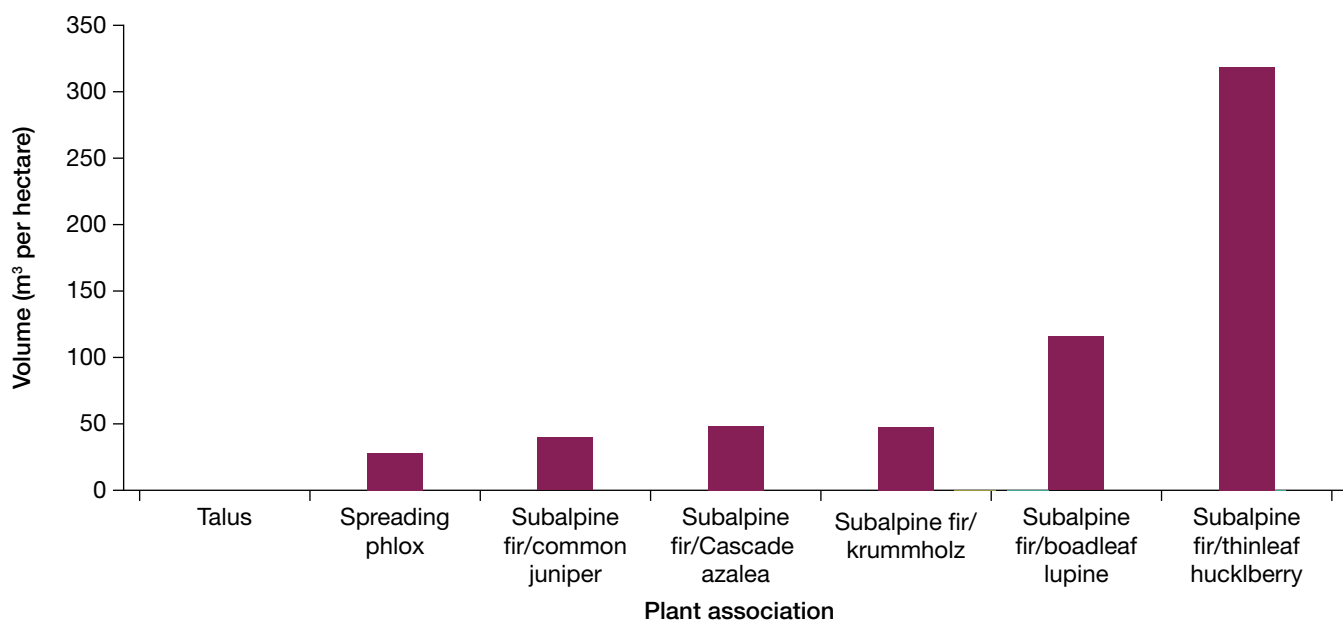


Figure 62—Mean coarse woody debris volume for each plant association having more than one plot in the Olympic Mountain whitebark pine communities study.

Surficial Organic Layer (Litter) Depth

- Litter depth ranged from 0.03 to 9.7 cm and was negatively correlated with mean monthly soil temperatures in July and August, and the mean growing-season soil temperature, and was positively correlated with total plot basal area and summer soil moisture.
- A multiple linear regression model including summer soil moisture and total plot basal area accounted for 61 percent of the variation in litter depth.
- Deeper organic layers tended to be in moister plant associations with older trees; however, one of the deepest layers was on a nonforest, black alpine sedge meadow community type.
- Although not directly measured, we found the densest organic layers in the black alpine sedge and subalpine fir/green alder community types and areas that were compressed by the deepest snowpacks.

Litter depth ranged from an average of 0.03 cm on a nonforested plot that was dominated by bracken fern to 9.7 cm on the subalpine fir/green alder community type plot (fig. 63). In our initial screening of potential explanatory variables, the five variables with strongest significant Pearson product-moment correlation coefficients were mean monthly soil temperature in July ($r = -0.57$), mean monthly soil temperature in August ($r = -0.52$), total plot tree basal area ($r = 0.52$), mean growing-season soil temperature ($r = -0.51$), and mean summer soil moisture ($r = 0.48$).

Weaker but still significant negative correlations included mean monthly soil temperature in June, slope steepness, and elevation. Weaker but significant positive correlations were number of frost-free days, subalpine fir basal area, and age of the oldest tree on the plot. Variables that were not significantly correlated with litter depth were mean monthly soil temperature in September, mean annual soil temperature, aspect, and mean annual air temperature.

The strongest multiple linear regression model resulting from combinations of the five strongest variables included the mean summer soil moisture measured over 5 years and total plot basal area (both variables were highly significant in the model) (adjusted $r^2 = 0.61$, $P < 0.01$, $n = 36$):

Litter depth (cm) = $-0.45942 + 0.29297 \times \text{mean summer soil moisture} + 0.03986 \times \text{total plot basal area}$

In figure 63, the plant associations or community types to the right are generally moister and with older forest than those to the left, although these relationships are not entirely straightforward. For example, the black alpine sedge plot is nonforested but wet, and the soil was mostly organic. The talus plots were dry because of a dearth of soil. The soil there consisted of organic material over boulders and cobbles in a few places and none in most of the area. The two plots that we are calling krummholz included krummholz trees within their boundaries, but most of the plot area was tundra. The non-krummholz portions of both of those plots had affinities to the spreading phlox community type.

Although we did not measure the density of the litter layer, it was obvious that litter density also varied. The litter layers of the black alpine sedge and subalpine fir/green alder community types were denser and more decomposed than those of the other plant associations or community types. In these cases, most of the organic material consisted of dark humus. Also, in plant associations or community types that accumulated greater snow depth, such as the subalpine fir/Cascade azalea plant association, the weight of the overlying snow greatly compressed the litter layer. If we had used dry weight as the measure of the amount of litter instead of depth, the order depicted in figure 63 would change somewhat, but an overall similarity would remain.

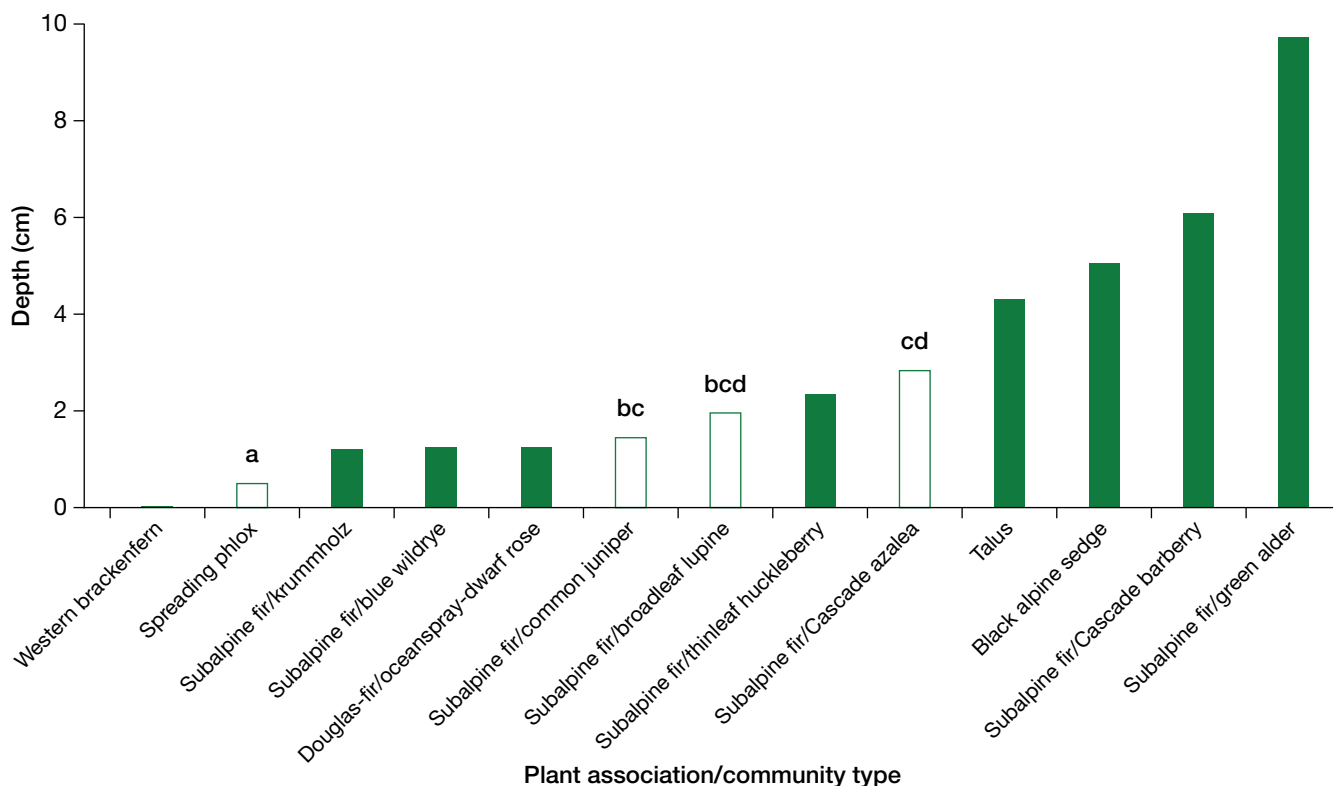


Figure 63—Mean litter depth by plant association or community type for the Olympic Mountain whitebark pine communities study. All the plant associations or community types that were identified are shown; however, only the plant associations or community types shown with white bars had enough plots (4 to 8) to conduct analyses of variance. Letters over the white bars indicate which plant association or community types did not have significantly different litter depths (e.g., the spreading phlox plant communities had significantly lower litter depths than subalpine fir/common juniper, subalpine fir/broadleaf lupine, and subalpine fir/Cascade azalea plant communities).

Foliar Nitrogen and Carbon

- Whitebark pine and subalpine fir, on average, had 1.3 percent foliar nitrogen and 47 to 48 percent foliar carbon, with subalpine fir having a marginally higher carbon-to-nitrogen ratio.
- Whitebark pine foliar carbon increased with direct solar radiation in June and summer soil moisture.
- Subalpine fir foliar carbon increased with minimum annual air temperature and decreased with elevation.
- In both species, foliar nitrogen tended to increase with warmer aspects and temperatures.

Whitebark pine and subalpine fir were not significantly different from each other in terms of percentages of foliar carbon and foliar nitrogen, and the levels in one species were positively correlated with the levels in the other species (table 32). Both species had 1.3 percent foliar nitrogen and between 47 and 48 percent foliar carbon. However, the carbon-to-nitrogen ratio for subalpine fir was marginally higher than for whitebark pine, although they still correlated.

Several environmental factors were significantly correlated with foliar nutrients (table 33). Whitebark pine percentage of foliar carbon was positively correlated with direct solar radiation in June, while subalpine fir percentage of foliar carbon was positively correlated with the mean of the 10 minimum annual air temperatures for each plot (i.e., more carbon with higher minimum temperatures) and was negatively correlated with elevation (i.e., less carbon at higher and cooler sites).

In both species, percentage of foliar nitrogen was negatively correlated with warmer aspects and the mean of the 10 maximum annual air temperatures for each plot. However, percentage of foliar carbon did not change significantly with these two variables. Generally, where both species had significant correlations, their correlations tended to be similar (table 33).

In whitebark pine, percentage of foliar nitrogen was positively correlated with several indicators of soil moisture, including summer soil moisture, length of snow season (first to last snowfall), and the amount of time the soil surface was at or below the freezing point, and was negatively correlated with slope steepness. Also, the presence of large trees and overstory canopy closure were negatively correlated with percentage of foliar nitrogen and were positively correlated with the carbon-to-nitrogen ratio in whitebark pine.

Table 32—Foliar carbon, foliar nitrogen, and carbon-to-nitrogen ratios (C/N) of whitebark pine and subalpine fir for 29 Olympic Mountain whitebark pine communities study plots and Pearson product-moment correlation coefficients (*r*) for the comparison of the values from each plot for each species and the *P* value associated with the correlation

	Whitebark pine	Subalpine fir	<i>P</i> for means	<i>r</i>	<i>P</i> for <i>r</i>
DRY WEIGHT PERCENT (STANDARD DEVIATION)					
Carbon	47.3 (0.90)	47.8 (1.11)	0.2078	0.64	<0.01
Nitrogen	1.3 (0.13)	1.3 (0.12)	0.2563	0.53	0.03
C/N	35.9 (3.60)	38.2 (3.90)	0.0643	0.49	0.05

Table 33—Spearman correlation coefficients for the correlations between percentages of foliar carbon and nitrogen and carbon-to-nitrogen ratios (C/N) and environmental and stand variables for the Olympic Mountain whitebark pine communities study

Variable	Whitebark pine			Subalpine fir		
	Carbon	Nitrogen	C/N ratio	Carbon	Nitrogen	C/N ratio
June direct solar radiation	0.43	—	—	—	—	—
Aspect	—	−0.65	0.55	—	−0.45	0.50
Mean of 10 maximum annual air temperatures	—	−0.59	0.55	—	−0.58	0.68
Mean of 10 minimum annual air temperatures	—	—	—	0.48	—	—
Elevation	—	—	—	−0.42	—	—
Summer soil moisture	—	0.65	−0.58	—	—	—
Snow season length	—	0.49	−0.54	—	—	—
Soil freezing	—	0.48	−0.56	—	—	—
Slope steepness	—	−0.44	—	—	—	—
Maximum diameter at breast height	—	−0.71	0.65	0.51	—	0.43
Subalpine fir diameter at breast height	—	−0.64	0.54	0.56	—	0.53
Whitebark pine age	—	−0.56	0.45	—	−0.51	0.58
Average tree diameter at breast height	—	−0.59	—	—	—	—
Overstory canopy closure	—	−0.47	0.43	0.41	−0.45	0.56
PAR at 1.3-m height	—	0.46	−0.48	−0.46	—	—

Notes: Correlation coefficients shown are significant at $P = 0.05$.

— = not significant; PAR = photosynthetically active radiation.

White Pine Blister Rust Infection of Whitebark Pine

CLUMP-LEVEL DATA—

For the 26 plots with clump data, there were 487 trees and 228 clumps. The average number of stems per clump was 2.14. There were 70 infected clumps, so 69 percent of clumps were healthy, and 31 percent were infected with white pine blister rust. The mean white pine blister rust infection severity code for infected clumps was 2.29 (SD = 1.19).

TREE-LEVEL DATA—

- 16 percent of stems were visibly infected with white pine blister rust.
- The mean white pine blister rust infection severity code for infected stems was 2.24 in 2010 and 2.9 in 2013 and 2016.
- Trees with more severe infections tended to be older, larger, and grew at lower elevations than uninfected trees.

For data collected during initial plot measurements, we surveyed 510 whitebark pine trees on 27 plots for white pine blister rust (table 34). There were 392 stems with no rust detected, so 84 percent were apparently healthy, and 16 percent were infected with white pine blister rust. The mean blister rust infection severity code for infected stems was 2.24 (SD = 1.18) (table 34). In 2013 and 2016, only 473 of these trees were resampled. In these years, 19 percent of trees were infected in each year, and proportionately fewer trees with severity code 1 infections and more with severity code 2 infections, which resulted in a higher mean blister rust infection severity code (2.9). On average, 20 (SD = 27) percent of

Table 34—Tree-level white pine blister rust infection severity code survey statistics for the Olympic Mountain whitebark pine communities study

Infection severity code ^a	Infected trees in 2010 ^b	Infected trees in 2013	Infected trees in 2016
	PERCENT		
1	43	2	2
2	5	33	33
3	36	41	41
4	16	24	24
Mean (SD)	2.2 (1.2)	2.9 (0.8)	2.9 (0.9)

SD = standard deviation.

^a For each stem forking below breast height (1.3 m), we assigned a rust infection severity code from 0 through 4, with 0 equal to no infection and 4 equal to severe infection.

^b The 2010 column refers to trees surveyed in 2007, 2008, and 2010. We surveyed each plot only once in that period. The total number of trees surveyed in the 2007 through 2010 period was 510 from 27 plots. In 2013 and 2016, we resampled 473 of these trees. We did not conduct the surveys for the percentage of crown dying and dead in 2007 through 2010.

the tree crown was dying, and 39 (SD = 35) percent was already dead among infected trees in 2013. In 2016, these numbers were 19 (SD = 27) percent dying and 40 (SD = 36) percent dead. Similar data was not collected for the 2007 through 2010 data.

Age, diameter at breast height, and elevation of trees (stems) in the five white pine blister rust infection severity codes differed significantly but not slope steepness, aspect, or summer soil moisture where they were growing (table 35). Trees with more severe infections tended to be older, larger, and grew at lower elevations than uninfected trees.

PLOT-LEVEL DATA—

- Mean white pine blister rust infection severity code, number of infected trees, and percentage of dead crown were highly correlated and gave similar results when correlated with other variables.
- All three white pine blister rust infection severity indicators were positively correlated with whitebark pine canopy cover, species richness, ground-level PAR, and canopy cover of alternate host species for white pine blister rust, which were present on 94 percent of our whitebark pine plots.
- Areas with higher summer temperatures (especially for soil and soil surfaces) tended to have more infections and more severe infections than cooler areas.
- The correlation between white pine blister rust infection severity code and the percentage of night temperature measurements that fell between the physiologically important range of 9 and 15 °C peaked in October, suggesting that white pine blister rust infection is more successful where higher night temperatures extended into October.

The Spearman correlation coefficient for the correlation between mean white pine blister rust infection severity code and number of infected trees on each plot was 0.83, and with percentage of dead crown, it was 0.92. Thus, it is not surprising that these three measurements gave generally similar results when correlated with other variables; however, they are not equivalent measures, so taken together, they facilitate a more robust interpretation of the results.

There were several significant correlations between blister rust infection severity indicators and plot physical and biological variables (table 36). All three of the rust infection severity indicators were positively correlated with whitebark pine canopy cover, plot species

Table 35—Mean tree age and diameter (tree-level variables) and elevation, slope steepness, aspect, and summer soil moisture (plot-level variables) by white pine blister rust infection severity code and analysis of variance probability values (*P*) for the Olympic Mountain whitebark pine communities study

Infection severity code ^a	n ^b	Age	Diameter at breast height	Elevation	Slope steepness	Aspect	Summer soil moisture
		YEARS (SD)	CENTIMETERS (SD)	METERS (SD)	PERCENT (SD)	DEGREES (SD)	PERCENT (SD)
0	392	46 (19)	6 (6)	1695 (97)	58 (10)	135 (27)	4.46 (1.30)
1	35	57 (37)	11 (9.3)	1694 (78)	61 (6)	134 (26)	4.12 (0.86)
2	3	58 (7)	13 (5)	1658 (144)	64 (5)	129 (21)	4.13 (0.83)
3	30	45 (10)	7 (7)	1620 (92)	58 (9)	131 (21)	4.27 (0.56)
4	13	65 (34)	16 (15)	1594 (76)	57 (9)	133 (24)	3.98 (0.56)
<i>P</i>		<0.01	<0.01	<0.01	0.41	0.96	0.33

SD = standard deviation.

Note: Means and standard deviations were calculated on a per tree basis for each white pine blister rust infection severity code.

^a For each stem forking below breast height (1.3 m), we assigned a rust infection severity code from 0 through 4, with 0 equal to no infection and 4 equal to severe infection.

^b n is the number of trees. These 473 trees came from 27 plots.

Table 36—Spearman correlation coefficients for the correlations between plot-level variables and indicators of white pine blister rust infection severity for the Olympic Mountain whitebark pine communities study

Variable	Infected trees	Mean infection severity code ^a	Mean percentage of dead crown
Whitebark pine canopy cover	0.73	0.71	0.70
Species richness	0.52	0.57	0.56
Standard deviation of ground-level PAR	0.44	0.38	0.41
Alternate host species canopy cover	0.37	0.49	0.55
Slope steepness	—	0.37	0.37
Summer soil moisture	−0.34		

— = not significant; PAR = photosynthetically active radiation.

Notes: Correlation coefficients shown are significant at *P* = 0.05.

^a For each stem forking below breast height (1.3 m), we assigned a rust infection severity code from 0 through 4, with 0 equal to no infection and 4 equal to severe infection.

richness, the standard deviation of ground-level PAR, and canopy cover of alternate host species for white pine blister rust. In addition, the number of infected trees was negatively correlated with summer soil moisture. The mean blister rust infection severity code as well as the mean percentage of dead crown were positively correlated with slope steepness.

We found alternate host species on most of our plots. We found giant red Indian paintbrush on 68 percent of our plots and sickletop lousewort on 43 percent of our plots. We found species of currants on 19 percent of our plots and other paintbrush species on 10 percent of our plots. Taken together, there were only five plots on which we found no alternate host species, and only two of those plots had whitebark pine on them. Thus, 94 percent of our whitebark pine plots had an alternate host species present, suggesting that infection sources are highly localized.

None of the correlations between white pine blister rust severity indicators and potential solar radiation variables were significant. The significant correlations between blister rust severity indicators and temperatures were all positive, but the number of correlations that were significant and the mix of air, soil surface, and soil temperatures varied by indicator. Even so, similar overall patterns appeared in each analysis (fig. 64). There were more

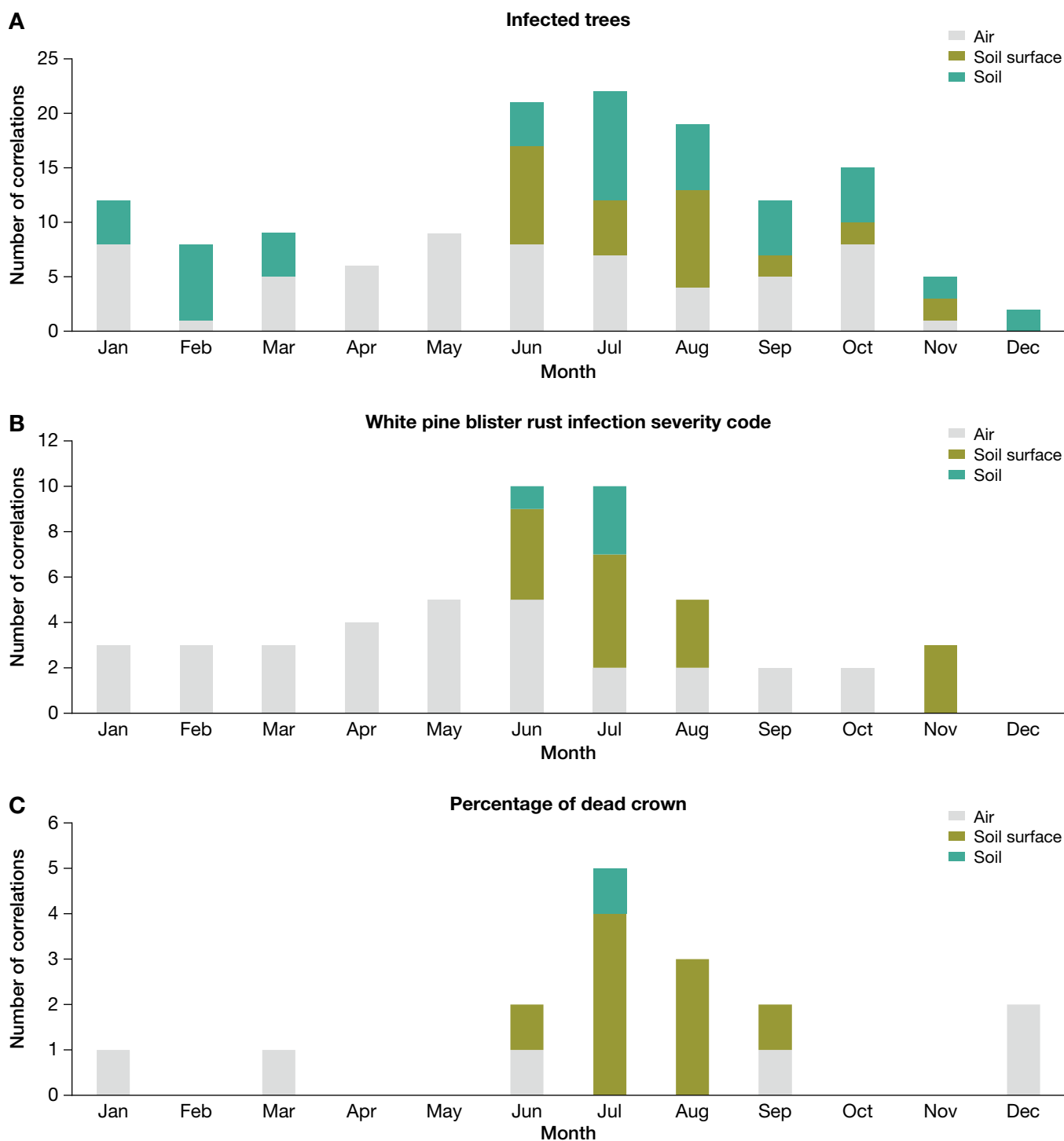


Figure 64—The number of significant correlations between three white pine blister rust severity indicators and 540 temperature variables by month for whitebark pine trees in the Olympic Mountain whitebark pine communities study. All the correlations were positive. Shown are the number of significant temperature variable correlations for (A) the number of infected trees on each plot, (B) the mean blister rust infection severity code assigned to each tree on the plot (0 through 4, with 0 equal to no infection and 4 equal to severe infection), and (C) the mean percentage of dead crown. We measured soil temperatures at 20-cm depth.

significant correlations with summer temperatures than with temperatures at other times of the year, and this was driven more by soil surface and soil temperature correlations than by air temperature correlations. Thus, warmer areas, particularly areas with higher summer temperatures, had more infections and more severe infections than the cooler areas. This was reinforced by the observation that infections of trees (as opposed to plot means) were significantly more severe at low elevations than at high elevations.

There were more significant correlations between mean white pine blister rust infection severity code and air temperatures than with soil surface temperatures, and fewest with soil temperatures. The significant correlations with air temperatures were equally divided between correlations with mean air temperatures and maximum air temperatures (fig. 65). There were no significant correlations between mean white pine blister rust infection severity code and minimum air temperatures, but the only significant correlations with soil temperatures were with minimums.

There were more significant correlations between mean white pine blister rust infection severity code and quarter-day 3 than with any other quarter-day, and most of those were with air or soil surface temperatures (fig. 65). The number of significant correlations for soil surface temperatures also peaked in quarter-day 3, and the number of significant correlations for soil temperature were symmetrical about quarter-day 3.

Thus, white pine blister rust was associated with places that had higher air, soil surface, and minimum soil temperatures, primarily in summer and fall months and especially during the afternoon hours.

Air temperatures at night between 9 and 15 °C are considered the most physiologically active for white pine blister rust basidiospore germination and germ tube growth (Hansen and Patton 1975). Both the mean night air temperature and the percentage of night air temperatures between 9 and 15 °C peaked in August (table 37). From there, they diminish to negative temperatures and infrequent occurrences by November.

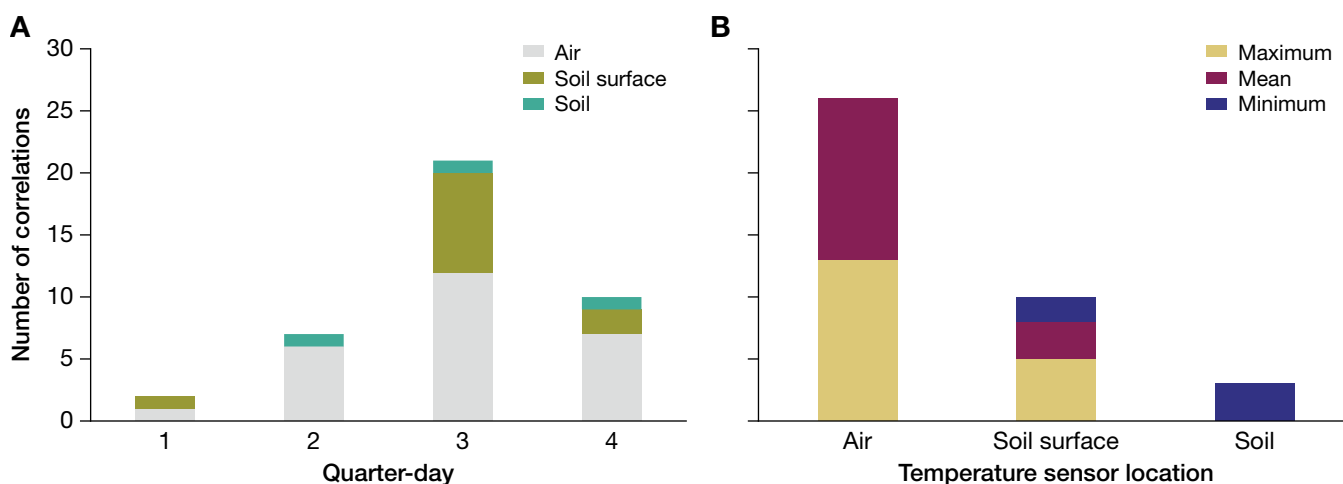


Figure 65—(A) The number of significant correlations between mean white pine blister rust infection severity code and mean air, soil surface, and 20-cm-deep soil temperature variables by quarter-day (of 432 possible). (B) The number of significant correlations between mean white pine blister rust infection severity code and minimum, mean, and maximum air, soil surface, and 20-cm-deep soil temperature variables (of 540 possible) for the 26 Olympic Mountain Whitebark Pine Communities study plots with quarter-day temperature data. Quarter-day 1 = 0000 to 0600, quarter-day 2 = 0600 to 1200, quarter-day 3 = 1200 to 1800, and quarter-day 4 = 1800 to 2400.

Table 37—Mean air temperatures and percentage of night air temperature measurements that fell between 9 and 15 °C and Pearson’s correlation coefficients (*r*) for the correlations between the mean percentage of night air temperature measurements that fell between 9 and 15 °C and the mean white pine blister rust infection severity code by month for the Olympic Mountain whitebark pine communities study

	July	August	September	October	November
Degrees Celsius	11.0	11.2	8.0	3.7	−1.5
Percentage between 9 and 15 °C ^a	45.0	50.9	36.2	17.0	0.5
<i>r</i>	−0.17	−0.12	0.05	0.37	0.01

^a Percentage of night air temperature measurements that fell between 9 and 15 °C were averaged over all whitebark pine plots and over quarter-days 1 and 4.

The correlation between mean white pine blister rust infection severity code and the mean percentage of night air temperature measurements that fell between 9 and 15 °C peaked in October, suggesting that white pine blister rust infection was more successful where higher night temperatures extended into October.

On average, the minimum air temperature did not reach the freezing point until October 27 on plots with ≥ 1 percent whitebark pine canopy cover (fig. 66). Although the pattern was similar for plots with < 1 percent whitebark pine canopy cover, the mean minimum air temperature was generally lower and fell below freezing for the first time on October 5.

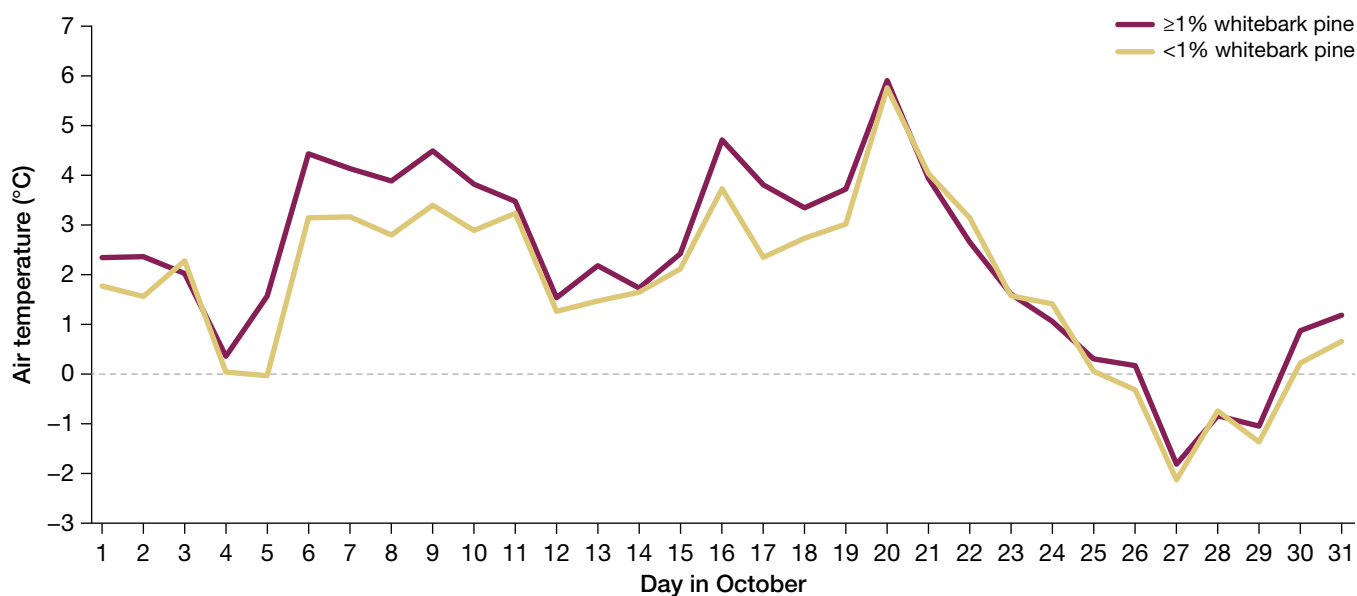


Figure 66—Mean minimum October air temperature for Olympic Mountain whitebark pine communities study plots with ≥ 1 percent whitebark pine canopy cover ($n = 24$) and for those with < 1 percent whitebark pine canopy cover ($n = 10$). Each plot mean was based on 2 to 5 years of data.

Fire and Establishment History

- We found no charcoal, fire scars, or charred bark on trees in our plots, and although we observed small amounts of bark char on some lower elevation Douglas-fir trees outside of our plots, we were unable to identify any fire scars on our core samples.
- A 132-cm-d.b.h. Douglas-fir with internal rot established between 1667 and 1808, but smaller Douglas-fir trees that were 75-, 84-, and 89-cm d.b.h. established around 1797, 1809, and 1808, respectively.
- The population structures of all the major tree species, except shore pine, were skewed to younger age classes and mostly increased after 1900.
- Although most tree species were present somewhat before the end of the Little Ice Age (around 1850), scattered whitebark pine trees grew at the highest elevations long before the end of the Little Ice Age, with one krummholz-form tree dating to around 1384.

We found no charcoal, fire scars, or charred bark on any of the trees in our plots. However, we observed small amounts of char on the bark of some Douglas-fir trees in the lower part of our study area outside of our plots, especially near plot 3. Several of these trees appeared to have healed scars, but in attempts to core sample these trees, we encountered rotten interiors. We noted that these Douglas-fir trees had many large, lower limbs, suggesting that they grew in the open throughout their lives.

The largest of these Douglas-fir trees that we attempted to sample was 132-cm d.b.h. However, we were only able to extract a core that was 15 cm in length with only 59 rings because of internal rot. Assuming the tree grew symmetrically and at the same rate throughout its life, this tree was around 340 years old and thus established around 1667 (fig. 67). However, both assumptions are unlikely to be accurate as trees usually have wider rings near the center than near the outer edge. We bored the tree on the uphill side on a steep slope, and the pith was likely offset toward the uphill side, so this tree was likely younger than our estimate. However, near this tree, we bored another tree that was only 75-cm d.b.h. and came close to the pith (we estimated one missing ring). The establishment date for this tree was around 1797 (fig. 67), so the larger, forementioned tree was at least this old. Two other nearby trees (84- and 89-cm d.b.h.) established around 1809 and 1808, respectively. The cores from these trees also passed close to the pith. These were the four oldest Douglas-fir trees that we found; however, observations from along the Dungeness River trail, within 2 km of the study site, suggest at least one much older age class of Douglas-fir is present in the area.

We were not able to identify an unequivocal fire scar on any of our core samples. We found five pitch-soaked rings on four Douglas-fir trees corresponding to the dates 1851, 1901, 1903, 1922, and 1948. There was no apparent reproductive cohort following any of these dates. If any of the pitch rings represented a fire, at least in the study area, the fire must have been a ground fire that failed to create new growing space. The Olympic National Forest has no historical records of a fire in this area.

The population structures of all the major tree species, except for shore pine, were skewed to younger age classes (fig. 67). The oldest shore pine tree that we aged established around 1788, an age that we have considerable confidence is accurate, as the core sample included the pith. Although this shows that its presence in the area pre-dates the end of the Little Ice Age, the shore pine population grew mostly after the end of the Little Ice Age, reaching a peak between 1901 and 1920. It has since been in reproductive decline. Douglas-fir and

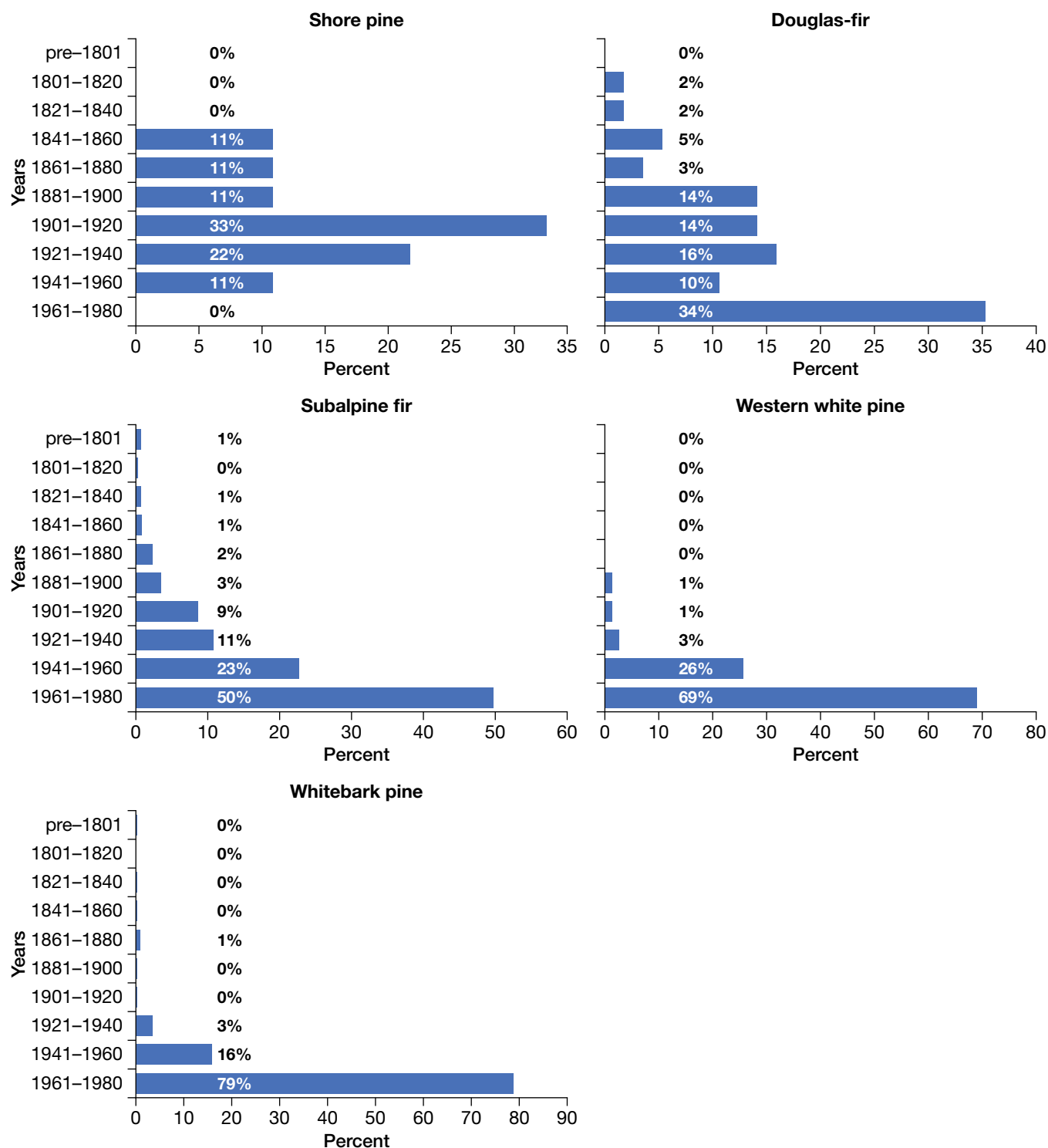


Figure 67—Percentage of core sampled trees (≥ 1.3 m tall) by 20-year age classes that originated on or before 1980 in the Olympic Mountain whitebark pine communities study. The numbers in each bar show the total percentage of the sample that germinated during that age class. Note that “pre-1801” is not a 20-year interval. Also, we do not show data for post-1980 as many, if not most, of the trees originating after 1980 would be too small to core sample.

subalpine fir were both present before the end of the Little Ice Age, but their populations mostly increased afterward in the mid- to late 1800s. In both cases, most of the population established after 1920. However, for western white pine and whitebark pine, most of the population has been recruited since about 1940. There were a few older whitebark pines in the area. One of the oldest whitebark pine trees in the study area that we core sampled established around 1774, and it grew on one of the lowest elevation plots. But the abrupt transition from a low percentage of trees before 1940 to a rapid increase after 1940 suggests that white pine blister rust eliminated most of the older trees, thus distorting the shape of the population curve.

Scattered whitebark pine trees appeared to have been present at even the highest elevations long before the end of the Little Ice Age. We found one krummholz-form tree dating to around 1384, although it was not on one of our plots and was outside of the main study area (fig. 68). This tree had a single, thick, short stem emerging from the ground, with the first major branches emerging less than 50 cm high. We estimated the date for this tree from a core sample taken from a low, horizontal limb about a meter from where the bole emerged from the ground. We estimated that the core sample missed the pith by 22 rings. This tree was the highest elevation tree that we core sampled (1936 m).

The basal area increments from this tree showed a pattern of accelerating basal area increment accumulation throughout the tree's life. This accumulation occurred in waves, with peaks around 1562, 1652, 1802, 1932, and 1982 (middle values of decadal increments are given). Each peak surpassed the previous peak in height. The low points in this chronology occurred in 1472, 1592, 1712, 1862, and 1952 (middle decadal values). The first (1422) and last (2002) intervals were low but undefined, as we cannot see the pattern beyond them. The highest peak (around 1982) is the most recent one that began from a low around 1952. Other than the brief low around 1952, the longest and steepest increase in basal area increment has occurred since the end of the Little Ice Age around 1850.

Subalpine fir also existed in the area in krummholz form, although we were not able to get ages from these trees that we felt closely approximated their true age. Nevertheless, none of their ages appeared to approach the age of the krummholz whitebark pine just mentioned.

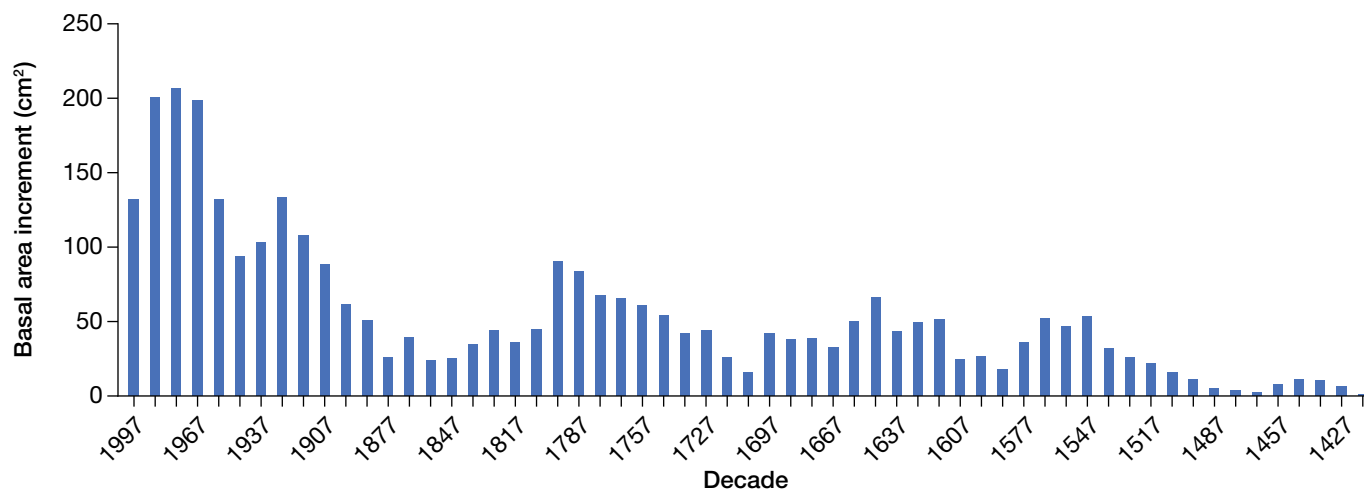


Figure 68—Decadal basal area increments for the oldest krummholz whitebark pine tree that we core sampled in the Olympic Mountain whitebark pine communities study. The horizontal axis is labeled with the first year of the decadal basal area increment.

Discussion

Physical and Climatic Environment

Geographic and Climatic Context

- The Olympic Mountains are a roughly circular range rising to 2300 m, with a maritime climate and prevailing southwest winds that create a rain shadow in the northeast where the study was located.
- Only about 8 percent of the total annual precipitation (1623 mm) occurs in summer.
- The steep, dissected, west-facing mountain ridge interacts with solar radiation and weather to strongly affect the distribution of temperature and moisture.
- The vegetation was typical for the northeastern Olympic Mountains and resembles northern Rocky Mountain vegetation more than southwestern Olympic Mountains vegetation.

The Olympic Mountains are a roughly circular range with a radius of about 50 km rising from sea level to peaks higher than 2300 m. The prevailing winds from the southwest create a decreasing precipitation gradient toward the northeast where our study was located. Within 88 km, rainfall decreases from 3353 mm at Lake Quinault, near the southwest base of the mountains, to 432 mm at Sequim, near the northeast base of the mountains. However, near sea-level cities scattered around the edges of the Peninsula, all report mean annual temperatures within 1.4 °C of each other. The combined effect of temperature and precipitation raises the elevation of comparable tree zones 730 m from southwest to northeast (Henderson et al. 1989).

Although generally maritime, these mountains harbor important climatic differences. The study area is on a deeply dissected, west-facing mountain ridge with dissected slopes varying from south to north. Although no east-facing slopes were present, the study area is otherwise typical of similar elevations in the rain shadow of the Olympic Mountains. Topography interactions with solar radiation and weather strongly affect the local distribution of temperature and moisture.

The climate of the study area is best characterized as a maritime rain shadow. The vegetation more closely resembles that of the northern Rocky Mountains than that of the southwestern side of the Olympic Mountains, yet the climate differs in important ways from that of the northern Rocky Mountains. To provide context for the study area climate, we compared the annual precipitation and range of temperatures of several Olympic Mountains locations to locations in the Cascade Range, Rocky Mountains, and the Black Hills in the continental interior (table 38). Generally, precipitation decreases and temperature range increases when going from a maritime climate to an interior continental climate, and the points we selected show this (table 38).

Within the Olympic Mountains, the temperature range changes little, while the precipitation declines sharply from southwest to northeast. However, east of the Olympic Mountains, the range of temperature increases, and the precipitation decreases. Note that the best comparison of Snowgrass Mountain to the three Olympic Mountains sites is with Mount Lawson, as both Snowgrass Mountain and Mount Lawson are on the western aspects of their respective ranges.

Although the Olympic Mountains have generally high precipitation, their summers are relatively dry. At the Dungeness SNOTEL weather station site, just 8 km to the northeast of our study site, the June through August precipitation was only 8 percent of the annual

total over a 20-year period. During the years of our study, this figure was closer to 11 percent, suggesting that we sampled in slightly moister than average conditions. This is in keeping with the Oceanic Niño Index of -5.5 ($SD = 5.5$) for the years of our study, indicating that most of the study occurred during moderate to weak La Niña conditions, with only one brief, weak El Niño (USDC NOAA 2021). In the Pacific Northwest, La Niña years tend to be cooler and wetter than average.

Temperature and moisture physiologically constrain plants and are implicated in their distributions and migrations. Our temperature data facilitated an understanding of the species distributions and vegetation dynamics within the study area. Although we studied a limited area, we are confident that our findings have wide application within the rain shadow of the Olympic Mountains. Moreover, much of what we investigated was of such a fundamental nature as to be of much wider interest. Thus, although we did not collect our data with the intent of understanding larger climatic phenomena or more widespread species and community relations, some may find use for our findings in those contexts.

Air Temperature

1.5- AND 3-METER-HIGH AIR TEMPERATURES—

- We attached temperature sensors to the north side of trees at 1.5- and 3-m heights and found that they agreed well with traditional methods.
- Our air temperatures compared favorably with Olympic Mountains SNOTEL weather station records.
- Some of our 1.5-m-high air temperature sensors, but not the 3-m-high sensors, were affected by tree wells in the snowpack, which partly insulated them from nocturnal reradiation.

Aboveground temperature measurements are usually taken in screened and ventilated enclosures, but because of wilderness area regulations restricting visually obvious hardware, we were required to take a minimalist approach. We enclosed temperature sensors in white PVC pipe endcaps nailed to the north side of trees and used natural screening provided by the tree to protect them from direct solar exposure. Where there were no trees, we were not able to obtain air temperature measurements, and no doubt, sunflecks occasionally struck our sensor enclosures in the trees. Minder et al. (2010) found iButton sensors installed in trees to be a satisfactory method, and removal of suspected sunfleck-induced temperature spikes had minimal effect on mean seasonal temperatures. Lundquist and Huggett (2008) showed that sensor measurements deployed in

Table 38— Geographic and climatic data for sites along a maritime to continental interior climate gradient from Washington State to South Dakota

Variable	Washington, Olympic, Mount Lawson	Washington, Olympic, Buckinghorse	Washington, Olympic, plot 23	Washington, Cascade, Snowgrass Mountain	Idaho, Rocky, Idaho Point	South Dakota, Black Hills, Black Hills
Annual temperature range ($^{\circ}\text{C}$) ^a	14.1	14.8	14.9	17.4	20.4	25.6
Mean annual precipitation (mm)	5004	2531	1632	2414	1296	495
Distance from previous site (km)	0	12	26	156	376	1010
Longitude	-123.59194	-123.46614	-123.14717	-120.95410	-115.95071	-104.29106

Note: The first three sites form a southwest to northeast transect over the Olympic Mountains, showing the development of the rain shadow. The next three sites lie along a gradient of increasingly continental climate from the Olympic Mountains to the continental interior. All sites are near to slightly above 1520-m elevation. All except the Buckinghorse SNOTEL weather station site and plot 23 are on the west side of a mountain range. All have a western aspect.

^a The annual temperature range is the difference between the highest and lowest mean monthly temperatures. All data provided was from the Parameter-elevation Relationships on Independent Slopes Model (PRISM), except for plot 23 temperature, which was measured data from the Olympic Mountain whitebark pine communities study. The value indicated by the PRISM model for plot 23 temperature was 14.4°C .

dense stands of trees were in close agreement with measurements from traditional instrumentation and that tree shade was more important than additional shielding. Thus, we believe our similarly deployed sensors provided temperature data of similar quality to more traditional methods.

By monitoring air temperature at two heights and choosing the lowest temperature, we minimized sunfleck error, as it is less likely that both sensors would be struck by sunflecks simultaneously. Most of our interpretations are based on monthly or longer averages, further minimizing effects of occasional errors. Our air temperatures compared favorably with four Olympic Mountains SNOTEL weather stations and a dataset from Mount Townsend, 9 km distant. Differences between our data and these other stations were mostly accounted for by differences in elevation and location.

The height above the surface of fixed temperature sensors changes in winter as snow accumulates, and there is a concern that as the snow approaches the sensor, its temperature may decline because of near-surface temperature inversion (Minder et al. 2010). However, our 3-m-high sensors recorded slightly lower temperatures than the 1.5-m-high sensors (0.5 to 0.8 °C lower in winter and 0.1 to 0.2 °C lower in summer). We believe the 1.5-m-high air temperatures, but not the 3-m-high air temperatures, were affected by the development of tree wells in the snow during times of deep snowpack, which partly insulated them from nocturnal reradiation. Most of the 1.5-m-high sensors were not buried by snow, as their daily fluctuation was like that at 3 m. However, on 11 plots, there was some reduction of daily fluctuation, suggesting shallow snow burial. The effect of the shallow covering of snow over these sensors and the partial enclosure by tree wells of others prevented efficient air exchange and radiational heat loss unlike at 3 m. By using the lower of the two temperatures—usually the more exposed 3-m-high sensor—we avoided the issues with snow at 1.5 m. We speculate that the summer difference also had to do with air exchange in that many of our stands had open canopies that permitted the ground to heat up but restricted efficient mixing of the air by the wind. The 1.5-m-high sensors, being closer to the ground, were less exposed to cooling winds than the 3-m-high sensors.

AIR MICROCLIMATIC OVERVIEW—

- The mean annual air temperature was 2.7 °C. February had the lowest mean monthly air temperature at -2.1 °C, and July had the highest mean monthly air temperature at 14.6 °C.
- Maximum annual air temperatures ranged from 29 to 31.1 °C, occurring in the lower third of the area on southwestern aspects in large canopy gaps.
- Minimum annual air temperatures ranged from -15.5 to -21.5 °C, occurring in the upper third of the area on steep, western to southern aspects and level benches with open canopies that allowed unobstructed nocturnal reradiation of heat.
- Variation in monthly air temperature among study plots was highest in May (SD = 1.1 °C), when cold air over snow under tree canopies contrasted with air over sun-warmed, bare soil in melted openings, and was lowest in December (SD = 0.61 °C) in a snow-covered landscape with weak low-angle sun.

Over three years, the mean annual air temperature over all plots averaged 2.7 °C, which according to the PRISM model (PRISM Climate Group 2020) was about 7 °C lower than at sea level along the Pacific Ocean to the west or Hood Canal to the east. SNOTEL weather stations at comparable elevations in the Cascade Range to the east on sites that are dominated by subalpine fir reported mean annual air temperatures of 1.6 °C (Rainy Pass), 1.8 °C

(Lyman Lake), and 2.7 °C (Corral Pass). A wetter site that was dominated by mountain hemlock in the Middle Fork Nooksack River drainage recorded a mean annual air temperature of 4.8 °C. All but the Middle Fork Nooksack River drainage temperature fell within the range of the mean annual air temperatures from our plots. The Middle Fork Nooksack River drainage temperature was 0.7 °C higher than our highest mean annual air temperature and was closer to the more maritime Buckinghorse SNOTEL weather station in the Olympic Mountains (5.1 °C). Thus, our study site was generally slightly warmer than comparable Cascade Range stations, which were farther from the ocean.

February was the coldest month at our site (mean = -2.1 °C, SD = 1.1 °C), and July was the warmest (mean = 14.6 °C, SD = 0.9 °C). The maximum air temperatures for each year ranged from 29 to 31.1 °C and occurred mostly in plots with large canopy gaps and in the lower third of the study area on western to southwestern aspects. This kind of gap environment is prone to elevated daytime air temperature (de Freitas and Enright 1995).

The minimum air temperatures for each year ranged from -15.5 to -21.5 °C and occurred between December 7 and January 16, from midnight to mid-morning. The open canopies on these plots allowed unobstructed nocturnal reradiation of heat, and all were in the upper third of elevations in our study area. These sites were on steep, western to southern aspects except for one on a nearly level bench subject to cold-air accumulation. Thus, open conditions prevalent on droughty southern and western exposures that led to the highest daytime air temperatures at lower elevations led to the lowest nighttime air temperatures at higher elevations.

The highest variation in monthly air temperature among study plots occurred in May (SD = 1.1 °C), and the lowest was in December (SD = 0.61 °C). Overall, the plot variation in air temperature was low compared to soil surface and soil temperatures (see below) because of convective mixing of the air. The difference between May and December was because of snow cover (complete cover in December and partial in May) and solar angle (low in December and high in May). The high-angle sun in May warmed exposed soil, which warmed the air above it, but the air over snow, especially under an overstory canopy, was cooled. These contrasting conditions created a wide range in temperature. In December, not only was nearly all the land surface covered with snow, but the low-angle sun was less effective in producing warming, so we found little variation in temperature at that time.

TEN MAXIMUM AND TEN MINIMUM AIR TEMPERATURES—

- Because the 10 maximum air temperatures, which occurred mostly in July and August, were broadly distributed over the sample area, they were unlikely to differentially affect plant communities.
- Because the 10 minimum air temperatures, more of which occurred in January than other months, were broadly distributed over the sample area, they were unlikely to differentially affect plant communities.

We examined the distribution of air temperature extremes with the 10 maximum and 10 minimum air temperature readings from each plot for each of the three years (thus 30 total measurements). Although July was the warmest month (mean = 14.6 °C), August had slightly more of the 10 maximum air temperatures (38 vs. 36 percent). The set of maximum air temperatures was broadly distributed over the sample area, suggesting that maximum summer air temperatures are unlikely to differentially affect plant communities in the study site.

Almost all the minimum air temperatures occurred from November through March. February was the coldest month overall (mean = -2.1°C), but more of the minimum air temperatures occurred in January than in any other month. The mean of the 10 minimum air temperatures was lower in December and February than in January (-16.2 , -16.8 , and -12.6°C , respectively). Thus, by this measure, December and February had the most extreme events, and February was also the coldest month. The measurements were broadly distributed over the sample area, suggesting that extreme winter air temperatures would not differentially affect plant communities within the study area.

FREEZING AIR TEMPERATURES—

Freezing air temperatures were most common in February (81 percent of the time) and were uncommon in summer. However, one plot in a cold-air drainage and two plots located on ridge summits froze occasionally during summer. The ridgetop plots had wide sky exposure and open tree canopies with considerable potential for nocturnal reradiation of heat.

FROST-FREE INTERVALS—

- The mean frost-free interval ranged from 48 to 132 days and averaged 94 days.
- The 10 lowest elevation plots included the 7 longest frost-free seasons as well as 3 frost pockets with frost-free seasons <90 days.
- Aside from these frost pockets, all the plots with a frost-free season <90 days (8 plots) were on exposed ridgetops and upper slopes and were among the highest elevation plots.
- The longest frost-free season was at plot 23, our lowest elevation plot and on a southwest-facing lower slope.

The mean frost-free interval over our study site ranged from 48 to 132 days (mean = 94 days). Plots with <90 -day frost-free intervals were either high in elevation or in an area where cold air accumulates. Elevation had a negative effect on temperature (discussed later in relation to lapse rates), but slope steepness was also important. Steeper slopes were generally warmer than flatter areas because cold, dense air flows off the slopes and accumulates in low or flat areas (Yoshino 1984). This was especially likely during cold, clear nights, culminating around sunrise. Exposed soil and especially snow, which is nearly a perfect blackbody radiator in the far infrared (Campbell 1977), rapidly radiate heat to clear skies. As this occurs, the air in contact with the soil or snow cools and flows downslope, concentrating in stream drainages and pooling behind blocking structures. Substantial frost pockets develop behind structures as low as 6 m (Fonda et al. 1971). As cold air flows off a slope, it is replaced by warmer air from above, but if the topography is flat, the cold, dense air accumulates in place (Yoshino 1984). As cold air moves downslope, it compresses and warms, thus it is rarely as cold or dense as cold air that forms in place on a flat area. In this situation, cold-air drainage tends to override rather than displace the locally generated cold air (Yoshino 1984). This was likely the situation on the bench plot (plot 18), while plot 7 was likely cold because of flowing cold air.

The shortest frost-free interval occurred on plot 7. Although the plot was on a moderately steep western aspect and in the lower part of the middle third of elevations, it was in the bottom of a talus-filled basin. Plot 8, with the third shortest frost-free season, was only 114 m away at nearly the same elevation as plot 7, but it was on a southwestern aspect. Trees in and around plot 8 likely deflected the cold air, which was not the case with plot 7. These slight differences contributed an additional 20 days to the frost-free season of plot 8 relative to plot 7. Plot 18 (with the eighth shortest frost-free season) was on a relatively flat, upper

slope bench and was colder in quarter-day 1 than plots above or below it. Another plot (plot 28) with a short frost-free season was on a steep, northwest-facing aspect near the top of a spur ridge (1828-m elevation). Aside from these plots, all the plots with a frost-free season <90 days (10 plots) were on exposed ridgetops and upper slopes and were among the highest elevation plots. The longest frost-free season was at plot 23, our lowest elevation plot situated on a southwest-facing lower slope. The 10 lowest elevation plots included the 7 longest frost-free seasons as well as 3 frost pocket plots with frost-free seasons <90 days.

SNOTEL DATA AND OTHER AIR TEMPERATURE COMPARISONS—

- Our mean annual air temperatures (1.1 to 4.1 °C) were slightly lower than those estimated by the PRISM model (2 to 4.5 °C).
- The mean annual air temperature at the Waterhole SNOTEL weather station site (3.6 °C) was comparable to plot 33 (3.3 °C), which is at similar elevation and aspect.
- Our study area lapse rate relationship accurately estimated the mean annual air temperatures of the Mount Crag and Waterhole SNOTEL weather station sites, but estimations for the Buckinghorse and Dungeness sites were 1 to 2 °C low.

Mean annual air temperatures ranged from 1.1 to 4.1 °C, slightly lower than PRISM model (PRISM Climate Group 2020) estimations of 2 to 4.5 °C. Waterhole was the SNOTEL weather station site most like our site in terms of elevation and vegetation. Its mean annual air temperature of 3.6 °C was comparable to plot 33 (3.3 °C), which is closest in terms of elevation and aspect. The other Olympic Mountains SNOTEL weather station sites were substantially lower in elevation and warmer than our study site and were warmer than our warmest plot. The mean annual air temperature over all plots in our study site (2.7 °C) was lower than the Waterhole SNOTEL weather station site record, which was expected because the Waterhole site is lower in elevation than the mean elevation of our plots.

By using our overall site lapse rate relationship to extrapolate air temperatures to these SNOTEL weather station sites, we were able to accurately predict the mean annual air temperatures of the Mount Crag and Waterhole sites. However, our estimations were 1.4 °C low for the Buckinghorse and 1 °C low for the Dungeness sites. The Buckinghorse SNOTEL weather station site is 26 km to the west-southwest of our study site, several prominent ridgelines away toward the ocean, and has one-third more precipitation, meaning that its climate is more maritime. On this basis, we expected its mean annual air temperature to be lower than at a comparable elevation in our site (Henderson et al. 2011). Although we cannot explain the discrepancy, we note that the PRISM model (PRISM Climate Group 2020) also estimated a mean annual air temperature that was 1.3 °C lower than the measured air temperature at the Buckinghorse site. It is also not clear why the estimation for the Dungeness site was not accurate, as this site was only 8 km to the northeast and on a western aspect. However, according to the PRISM model (PRISM Climate Group 2020), the Dungeness site has only 1320 mm of precipitation compared to 1810 to 2404 mm at our study site, so the climates differ importantly. The PRISM modeled mean annual air temperature for the Dungeness site was 4.75 °C, which is close to our estimation and 1.3 °C lower than the Dungeness SNOTEL weather station site records.

Soil Surface Temperature

SOIL SURFACE MICROCLIMATIC OVERVIEW—

- Soil surface temperatures fluctuated (−16 to 58.5 °C) more than air temperatures, and on average were 1.6 °C higher because snow-insulated surfaces remained within 0.2 °C of freezing, and in summer, surfaces in openings were warmed by sunlight.
- Soil surface temperatures varied greatly from May through October because of aspect and uneven tree cover, but the highest mean monthly soil surface temperature was 17.1 °C in July, with the highest soil surface temperatures (between 50 and 60 °C) potentially causing tree seedling mortality.
- Solar heating of the surface is an important driver of growing-season daytime air temperature in the open, but under tree shade, the soil surface temperatures followed air temperatures, except in spring when some plots were still snow covered and others were not, resulting in the greatest variation in soil surface temperature among the plots.
- The lowest soil surface temperatures occurred near dawn in November and December before a snowpack formed and again in March and April in the earliest melting plots.
- Under shallow snow, especially in October and November, soil surface temperatures dropped below 0 °C in response to cold air or radiational heat loss but rose only to 0 °C during warm days because of melting while the snow lasted.

Changes in soil temperature are controlled by the rate at which energy is exchanged at the surface of the soil. The surface interacts with both the air above and the soil below and is a heat source or sink to each depending on solar exposure, time of day, time of year, and weather. In this study, the surface was exposed to much greater temperature fluctuation than the air or deeper soil. Over all our plots, the extreme temperatures recorded in the 3-year soil surface dataset were −16 to 58.5 °C. Under dense vegetation, soil heat flux is small, and the net daily input of energy to the soil is near zero (Oliver et al. 1987). Under these conditions, heat travels through the surface downward when the soil is cooler than the air or upward under reverse conditions, but the flux will generally be small. However, where vegetation cover is sparse, the soil heat flux can contribute significantly to the soil energy balance (Oliver et al. 1987), downward under solar irradiation or upward under clear, cold night skies.

Our soil surface temperature sensors were shielded by white PVC pipe endcaps and in some cases by natural shade. We sought an indication of the environment experienced by emerging seedlings and small, low-growing plants. We reasoned that our PVC pipe endcaps acted similarly to pebbles on the soil surface. However, to the extent that this is not true, these measurements may be less useful. The PVC plastic is whiter, less dense, and smoother than the native rock and lighter than native soil or organic matter. However, it was in intimate contact with the soil materials, being typically half buried, and thus probably experienced relevant surface temperatures. Also, these issues affect mostly daytime performance when being struck by high-angle sun.

As with air temperature, soil surface temperatures were generally lower in year 1 than in years 2 and 3, but the differences in all 3 years were negligible from December through March. The mean annual soil surface temperature ranged from 4.1 to 5.4 °C, which was higher than the air or the soil at 20-cm depth. The highest mean monthly surface temperature was in July (17.1 °C) and the lowest occurred from December through March, which were all within 0.2 °C of freezing, reflecting the deep covering of snow. The mean annual

soil surface temperature averaged 1.6 °C higher than the mean annual air temperature both because the surface was insulated by snow in winter and because the surface in many plots was exposed to direct sunlight in summer, causing those surfaces to heat up much more than air temperatures. Under these conditions, solar heating of the soil is an important driver of daytime heating of the air. This is an important difference between shaded areas and open areas. Under tree shade, the soil surface responds mostly to air temperature when not covered with snow.

The soil surface exposed to sun heats up much more than the air, especially in summer, and is maintained at higher temperatures than the air by outflux of residual soil heat late into the evening. The highest soil surface temperatures we recorded were between 50 and 60 °C and occurred from mid-July through mid-August between 1300 and 1600. It seems likely that darker colored pebbles or soil might be heated to even higher temperatures, so these temperatures should be viewed as conservative estimates for the surface. Even so, the soil surface temperatures we measured are like temperatures associated with the onset of seedling mortality that others found, ranging from 52 to 66 °C (Helgerson 1990).

During winter, the soil surface is generally warmer than the air because of outflux of stored soil heat under snow insulation (Zhang 2005). However, the lowest soil surface temperatures occurred around dawn in November and December before a deep snowpack built up. Although air temperatures continued to decline into January, heat loss from the soil was restricted by a deepening snowpack. This is a principal reason why the mean annual soil surface temperature was 1.6 °C higher than the mean annual air temperature. In this environment, the minimum air and soil surface or soil temperatures do not co-occur, and none of the lowest soil surface temperatures occurred under a snowpack. Under a deep snowpack, the soil surface temperature was close to 0 °C. In late March and April, soil surfaces in the earliest melting plots were exposed to cold nights, resulting in the freezing of shallow soil. This is reminiscent of what was observed in November before snow accumulation, but by May, and especially by June, the nights were warmer and most soils and their surfaces were rapidly warming.

Under a shallow snowpack, soil surface temperatures decline in response to colder air above, but no matter how warm the air becomes, the soil surface temperature cannot rise over 0 °C so long as snow is present. At our study site, when the air temperature warmed during the day after an early season snowfall, the soil surface temperature warmed to 0 °C and remained at that temperature until the snow over the sensor finished melting. If at the end of the day there was still a shallow layer of snow over the sensor, the soil surface temperature would again drop below freezing until snowmelt resumed the next day or until a deeper layer of snow accumulated. Thus, soil surface temperatures dropped in response to cold air above the shallow snow or radiational heat loss from the snow surface but rose back only to 0 °C during warmer days. We frequently saw this decapitated daily pattern in October and November in response to the first few snowfalls. It usually occurred several times before the seasonal snowpack became deeper. However, fresh snow is a highly efficient insulator. Zhang et al. (2005) found in Alaska that although fresh snow cover was relatively shallow in November, it nevertheless insulated well because of its low density and thermal conductivity. Snow depths >40 cm had little additional insulative value (Zhang et al. 2005).

The snowpack at our site lasted into April on most plots, and the last plot (plot 18) melted out in June. The effect of snow varied considerably by plot and year. Year 3 was a light snow year, and on plot 7, the snow did not damp daily fluctuations for more than a day or two until

the first week of January. In the previous year, daily damping occurred shortly after the minimum recorded soil surface temperature in mid-November.

While soil surface temperature variation among plots was minimal when most of the landscape was under snow, it was considerable from May through October. Once the snow melted, various levels of tree shade, topographic exposure, surface materials of different thermal properties, and elevation came into play, creating a range of surface temperatures. Landscape variation was greatest during spring when some plots had melted out and others had not.

TEN MAXIMUM AND TEN MINIMUM SOIL SURFACE TEMPERATURES—

- The highest soil surface temperatures occurred on open plots with southwestern aspects (July and August, up to 58.5 °C) and were high enough to kill tree seedlings, contributing to the openness.
- Factors determining the maximum soil surface temperatures were season, aspect, and canopy closure.
- The lowest soil surface temperatures occurred in early winter around dawn in topographic lows where cold air accumulated and little solar radiation was received, or on windy, highly exposed plots with little vegetative cover where snow was slow to accumulate or removed by wind.
- The lowest soil surface temperatures mostly occurred in November before snow accumulation, but after November, the lowest soil surface temperatures were where shallow snow cover caused by wind removal or winter melting on warm aspects occurred.

The 10 maximum soil surface temperatures averaged 27 °C higher than those for air, and the 10 lowest soil surface temperatures averaged 5.5 °C degrees higher than those for air. Temperatures from May through October were among the set of maximum temperatures, but most occurred in July and August. We recorded soil surface temperatures as high as 58.5 °C on open-canopy plots with southern to western aspects, which are high enough to kill tree seedlings. Baker (1929) concluded that stem damage could occur at soil surface temperatures as low as 47 °C but became more general above 54 °C. Helgersson (1990) reviewed tree seedling stem damage literature and concluded that seedling stem damage began when the soil surface reached about 52 °C, mortality accelerated as temperature increased, and few seedlings survived soil surface temperatures above 66 °C. Daubenmire (1943) found that 70-day-old subalpine fir seedlings displayed evidence of heat injury with 6-hour exposures to 45 °C, which increased to high levels at 55 °C. Of 33 plots for which we had enough soil surface temperature data, 13 plots exceeded 55 °C. Kuramoto and Bliss (1970) found that soil surface temperatures in this range were not uncommon in Olympic Mountains mesic and dry, open habitats, which was also where we found them.

Daubenmire (1943) progressively exposed tree seedlings to a series of higher heat treatments, allowing them time to adapt physiologically. He made the reasonable argument that this partly emulated natural seasonal warming. In this experiment, 17 percent of the subalpine fir seedlings and 64 percent of Douglas-fir seedlings survived 70 °C treatments. Temperatures this high may occur in our study area on dark soils, but our methods did not detect them. However, this implies that the rate of seasonal and daily warming as well as the frequency of heating interruption by such things as shade dappling and physical land features may be important determinants for the level of mortality from surface heating.

We found that season, aspect, and total plant canopy cover were important factors in determining the maximum surface temperatures. Elevation, although significant along with these variables for estimating the mean annual soil surface temperature, was not important in determining the maximum soil surface temperature, which is strictly a summer afternoon phenomenon. Perhaps it plays a role over wider spans than the 364 m of elevation change in our study area. Thus, southwestern aspects with minimal shade produced soil surface temperatures potentially damaging to tree seedlings, and this could be one of the reasons these slopes remain unforested. It seems likely that our maximum soil surface temperatures are conservative estimates of actual surface temperatures, given that the soil surface temperature sensors were enclosed in white plastic casings. Thus, plants growing in these environments may experience even more damaging temperatures.

Our minimum soil surface temperatures were recorded during morning hours in topographic lows where cold air accumulated and where little solar radiation was received in early winter, although some also came from windy, highly exposed plots with little vegetative cover where snow was slow to accumulate or removed by wind. The set of minimum soil surface temperatures occurred from September through May, but most occurred in November, and the lowest soil surface temperature occurred in December. After November, minimum soil surface temperatures moderated to values around 0 °C through March, reflecting the accumulating snowpack. We believe the plots that registered minimum soil surface temperatures well below 0 °C after November had shallow snow cover either due to wind removal or a combination of low elevation and an exposed, warm aspect. In these cases, we saw decapitated daily fluctuation, and occasionally, complete melting resulted in full daily fluctuation. However, by March, snow effectively insulated all surfaces.

Soil Temperature

- Soil temperatures at 20-cm depth are biologically meaningful because a large proportion of roots are restricted to shallow soil depths in cold, montane environments.

Our soil temperatures at 20-cm depth provide the most accurate representation of the environment in which they were placed, as they were not subject to distortions associated with direct solar exposure. This is one reason why soil temperatures have been used in studies examining temperature effects on tree line processes (Körner and Paulsen 2004). The soil temperature recording at 20-cm depth is biologically meaningful. Li et al. (2011) found that root biomass decreased exponentially with depth in Tibetan plateau alpine soils and that 85 percent of the root biomass was in the top 20 cm of soil. We also observed many roots in the top 20 cm of soil, and our soil temperature measurements represent the primary rooting zone with important physiological implications.

SOIL MICROCLIMATIC OVERVIEW—

- The range of soil temperatures (−14 to 27 °C) was narrower than the range of air temperatures because of soil thermal mass, winter snow cover, evaporative cooling, and vegetative shade, and for the same reasons, soil temperatures change more slowly.
- The highest soil temperatures occurred on western and southwestern aspects with open to scattered overstories in quarter-day 4 from mid-July through mid-August.
- The lowest soil temperatures occurred mostly in the morning hours (0330 to 1200) in late fall or early winter, with little or no snow present and strong radiational heat loss.
- The soil temperature under the snow over all plots averaged 0.1 °C.

- The mean annual soil temperature was 1.2 °C higher than mean annual air temperature because the soil stores heat during summer and is insulated from heat loss by snow in winter.
- Frost penetration of the soil was minimal, but on a few plots, it occurred in late fall or early winter before the snowpack built up or after wind eroded or thaw reduced the snowpack.

Extreme air temperatures in our study area ranged from −21.5 to 31.1 °C, but soil is buffered from these extremes by its thermal mass and by snow cover in winter, evaporative cooling in spring, and vegetative shade in summer. Thus, the range in soil temperatures over all plots was −14 to 27.5 °C.

Winter soil temperatures from year 1 were slightly lower than those from years 2 and 3, like what was found for air and soil surface temperatures. During 3 years of record, the highest soil temperatures were recorded on plot 5 (26.5 to 27.5 °C) and plot 35, which tied the highest soil temperature on plot 5 in year 3. Plot 35 was about 230 m upslope from plot 5 on an entirely open, west-facing slope, while plot 5 was on a southwest-facing slope with a scattered but mostly open overstory. All these maximum temperatures were recorded between 2136 and 2236 Pacific Standard Time from mid-July through mid-August.

Soil temperatures at 20-cm depth changed much more slowly than air or soil surface temperatures. Each daily minimum temperature that we recorded was maintained for more than one consecutive 4-hour recording interval. Most of the lowest soil temperatures occurred in late fall or early winter when there was little snow cover but strong radiational heat loss. The lowest soil temperatures among the plots occurred mostly in the morning hours from around 0330 to 1200 and ranged from −14 to −0.5 °C. The lowest soil temperature in year 1 (−7 °C) occurred in mid-January on plot 12, a barren, windswept slope showing clear signs of solifluction. The soil surface sensor had a decapitated daily fluctuation pattern expressing temperature drops, but no rises above 0 °C for much of winter, indicating continuous but shallow snow cover, which was probably kept shallow by wind removal.

Deeper snow accumulated earlier in year 2, which was reflected by a soil temperature of −0.5 °C occurring continuously in November over 3 days on three plots. Several other plots recorded similar but slightly higher soil temperatures, signifying the arrival of an early heavy snowfall over most of the study area. The lowest soil temperature of −14 °C occurred on plot 7 on December 8 in year 3 and was maintained from predawn to late afternoon, suggesting there was little snow cover at this time. Air temperatures had been cold, reaching −20 °C in quarter-day 3 on December 7 and warming gradually to −11.5 °C by quarter-day 3 on December 8. All plots, including plot 7, eventually attained a deep enough snow cover to eliminate daily temperature fluctuations before snowmelt in spring. Thus, the temperature of the soil surface under the snow remained close to, but often slightly below, 0 °C for as long as deep snowpack was present and indeed until the last of it melted. The soil temperature under the snow at 20-cm depth averaged over all plots was 0.06 °C, which is similar to what others have found, including in colder climates (Zhang et al. 2005).

The mean annual soil temperature was 1.2 °C higher than the mean annual air temperature, and at the plot level, the lowest mean annual soil temperature was higher than the highest mean annual air temperature (mean annual soil temperature: 3.7 to 5.1 °C, mean annual air temperature: 2.1 to 3.5 °C). The reason for this is that the soil stores heat both from solar

exposure and from the air whenever the air temperature exceeds that of the soil during summer, but during winter, the insulation that snow provides prevents soil from cooling as much as the air. This effect is observable even where winters are much colder, such as on the north slope of Alaska where the mean annual air temperature was -13°C , but the mean annual ground surface temperature was only -5 to -10°C because of seasonal snow cover (Zhang et al. 2005). In Ottawa, Canada differences as great as 3.25°C were found between the mean annual air and 10-cm-deep soil temperatures (Gold 1963). This effect has interesting implications. For example, in Russia, increased snowfall associated with climate change contributed to warmer permafrost by limiting winter heat loss that had previously occurred under shallower snow (Park et al. 2014). Beyond the quantity of snow, the timing of its arrival and departure is important. Late arriving snow enhanced soil cooling by permitting greater pre-snowpack heat loss, and late melting snow contributed to cooler soils by delaying spring and summer warming (Park et al. 2014). In looking at combinations of fall dates of snow arrival and spring dates of snowmelt, early snow arrival with early snowmelt had the largest positive effect on soil temperature, increasing the mean annual ground surface temperature by up to 6°C on the north slope of Alaska, but late snow arrival with late snowmelt decreased the mean annual ground surface temperature by up to 3°C (Zhang et al. 2005).

In our study, frost penetration of the soil before the arrival of the snowpack was usually minimal, but where it did occur, once covered by a deep snowpack, the soil temperature moderated to near 0°C . On a few plots, frost penetration of the soil occurred in late fall or early winter before the snowpack built up or after a winter thaw that reduced or removed the snowpack. Goodrich's (1982) model suggests this is normal and closely reproduced the patterns that we saw.

TEN MAXIMUM AND TEN MINIMUM SOIL TEMPERATURES—

- Few of the 10 maximum soil temperatures occurred in June, likely because of high soil moisture, but most of the 10 maximum soil temperatures, along with the highest soil temperature, occurred in July, with fewer occurring in August and September.
- The number of plots contributing to the 10 minimum soil temperatures peaked asymmetrically in November after a sharp rise in October and then tapered off into winter as snow accumulated.
- The lowest soil temperatures occurred after November in areas with low vegetative cover close to the windward side of a ridgetop where snow was removed by wind and often showed signs of solifluction.
- When snow melted in spring, soils generally heated up rapidly, but soil freezing similar to what occurred in November occurred in some of the early melting, lower elevation plots during cold nights.

The 10 maximum soil temperatures closely followed the patterns but not the magnitudes observed for the 10 maximum soil surface temperatures. The greatest proportion of the 10 maximum soil temperatures and the highest monthly mean of those temperatures occurred in July, and more plots contributed to the 10 maximum temperatures in July and August than in September. This fits with both the peak mean air temperature, which occurred in July, and the high angle of solar radiation at that time. It might be expected for open plots that the highest soil temperatures would occur in late June as this is when solar radiation is the most direct; however, it is likely that soil moisture at that time of year prevents high

soil temperatures, and few of the 10 maximum soil temperatures occurred in June. We did not measure soil moisture in June, but when we measured soil moisture by the end of July and August, it was quite dry. The overall mean monthly soil temperature was similar to or slightly higher in August, but mean air temperature was beginning to trend downward, and the solar angle was decreasing, limiting extreme temperatures.

Whereas the 10 minimum air temperatures from November through March came from a broad base of plots in each month, the number of plots contributing to the 10 minimum soil temperatures peaked asymmetrically in November after a sharp rise in October, and then tapered off into winter. This pattern reflects the onset of plunging winter air temperatures in November before the snowpack, which is usually ephemeral until mid-November or even December or January in some years and on some sites. More of the 10 minimum soil temperatures occurred in November than in any other month, which is also when the most plots had low soil temperatures (i.e., widespread cooling). Thereafter, as snow began to accumulate, a few plots contributed sporadically and under highly specific conditions, such as late arriving snow or snow removal by wind or winter snowmelt. Although fewer in number, the lowest soil temperatures occurred in December and January under these special conditions when air temperatures were lower than in November. In general, the characteristics of these plots included low vegetative cover, proximity to a ridgetop, and west to southwest exposure (windward) predisposing them to snow removal by wind (fig. 69). They also tended to show signs of solifluction. Even when snow is not entirely removed by the wind, wind-packed snow is less insulative than fresh snow, and a shallow covering of high-density



Figure 69—Lingering snowbanks below the ridgeline on north-facing slopes showing the relation of snow removal and deposition by prevailing winds from the south and southwest in the Olympic Mountain whitebark pine communities study area. Snow removed from the south-facing slopes is redeposited on the north-facing slopes. Where removal was extreme, as with plots 35 and 12, winter soil temperatures became much lower than in other areas where the snowpack was deeper. Google Earth image, July 30, 2017.

snow with high albedo has been shown to cool the soil surface (Zhang et al. 1997). The plot with the greatest number of freezing temperatures in late fall was a ridgetop krummholz subalpine fir plot (plot 35), but plot 12 behaved similarly for similar reasons. These plots were in highly exposed south- to southwest-facing, upper slope positions. The prevailing winds come from the south and southwest, removing snow from the same slopes that are most likely to receive the highest winter solar radiation, which could result in further loss of snow. The snow removed from these slopes contributed to snowbank deepening on north- and northeast-facing slopes where solar exposure was least.

Snowpack was also slow to form on plot 7, and soil temperatures at 20-cm depth plunged to -10°C more than once as late as late January. It is difficult to see why this plot was so different in snowpack and thermal characteristics from surrounding plots, although it has a bouldery substrate and is in a severe cold-air drainage.

When snow melts in spring, soils and soil surfaces generally heat up rapidly but at different levels depending on their exposure to solar radiation, elevation, and cold-air drainage. However, we found that as the earliest lower elevation plots (plots 3, 22, and 23) began to melt out in March, April, and May, cold nights occasionally caused soil freezing to occur similar to what had occurred in November on some plots. With continued seasonal warming, this soon stopped, and by the time higher elevation plots melted out, this no longer occurred anywhere.

TEMPERATURE PULSE MOVEMENT—

- We estimated that daily summer temperature pulses moved through the soil at about 3.93 cm per hour.
- Our analysis suggests that roots are warmest and best able to grow or take up water and nutrients around or after sunset, as opposed to when heat stress is greatest.
- On average, the lowest soil temperature occurred at around 1015, so much of the morning light had been received while the roots were at their coldest.

The process of heat movement in soil is complex (de Vries 1987), and an understanding of this process requires detailed knowledge of the soil moisture profile, the thermal properties of the soil, and how these properties vary with depth (Oliver et al. 1987). We estimated that a daily summer temperature pulse moved through the soil at about 3.93 cm per hour based on one open-canopy plot (plot 3) and one closed-canopy plot (plot 32). This estimate is specific to local conditions but nevertheless helps to build an understanding of the daily patterns that we observed. Hausenbuiller (1972) gives rates of 3.8 to 5.1 cm per hour as being typical. Other things being equal, a moist soil may conduct heat 10 times more readily than when it is dry (Hausenbuiller 1972), and the thermal diffusivity of quartz is about 3 times that of clay minerals, which are both higher than organic matter (Wells et al. 1979). Thus, the rate of heat movement in soils can be highly variable from place to place and season to season but would be relatively constant within a given soil type and season. What our analysis tells us is that in these already cool soils, the time when roots are the warmest and best able to grow or take up water and nutrients, at least in July, is around or after sunset, as opposed to when heat stress would be greatest. As the soils in July were already relatively dry, this situation would become even more limiting as summer progressed, the soils further dried, and the heat transfer slowed even more. In the morning, the lowest soil temperature occurred on both plots, on average, at around 1015, so much of the morning light was received when the roots were at their coldest.

SOIL TEMPERATURE REGIME—

- The cryic soil temperature regime was present in most of the study area.
- The lower fringe of the study area is transitional between the cryic and frigid or isofrigid soil temperature regimes.

The cryic soil temperature regime was present in most of our study area. Soil temperature regimes are based on 50-cm-deep soil temperatures (USDA NRCS 1999), which we did not record. However, we used three methods of estimating the 50-cm-deep soil temperatures from our 20-cm-deep soil temperatures, which pointed to similar results. Two estimates indicated that two of our lower elevation plots on warm aspects with open canopies had a frigid soil temperature regime, but the rest were cryic. A third estimate supported this but also indicated that one other low-elevation plot on a warm aspect with a closed canopy had an isofrigid soil temperature regime. Thus, the lower fringe of our study area is transitional between the cryic and frigid or isofrigid soil temperature regimes. We expect that the frigid regime predominates downslope, whereas the cryic regime would be increasingly restricted to colder aspects and cold-air drainages and would eventually disappear from the landscape. Moreover, the isofrigid regime may be more common than the frigid regime under dense tree canopies below our study area.

Relationships Between Annual and Daily Temperature Patterns and Overstory Canopy Closure

- In summer, open areas had strong radiative heat loss in quarter-day 1, followed by near-neutral flux in quarter-day 2, strong solar heating in quarter-day 3, and progressive heat loss to the air in quarter-day 4; but soil heat flux was minimal under closed canopies except for modest input in quarter-day 3, followed by progressive nocturnal loss.
- Because fine root growth is faster when the soil is warm, we expect the greatest root growth and soil organism activity in quarter-days 3 and 4.
- In 2 of 20 plots, there were only 50 days when soil temperatures were conducive to root growth ($>9^{\circ}\text{C}$ at 20-cm soil depth), and 11 plots had fewer than 100 such days.
- Overstory canopy closure and elevation (both negative estimators) estimated the number of days in a year that the soil temperature was above the root-limiting 9°C threshold, suggesting the potential of shade in limiting root growth.

During the snow-free season, the average soil heat flux was neutral under closed canopies in all quarter-days except quarter-day 3, when there was a modest input of heat into the soil. In these shaded stands, soil surface temperatures closely followed air temperatures. Stands with open canopies were more dynamic, with strong radiative heat loss in quarter-day 1, neutrality in quarter-day 2, strong solar heating in quarter-day 3, and progressive heat loss in quarter-day 4. Because the soil surface strongly absorbed solar radiation, in open-canopy plots it often heated up sufficiently by quarter-day 3 to heat both the air above and the soil below. Some of this stored heat may continue to heat the air above in quarter-day 4, even as the afternoon heat pulse moves deeper into the soil. However, the soil surface is an efficient radiator of heat, and at some time in quarter-day 1, it is likely to be cooler than the air above it as conduction from deeper soil is slower than the radiative process. This is when dew or frost forms. Thus, the soil surface plays an important regulatory role in both air and soil temperatures. However, our study suggests that it takes about 4 hours for surficial heat to be delivered to 20-cm soil depth; so at that depth, the peak temperature occurs in quarter-day 4.

Mahmud et al. (2018) found that fine root growth followed a daily pattern that was closely associated with soil temperature. Root growth was fastest when the soil was warmest and slowest when it was coolest. Thus, we would expect the greatest root growth and soil organism activity would occur in quarter-day 3 and early in quarter-day 4 at our study area. Nagelmuller et al. (2016) found that root growth of three alpine species was limited by cold soils. Alvarez-Uria and Körner (2007) found that five of six species tested, including three coniferous species, grew hardly any roots below 6 °C, and 85 percent of all root growth occurred above 9 °C. In our study, 2 of 20 plots averaged fewer than 50 days that were warmer than 9 °C at 20-cm depth in the soil, and 11 plots had fewer than 100 days that were warmer than 9 °C at a soil depth of 20 cm.

A model incorporating overstory canopy closure and elevation estimated the number of days in a year that the soil temperature was above 9 °C (table 5). Each variable had a negative relation. This suggests the powerful role of shade in this ecosystem in driving ecological outcomes and thus succession. Another factor, aspect, which has been similarly implicated in other analyses, was not a significant factor in this analysis, but this is likely because of the limited arc of aspects available in our study area.

In highly maritime climates around the world, such as the Cairngorms of eastern Scotland and Mauna Kea in Hawaii, the temperature at which the tree line occurs is about 3 °C higher than in temperate continental climates and thus at correspondingly lower elevations (Körner 1998). The windward side of the Olympic Mountains has a highly maritime climate and a tree line at around 1067-m elevation (Henderson et al. 2011). But in the maritime rain shadow of the Olympic Mountains, the tree line occurs above 1524-m elevation (Henderson et al. 1989, 2011). By using relationships from Henderson et al. (2011), the mean annual air temperature at 1067 m on the windward slopes of the Olympic Mountains would fall between 5.1 and 5.4 °C, which is 2.4 to 2.7 °C higher than the mean annual air temperature at our study area (mean elevation 1627 m). At our study area, the tree line is indistinct and lower on south-facing slopes than north-facing slopes, but on average, the study area appears to straddle it. Thus, the tree line occurs at lower elevations and higher temperatures on the windward side of the Olympic Peninsula than on the lee side, suggesting the lee side is somewhat less maritime in nature than the windward side. However, as already discussed, the principal difference between these portions of the Olympic Mountains is precipitation, not temperature, suggesting that soil drought and temperature seasonality related to differential snowmelt are important. This is likely why the tree line appears to be lowest on the south-facing slopes in our study area.

Körner (1998) reviewed the literature on the relation between alpine tree lines and temperature and elevation around the world, concluding that the mean growing-season soil temperature was the strongest estimator of tree line elevation because of root growth limitation. Körner and Paulsen (2004) found that climatically driven tree lines worldwide are associated with a seasonal mean ground temperature under an overstory canopy of 6.7 °C (range of 6.4 to 7.8 °C), also suggesting that temperatures this low inhibit root growth. They used soil temperatures at 10-cm depth in a season bracketed by first occurrences of 3.2 °C under tree shade in spring and fall. They found that at the tree line, soil temperatures in the open were high enough for root growth of most plants, but as trees grew, their shade cooled the soil at their bases, limiting their growth. This, they say, prevents forest canopy closure, resulting in parklands, and in progressively cooler areas, eventually prevents trees from growing at all. However, de Andrés et al. (2015) provide evidence that tree lines vary with a

combination of soil temperature and soil moisture in drier areas, so soil drought in combination with cool soils may contribute to even lower tree lines in some areas, which is what we found on south- and west-facing slopes in our study area. Much of the study area on warmer aspects was open, even though soil temperatures as low as those suggested by Körner and Paulsen (2004) did not occur. Thus, we conclude that these open areas must be limited in some other way, and we suspect that soil moisture plays an important role. Our summer soil moisture data revealed areas of relative drought that had few trees and so circumstantially support this argument.

Using similar methods as Körner and Paulsen (2004) to calculate the mean growing-season soil temperature for each of our plots produced two distinct clusters of data: a cooler cluster of 6 plots with high percentages of canopy closure (temperature and canopy closure means: 8.2 °C; 82.5 percent), or closed canopy, and a warmer cluster of 28 plots with low percentages of canopy closure (temperature and canopy closure means: 11.5 °C; 24.1 percent), or open canopy. These groups were significantly different in mean growing-season soil temperature and percentage of overstory canopy closure (both $P < 0.01$). The range of soil temperatures in cool, closed-canopy plots was 7.4 to 9.6 °C, thus all (including shaded plots) were warm enough for root growth and above the threshold temperature for tree line as defined by Körner and Paulsen (2004). However, as we have already discussed, some areas had much longer root growth seasons than others, even within our relatively small study area.

Relationships Between Temperature and Topography

RELATIONSHIPS BETWEEN AIR TEMPERATURE AND ELEVATION—

- Our annual air temperature lapse rate of -4.94 °C per kilometer gain in elevation varied by the time of day (-3.99 to -5.53 °C in quarter-days 2 and 3, respectively), by level of canopy closure (-8.53 °C for closed-canopy plots, -7.13 °C for open-canopy plots), and by month.
- Variation in monthly air temperature lapse rates (-3.83 °C per kilometer in August to -6.29 °C per kilometer in April) was accounted for best by a model that included the number of clear days (positive relation) and the standard deviation of potential solar radiation among plots (negative relation).
- Closed- and open-canopy plots had opposite daily air-temperature lapse-rate patterns; open-canopy plots had flatter air-temperature lapse rates in quarter-days 1, 2, and 4 but a steeper rate in quarter-day 3 than closed-canopy plots.
- The progression of monthly air-temperature lapse rates, which changed from flatter summer rates to steeper late-winter and spring rates, were best modeled with snow cover and solar radiation (positive relations), but the progression was steeper for closed-canopy plots (from around -4 °C per kilometer in summer to -14.07 °C per kilometer in May) than for open-canopy plots, which was subtle and nearly flat.
- The steeper spring air temperature lapse rate for closed- compared to open-canopy plots is due to more rapid and even snowmelt from the primarily south- and west-facing open slopes having open canopies than from areas with closed-canopy plots where air trapped with unmelted snow under higher elevation tree canopies was colder than in lower elevations where snow melted earlier.

Although the lapse rate is a fairly simple concept, topographic interactions with weather and differences in vegetation can cause substantial near-ground distortions. These near-ground distortions provide challenges to weather modeling but represent real habitat characteristics for plants and animals. Several studies have shown substantially different lapse rates by using local temperature sensor networks (Blandford et al. 2008, Bolstad et al. 1998, Gardner et al. 2009, Rolland 2003, Tang and Fang 2006). However, variation over time is apparently less. Minder et al. (2010) found only modest year-to-year variation in Quillayute, Washington, radiosonde data from the Olympic coast, but where differences occurred, they were greatest from November through February and least from June through August, during the growing season.

Many studies have assumed lapse rates of -6 to -6.5 °C per kilometer gain in elevation for hydrologic, climatic, and environmental studies (e.g., Hamlet and Lettenmaier 2005, Maurer et al. 2002, Prentice et al. 1992, Roe and O'Neal 2009). Although this assumption may be suitable for large areas, these values ignore the complex landscape interactions with temperature gradients, such as location relative to valley cold-air drainage (Bolstad et al. 1998, Rolland 2003) and aspect of the slope (Tang and Fang 2006). In a study in the Cascade Range across the Puget Sound from our study area, Minder et al. (2010) showed how mountain hydrologic estimations can be improved by using locally developed lapse rates compared to using the commonly assumed lapse rate of -6.5 °C per kilometer.

Regional lapse rates may not be adequate for the study of local ecology where site-specific controls on temperature necessitate local observations (Minder et al. 2010). We used our temperature data to calculate local lapse rates by quarter-day, month, and year and to study the factors influencing them. Our lapse rates represent the local conditions that we were interested in for understanding the local plant community dynamics. Nevertheless, we were interested in how similar our findings were from those in other areas, as this influences the degree to which our study results can be extrapolated to other Olympic Mountains sites and other mountainous regions.

Over our entire plot base, we found an annual air-temperature lapse rate of -4.94 °C per kilometer gain in elevation, which is in the range of lapse rates (-3.9 to -5.2 °C per kilometer) derived in the Cascade Range on the other side of the Puget Sound (Minder et al. 2010). Use of our calculated relationship between mean annual air temperature and elevation to predict the mean annual air temperatures for each of the four Olympic Mountains SNOTEL weather station sites gave reasonable results for some but not other sites. The Mount Crag site was precisely estimated (5.1 °C). Our estimation for the Dungeness site was 0.97 °C lower than the measured value of 6 °C; the Waterhole site estimation was 0.07 °C low; and the Buckinghorse site estimation was 1.36 °C low. Also, Henderson et al. (2011) proposed the use of the mean annual temperature at sea level (the lapse-rate regression intercept) as a vegetation modeling variable. Their model suggests that this temperature should be slightly higher than 11 °C for our study area. Projecting our study area mean air annual temperature to sea level (the regression intercept) gives a temperature of 11.1 °C.

Minder et al. (2010) found a similar lapse rate of -4.8 °C per kilometer gain in elevation with a similar seasonal pattern and amplitude to what we found at our site by using radiosonde data from Quillayute, Washington, on the Pacific coast, 106 km west of our study area. Thus, our overall estimate provided a surprisingly distortion-free estimate of a measured free air-temperature lapse rate on the Olympic Peninsula.

Like others (Pepin 2001, Tang and Fang 2006), we found the annual air-temperature lapse rate was not constant through the day (e.g., -3.99 °C per kilometer in quarter-day 2 and -5.53 °C per kilometer in quarter-day 3). Pepin (2001) found steeper rates in the mid-afternoon and evening hours and flatter rates in the predawn hours, similar to what we found with our open-canopy and overall rates. However, Tang and Fang (2006) found the flattest rates at 0800 and the steepest between 1200 and 1400.

Our rates were not constant throughout the year, being steepest in April (-6.29 °C per kilometer) and November (-5.46 °C per kilometer) and flattest in summer (-3.83 °C per kilometer in July and -3.69 °C per kilometer in August). Others (Blandford et al. 2008, Bolstad et al. 1998, Gardner et al. 2009, Minder et al. 2010, Rolland 2003, Tang and Fang 2006) have found this too, but the seasonal patterns vary with location. In our data, lapse rates were flattest during the growing season, like what Minder et al. (2010) found in the nearby Cascade Range, but unlike what most others have found (Blandford et al. 2008, Gardner et al. 2009, Rolland 2003, Tang and Fang 2006). Interestingly, although Bolstad et al. (1998) showed that regional lapse rates were steepest in summer, their more local sideslope to ridge lapse rates were similar to ours, with a peak in April and lower summer values. Sideslope to ridge describes our plot network quite well. Xue et al. (2020) also found rates flattest in summer and steepest in March through May at Luya Mountain in China.

We assume the difference between our seasonal pattern and that of others is because of scale, topography, and differences in macroclimate and vegetative cover. Minder et al. (2010) compared lapse rates over several scales with data derived from soundings and found the weakest correspondence with a sensor network installed on a local mountainside. This suggested that local factors were important in addition to the regional air mass conditions (Minder et al. 2010). Our measurements describe the dissected mountain slope that we were interested in, whereas Blandford et al. (2008) and Roland (2003) were describing a larger region consisting of many mountain slopes and aspects. This suggests that regionally derived lapse rates may not be adequate for studies of local vegetation.

Most of the variation in the overall monthly air temperature lapse rates was accounted for by a model that included the number of clear days (positive relation) and the standard deviation of the potential direct solar radiation among plots (negative relation) (table 7). The number of clear days accounted for about two-thirds more variation in the model than did the standard deviation of the potential direct solar radiation. From October through June, there were only 2 to 3 clear days per month, but this number increased to between 5.1 to 6.4 days from July through September, resulting in flatter lapse rates. Thus, the effect of this variable was constant until the arrival of summer, when its effect became much larger until September, after which the effect of the number of clear days once again decreased. Others have found relations to sky and cloud cover but with some differences. Pepin (2001) found that the median lapse rates were steepest for intermediate levels of cloud cover and when cloud cover was over the uplands (suggesting convection). However, during times of general cloud cover or general clearing, the lapse rates became flatter. This last statement comes close to describing our observation. Summer months, especially July and August, are generally clear in the Olympic Mountains, and this is when some of the flattest air temperature rates were observed. December and January were the cloudiest months, and they also had relatively flat air temperature lapse rates. However, November and February, which are only slightly less cloudy, had steeper air temperature lapse rates.

The other variable in the model, the standard deviation of the potential direct solar radiation among plots, accounted for less variation but was still significant. The standard deviation of potential direct solar radiation, a measure of heterogeneity of solar illumination over the landscape, was lowest in December and January, increased in April, plateaued in September, then decreased in December. By itself, standard deviation of potential direct solar radiation did not correlate well with the monthly air temperature lapse rate, and its function in the model was somewhat opaque. From December through June, while the number of clear days were uniformly low, the changes in monthly air temperature lapse rate followed the pattern of the standard deviation of potential direct solar radiation over the landscape, which varied more at that time of year than the number of clear days. It was associated with a progressive steepening of air temperature lapse rates (more negative) from December through April when the clear days variable was relatively constant. Note, that although the standard deviation of potential direct solar radiation was significant in the model, the actual monthly potential direct solar radiation was not.

We also calculated air temperature lapse rates by two overstory canopy closure groups and found substantial differences. Over the entire year, the air temperature lapse rate for closed-canopy plots was -8.53°C per kilometer gain in elevation, and the air temperature lapse rate was -7.13°C per kilometer for open-canopy plots (both steeper than the overall average of -4.94°C per kilometer). There were opposite patterns of daily fluctuation between closed- and open-canopy plots. Open-canopy plots had flatter air temperature lapse rates than closed-canopy plots in quarter-days 1, 2, and 4 but a steeper air temperature lapse rate in quarter-day 3. We believe that the afternoon steepening of the air temperature lapse rate for open-canopy plots was because of greater wind dispersal of afternoon canopy gap-associated heating at higher than at lower elevations, partly because of more open-canopy plots at higher elevations. The afternoon flattening of the air temperature lapse rate for closed-canopy plots may be because of moderation of the subcanopy temperatures by transpiration.

There was also a difference in monthly air temperature lapse rates between closed- and open-canopy plots. In open-canopy areas, the monthly air temperature lapse rates varied little throughout the year, but in closed-canopy areas, there was a marked progression from flatter lapse rates in summer to steeper rates in the late winter and early spring (around -4°C per kilometer in summer to -14°C per kilometer in May).

Snow cover and solar radiation were positively related to monthly air temperature lapse rates in closed- and open-canopy relations. For both overstory canopy cover groups, the percentage of time that plots were covered by snow deep enough to moderate daily temperature variation was important. However, the mean potential direct solar radiation was important to the closed-canopy model, while in the open-canopy model, the measured direct solar radiation at the Waterhole SNOTEL weather station site was a better estimator. Measured direct solar radiation was more important to open-canopy than closed-canopy models because the tree shade damps the effect of the solar radiation fluctuation.

The air temperature lapse rates for closed-canopy plots were flatter in July and August, when summer potential direct solar radiation was high, and to a lesser degree from February through March, when the greatest number of plots were snow covered. The air temperature lapse rates for open-canopy plots followed a similar pattern to the lapse rates for closed-canopy plots but were much more subdued in amplitude. Thus, similar factors operate in both closed- and open-canopy areas but more effectively flatten the air temperature lapse rate in open-canopy situations.

From April through May, the snowpack melts progressively from low to high elevations. By June, the snowpack is gone from all but a few patches. While the snowpack is present, the air trapped under the canopy remains cold but warms once the snowpack is gone. Thus, during April and May, when the snowpack is still present at higher elevations, especially in the shade, but is gone from lower elevations, the air temperature lapse rate is greatest in the shade, but from June through October, there is less difference because there is no differential distribution of snow under the canopy. This difference did not exist in our generally south- and west-facing open areas because there was less canopy to interfere with insolation or air movement, and the snow melted more rapidly over a wide range of elevations. It seems likely that there is much less difference above the overstory canopy between closed- and open-canopy areas and less difference from low to high elevation over closed-canopy areas than under them. However, we were not able to obtain above-overstory canopy air temperature measurements. Nevertheless, for understory plants and animals living near the ground, these differences in air temperature lapse rates are important.

We explored the effect of several environmental variables on the seasonal air temperature lapse rate progression with stepwise regression analysis (table 7). This permitted a comparison of the factors influencing the seasonal air temperature lapse rate progressions in closed- and open-canopy situations. Both models were similar in that snow cover and solar radiation were important variables. However, in the model for open-canopy plots, solar radiation actually measured each month at the nearby Waterhole SNOTEL weather station site was significant in the model, but in the model for closed-canopy stands, the calculated potential direct solar radiation for each plot was significant. Although the variables in the closed- and open-canopy models were similar, the snow variable was relatively more important in the closed-canopy model than in the open-canopy model. Thus, snow was less influential in the open where it melts more rapidly and probably more evenly than in forested stands where the shade preserves it for a longer period. Air temperature sensors in a closed-canopy forest with a snow floor would be expected to reflect a lower late-spring or early-summer temperature than those in similar stands without a snow floor or in open stands with freer air flow.

Without an overstory canopy, convective mixing of air over a span of elevations is more efficient, which tends to even the temperature differential from low to high elevations. Under the overstory canopy, snowmelt proceeds more slowly both because convective air tends to move over more than under the overstory canopy and because the trees block direct insolation of the snow. Thus, the progression of snowmelt from low to high elevations proceeds more slowly, resulting in a longer period during which there are large elevational differences in the amount of snow and extending this period into a warmer season, effectively amplifying the effect.

RELATIONSHIPS BETWEEN SOIL SURFACE TEMPERATURE AND ELEVATION—

- Soil surface temperature variation was driven more by aspect and shade than by elevation, so soil surface temperature lapse rates were weak.
- Daily soil surface temperature lapse rates were only present in quarter-days 1 and 2, after the effects of daytime soil heating had decayed and were similar to air temperature lapse rates in quarter-days 1 and 2.
- A linear model combining elevation, aspect, and percentage of overstory canopy closure accounted for 72 percent of the variation in soil surface temperatures.
- Aspect and total canopy cover accounted for 41 percent of the variation in the highest soil surface temperature for each plot.

- Open-canopy areas had a daily pattern in soil surface temperature lapse rates, with the steepest lapse rate in quarter-day 3 and the flattest lapse rate in predawn hours.
- There was a similar daily pattern in soil temperature lapse rates but with a quarter-day delay.
- Open-canopy areas had a seasonal pattern in soil surface temperature lapse rates, with a steeper lapse rate during snowmelt, when elevational differences in snow cover were greatest, and a nearly flat lapse rate just before snowmelt, when soil and soil surface temperatures had equilibrated with the snow.

Overall, soil surface temperatures mostly did not exhibit monthly or annual lapse rates. Throughout summer, temperature variation imposed by aspect and shade (see below) appeared to be more important than elevation, and from mid- to late winter and early spring, a blanket of snow maintained relatively even soil surface temperatures over most of the area. Monthly soil surface temperature lapse rates emerged only for October through January when low-angle sun, shorter day lengths, increased cloudiness, rain, and snow decreased differences between open and shaded sites, and the snowpack was still shallow on many plots.

We found significant annual soil surface temperature lapse rates for the quarter-days 1 and 2; the relationship for quarter-day 1 was strongest, but both were similar to the comparable air temperature lapse rates (quarter-day 1 air: -4.92 °C per kilometer, quarter-day 1 soil surface: -4.10 °C per kilometer; quarter-day 2 air: -3.99 °C per kilometer, quarter-day 2 soil surface: -4.02 °C per kilometer). Thus, when the effects of uneven heating by the sun have decayed during the night, the soil surface temperature lapse rates closely approximated the air temperature lapse rates.

We found that modeling surface temperatures as a function of aspect and elevation resulted in a highly significant and strong model. Adding percentage of overstory canopy closure to the model further improved it. Aspect and overstory canopy closure are related; overstory canopy closure increased from southwest to north. However, overstory canopy closure also increased downslope and with summer soil moisture availability. By itself, overstory canopy closure did not produce a significant soil surface temperature model, and aspect by itself only accounted for a modest portion of it. A multiple linear regression model combining elevation, aspect, and percentage of overstory canopy closure was highly significant and accounted for 72 percent of the variation, indicating important roles for all three variables. Increasing elevation and overstory canopy closure decreased soil surface temperature, while more south-southwestern azimuths increased it.

Because of the biological significance of high soil surface temperatures, we sought a model that would account for the distribution of the highest soil surface temperature from each plot. Two factors, total canopy cover and aspect, accounted for 41 percent of the variation in the highest soil surface temperatures (table 9). Soil surface temperature increased by 0.09 °C per 1° azimuth away from north-northeast, and soil surface temperature decreased by 0.15 °C per 1 percent added to total canopy cover. The modest model r^2 suggests that other factors were also involved, but inclusion of elevation actually decreased the model performance.

When we split the data into closed-canopy and open-canopy groups, there was insufficient soil surface temperature data in the closed-canopy set to enable statistical comparisons. For open-canopy plots, a strong daily soil surface temperature lapse rate pattern

emerged, with the flattest lapse rate in predawn hours and the steepest lapse rate in quarter-day 3 (afternoon). The same pattern, albeit subdued in comparison, was found in the air temperature lapse rates for open-canopy plots, and it seems likely that heating of the air at the surface is responsible for the similarity, and convective mixing of the air is the reason for its more subdued character. At 20-cm soil depth, a similar pattern is visible, but it is delayed by a quarter-day (see below). It seems likely that this pattern too is driven by afternoon surface heating, with the delay reflecting the time it takes the pulse of heat to reach a 20-cm depth in the soil.

For open-canopy plots, there was a seasonal pattern of soil surface temperature lapse rates; the lapse rate was steepest during the snowmelt period and flattest just before snowmelt occurred. By March or April, nearly all areas had been under deep snow for more than a month and for as long as three months. Under the snow, the soil and surface gradually equilibrate with the temperature of the snow. Thus, the soil surface temperature is at or near 0 °C as is the soil to a depth that depends on the time it has been under the snow and the depth of that snow.

Beginning in April and May, low-elevation areas melt out, allowing rapid warming of the soil surface to ambient conditions, while high-elevation areas are still under snow, so the elevational soil surface temperature differential is large. As the snow melts at higher elevations, soils warm there as well, and the differential decays. This differential continues to decrease in fall and winter as first rain, then snow, brings the soil surface temperatures over a wide span of elevations into a similar range.

RELATIONSHIPS BETWEEN SOIL TEMPERATURE AND ELEVATION—

- There was no overall annual soil temperature lapse rate.
- Air, soil surface, and soil temperatures followed a similar daily sequence, but this was delayed by a quarter-day in the soil because of the time required for heat to move through the soil.
- Soil temperature lapse rates were steepest during the hottest part of the day in open-canopy stands and during the coldest part of the day in closed-canopy stands.
- For open-canopy plots, soil temperatures followed the same seasonal pattern as the soil surface temperatures and for the same reasons.
- Fall rain and winter snow cooled and homogenized soil temperatures over a range of elevations, but differential melting of the snowpack from low to high elevations caused large spring elevational differences to develop, which gradually equilibrated through summer.

In the overall dataset, elevation by itself was not a significant estimator of soil temperature, and thus there was no overall annual soil temperature lapse rate. The only significant monthly soil temperature lapse rate occurred in January (−2.7 °C per kilometer gain in elevation). Thus, because of snow cover, there is little difference between low- and high-elevation soil temperatures in winter, and we believe that this degree of difference was due to wind eroding the snowpack on some high-elevation plots rather than from elevational differences per se.

By separating the data into closed-canopy and open-canopy groups, significant soil temperature lapse rates emerged. Thus, we found a significant lapse rate of −11.79 °C per kilometer for open-canopy plots and a marginally significant rate of −13.39 °C per kilometer for closed-canopy plots. Given the uniformity of soil temperatures under snow, these lapse rates

reflect mostly summer differences and are influenced by the differential spring melt from low to high elevations, which occurs more slowly under tree canopies than in open areas.

Open-canopy plots had significant daily lapse rates in all quarter-days; lapse rates were steepest in quarter-day 4 and flattest in quarter-day 2. Because of the time it takes for heat to move through the soil, the daily sequence of these lapse rates was delayed by a quarter-day from air and soil surface temperature lapse rates. Thus, air, soil surface, and soil temperature lapse rates all followed the same daily sequence, with the steepest rate associated with the hottest part of the day but with a delay by a quarter-day at 20-cm depth in the soil.

In closed-canopy plots, the daily soil temperature lapse rate sequence also tracked the air temperature lapse rates with a delay by a quarter-day. However, in this case, the pattern is opposite that of the open-canopy plots in that the steepest air temperature lapse rates were associated with the coldest part of the day, especially in quarter-day 1.

For open-canopy plots, soil temperature lapse rates followed the same seasonal pattern as the soil surface temperature lapse rates and for the same reasons. Soil cooling associated with fall rain and winter snow homogenized soil temperatures over a range of elevations, but differential melting of the snowpack from low to high elevations in spring and early summer caused large elevational differences in temperatures to develop, which gradually flattened through summer. In May and June, soils still under snow, especially at higher elevations, remained close to 0 °C, while exposed, lower elevation soils warmed rapidly to ambient conditions.

Although significant monthly soil temperature lapse rates had an overall similarity in seasonal pattern between closed- and open-canopy plots, there was a substantial difference in July and August when open-canopy plots had relatively steep lapse rates, while closed-canopy plot lapse rates were nearly flat. We could not derive an explanation from examination of air temperature lapse rates as they do not show differences developing at this time, but we caution that the July and August soil lapse rates for closed-canopy plots were not significant and were based on only five plots. In the absence of the July and August soil data points, the closed-canopy trend was like the open-canopy trend.

Relationships Between Temperatures and Aspect—

- Relationships between annual air, soil surface, and soil temperatures and aspect alone were weak but implied higher temperatures on southern and western than on northern and northwestern aspects.
- For annual air temperature, 79 percent of variation was accounted for by a model that included aspect and elevation, but elevation was not a significant variable in annual soil surface or soil temperature models because these temperatures depend mostly on direct solar exposure.
- The strongest quarter-day temperature regression models were quarter-day 4 for annual air temperature, quarter-day 1 for annual soil surface temperature, and quarter-day 2 for annual soil temperature. This sequence apparently reflects reradiation of soil heat into the atmosphere after sunset.
- For annual soil temperature, the importance of aspect relative to elevation increased through the day as solar heat was stored in the soil and decreased during the night as it decayed away, so the relative importance of elevation was greatest around dawn.
- Aspect and annual soil surface and soil temperature relationships were weaker than aspect and annual air temperature relationships because soil surface and soil temperatures were affected by more microsite factors than temperatures for air, which moves and mixes with convection.

Annual air, soil surface, and soil temperatures modeled as linear functions of aspect were significant, but of weak to moderate strength. Nevertheless, a measurable warming of temperatures on southern to western aspects compared to northwestern and northern aspects is implied. A stronger relationship between aspect and annual soil surface temperature than with annual soil temperature occurred because the surface is directly heated in the day and radiatively cooled at night, whereas these processes are indirect at 20-cm soil depth and mediated by the surface. The annual air temperature model was improved by using only plots with ≤ 75 percent canopy closure, which suggests the air was heated by directly insolated surfaces in canopy gaps.

Modeling mean annual air temperature as a function of both aspect and elevation resulted in a strong model (adjusted $r^2 = 0.79$). However, elevation was not significant in annual soil surface or soil temperature models, implying that any effect that it might have is small compared to aspect. This suggests that surface and soil heating is mostly caused by direct absorption of solar radiation, which in turn heats the air more on south- and southwest-facing slopes than on those with northern exposures. The heated air is convected away and adiabatically cooled as indicated by the significance of elevation in the air temperature model.

The strongest overall annual temperature regression models by quarter-day were quarter-day 4 for air, quarter-day 1 for soil surface, and quarter-day 2 for annual soil temperatures. This progression from evening through night and into the morning seemed to reflect the effect of reradiation of soil heat into the atmosphere after sunset. After sunset, the residual soil heat continued to warm the air in areas that were heated the most, but this effect decayed by quarter-days 1 and 2. However, the soil surface radiatively cooled below the temperature of deeper soils and became a temperature sink for deeper heat. This change apparently occurred in quarter-day 1, and the surficial cooling that occurred in quarter-day 1 appeared at 20-cm soil depth in quarter-day 2.

This sort of progression was also visible in the ratio of the elevation coefficient to the aspect coefficient. This ratio indexes the relative contribution of the two variables to the overall temperature effect. Thus, for air and soil surface, the ratio was greatest in quarter-day 1 and least in quarter-day 3; but for soil, there was a delay by a quarter-day, and the ratio was greatest in quarter-day 2 and least in quarter-day 4. So, in the early morning, at the time longest removed from the last solar radiation of the surface, and the previous day's radiation effect has decayed as much as possible, aspect was relatively unimportant compared to elevation, and the lapse rate was the main determinant of temperature. However, as the day advanced, aspect became increasingly important, until near sunset, when the day's heat at the surface will have decayed both upward to the air and downward to deeper soil. It is that downward pulse that arrived at 20-cm soil depth several hours later that was responsible for the quarter-day delay in soils relative to the surface. The elevation coefficient was significant in all quarter-days for air, only in quarter-days 1 and 2 for soil surface, and in no quarter-days for soil.

The annual soil surface and soil temperature relationships were weaker than with annual air temperature because there are many unmeasured microsite factors that can influence and add noise to the relationships (fig. 9). Factors such as the amount of understory over the measured point and amount of overstory vegetation in the vicinity can make a difference. Also, soil characteristics, such as soil moisture, rock content, soil surface color, and organic matter depth, can all add variation. However, microsite characteristics are less important to air temperature because air can move and mix with convection.

When we separated the data into closed-canopy and open-canopy groups, the closed-canopy models for air temperature were not significant, but open-canopy models were as strong or stronger than the combined model. It may be that the closed-canopy models were not significant because of their small sample size, but soil heating in the absence of direct solar radiation is minimal and derived from contact with air from warmer places moving to the shaded location through convection.

Other Annual Soil Temperature Relations—

- Mean annual air temperature accounted for only 35 percent of the variation in mean annual soil temperature, suggesting a more complex explanation for soil temperature was needed.
- Mean annual air temperature, elevation, and the length of the snow season accounted for 58 percent of the variation in mean annual soil temperature.
- Aspect and the standard deviation of ground-level PAR accounted for 52 percent of mean annual soil temperature variation, implying that the warmest soils occurred with a mix of around 50 percent tree cover and canopy gaps on southwestern aspects.

It is generally held that mean annual soil temperatures approximate the mean annual air temperature (USDA NRCS 1999). However, the amount and distribution of rain and snow, the presence of vegetation, and the shape of the land cause differences (USDA NRCS 1999). In our sample area, mean annual air temperature accounted for only 35 percent of the variation in mean annual soil temperature. Clearly other factors were important; however, by themselves, only a few factors (aspect and the standard deviations of ground-level PAR) proved to be significant (but weak) explanatory variables of mean annual soil temperature. Elevation, the length of the snow season, and overstory or understory canopy closure were not by themselves significant estimators. However, some of these variables worked well together in multiple linear regression models. The strongest model included mean annual air temperature, elevation, and the length of the snow season to account for 58 percent of the variation in mean annual soil temperature. Snow cover fixed the soil temperature within a narrow range near 0 °C, and the length of the snow season determined the length of the snow-free season when wider variation occurred. Air can heat or be heated by the soil depending on the time of day if the snow is gone from the soil and is influenced by elevation through the process of adiabatic cooling.

Aspect and summer plot-level standard deviation of ground-level PAR accounted for 52 percent of the variation in mean annual soil temperature. A high standard deviation of ground-level PAR implies high plot-level variation in shading (a mix of gaps and shade). The relationship was positive, which implies that variable structure contributed to warmer soils, and we would expect from this that the warmest soils would occur with around 50 percent tree cover on a southwestern aspect. The intent of taking meteorological observations at a standardized height of 1.5 to 2 m is that wind and convection would normally obscure localized microclimates at this height (Ashcroft and Gollan 2013). However, where trees are spaced so that sunlight still strikes much of the ground and thus warms it but obstructs wind from efficiently moving the heated air away, daily maximum temperatures may be raised (Daubenmire 1974, Day 1946, Smith 1926). In areas of savanna and parkland structure, decreased air flow has been shown (Kainkwa and Stigter 1994), and this results in an increase in air temperature within canopy gaps in summer (de Freitas and Enright 1995). Thus, stands with many canopy gaps, especially when on south- or southwest-facing slopes, attained the highest daytime summer temperatures, but as was already discussed, these stands also had lower nighttime temperatures due to cold air pocketing.

Seasonal Correlations Between Overstory Canopy Closure and Mean Annual Soil Temperature

Our linear regression analysis of mean annual soil temperature as a function of either overstory canopy closure or PAR (ground level or 1.3-m height) was not significant, implying that soil temperature is not strongly affected or is affected in more complex ways by these variables (see above). However, our correlation analysis suggested that there is an annual cycle, with the amount of overstory canopy closure positively correlated with soil temperature in winter and negatively correlated in summer, although the correlations were only significant in summer. This would seem to be a topic of interest for future study as it implies seasonally changing roles for vegetation in relation to soil temperature moderation. Our regression analyses on the effect of overstory canopy closure on soil temperature suggested that in summer, closed canopies lower soil temperature by 3.9 °C in June, 7 °C in July, and 5.6 °C in August compared to areas with open canopies.

Relationships Between Alpine Tree Line Position and Temperature

- We found scattered, isolated trees on dry, south- and southwest-facing slopes or north-facing slopes near ridgelines with obvious redistributed snow accumulation, but the alpine zone, as defined by low soil temperatures, lay mostly above the study area.
- Although half of the plots would have root-limiting cold soils (≤ 6.2 °C) if a closed overstory canopy developed, they did not display a pattern in terms of elevation, aspect, or slope steepness.
- Plots that were not available to trees because of drought or cold supported subalpine meadows and cushion plant communities.
- Some plots may have become physiologically available to trees because of the warming climate, but because trees have not yet dispersed to them, these plots retained the previous alpine flora.
- Soil temperature was only occasionally limiting for forest growth in our study area, and open slopes were more often due to drought, soil instability, redistributed snow accumulation, or cumulative limitations.
- The krummholz tree growth form was associated with windy ridgetops.
- Based on our findings and others, we believe the area is shifting from temperature limitation toward greater drought limitation on warm aspects, with increasing growth and vigor on northern aspects and moist sites, and shade-tolerant subalpine fir becoming especially competitive on all but the driest sites.

Confusion in the terminology around tree line, timberline, subalpine, and alpine is addressed in Körner's (1998) literature review. Because these phenomena are associated with gradients, the vocabulary associated with them is unclear. Although a fair amount of attention has been directed toward studying the causal mechanism(s) and the underlying physiology of the plants involved with the alpine transition, many questions remain. In this report, we adopt a simple model proposed by Körner and Paulsen (2004) for our terminology. They define "alpine" as the zone above tree growth. Well below that is the "montane forest zone" of continuous overstory canopy. Between these extremes is the "subalpine," a zone wherein trees grow upright but do not form a continuous canopy. The trees in the lower part of the subalpine zone form patches of various sizes within which continuous canopy exists, but at the upper extreme, only individual trees are found scattered below the alpine zone. It is within this fragmented canopy zone that Körner and Paulsen define the tree line,

with the actual line between areas where trees grow in clumps and the area where they only grow as individuals (Körner and Paulsen 2004). The rationale for this placement is based on temperature limitations on tree root growth (Körner 1998, Körner and Paulsen 2004).

The tree life form has evolved for light competition under warm soil conditions (Slatyer and Noble 1992). This is different from ground-hugging alpine plants, in which both the shoot apical meristems and roots benefit from radiant daytime warming and stored soil warmth (Grace and Norton 1990, Körner and Cochrane 1983). According to Körner and Paulsen (2004), the tree line occurs where overstory canopy shade depresses the root zone temperature below levels that would support forest-like structure and canopy. Although the soil temperatures under open vegetation might be warm enough to support tree germination above the tree line, as soon as the tree becomes large enough, shade from its canopy depresses the soil temperature, limiting subsequent increases in size. This enforces canopy fragmentation because to survive and grow, the tree must be able to grow roots beyond its canopy into warmer, open soils where the shade of another tree would prevent such growth.

Körner and Paulsen (2004) found that most temperate zone tree line sites had a sub-canopy growing-season soil temperature (at 10-cm depth) of 6.4 to 7.8 °C, which averaged 6.7 °C across biomes. They also found that soil temperatures in open areas were highly aspect dependent, but temperatures under tree canopies were not, which our data supports.

A visual inspection of aerial photography indicated only two areas within our study area where single trees were common on the landscape (fig. 70). Those areas were most of the dry, southern, and southwestern exposures in the study area and northern exposures near ridgelines where there was obvious snow accumulation. Other than these areas, trees formed clumps to the tops of the highest ridges.

Because we measured soil temperatures at 20-cm depth, we estimated that 6.2 °C is equivalent to Körner and Paulsen's (2004) 6.7 °C threshold at 10-cm depth. By using our 20-cm-deep soil temperatures, we estimated that 14 of 36 plots used in the analysis would fall in the range they indicated for root limitation, and 4 of these plots would cool to 6.2 °C or lower if an overstory canopy closed over them (fig. 71). The 14 plots that fell within Körner and Paulsen's (2004) root-limiting range did not differ from the remainder of the plots in terms of mean elevation, aspect, slope steepness, or overstory canopy closure. Nevertheless, they had significantly lower soil temperatures at 20-cm depth. Several plots were in situations of cold-air drainage, some were on northern exposures, and none were on ridge crests, but other than that, they were on a variety of lower to upper slope topographies and aspects. They included a wide variety of vegetation, including plots that were already mostly forested (subalpine fir/Cascade azalea plant association) to open alpine meadows and cushion plant communities (spreading phlox community). However, many alpine cushion plant communities and some forest plots would not cool to this range of temperatures. Indeed, one spreading phlox community plot would only cool to 11.7 °C in this exercise. Thus, it does not appear that the current vegetation is a particularly good indicator of how a forest overstory would affect the soil temperature. We suspect the reason for this is that subalpine meadows and alpine cushion plant communities are the default vegetation on sites that are not available to trees either because of temperature, moisture, or some combination of the two. Thus, some sites are warm enough to support trees but are not wet enough, and although some may have sufficient moisture for trees, they may be too cold; but in either case, similar species can be found in the nonforested community. There may also be sites that are physiologically available to trees because of the changing climate but to which trees have not yet

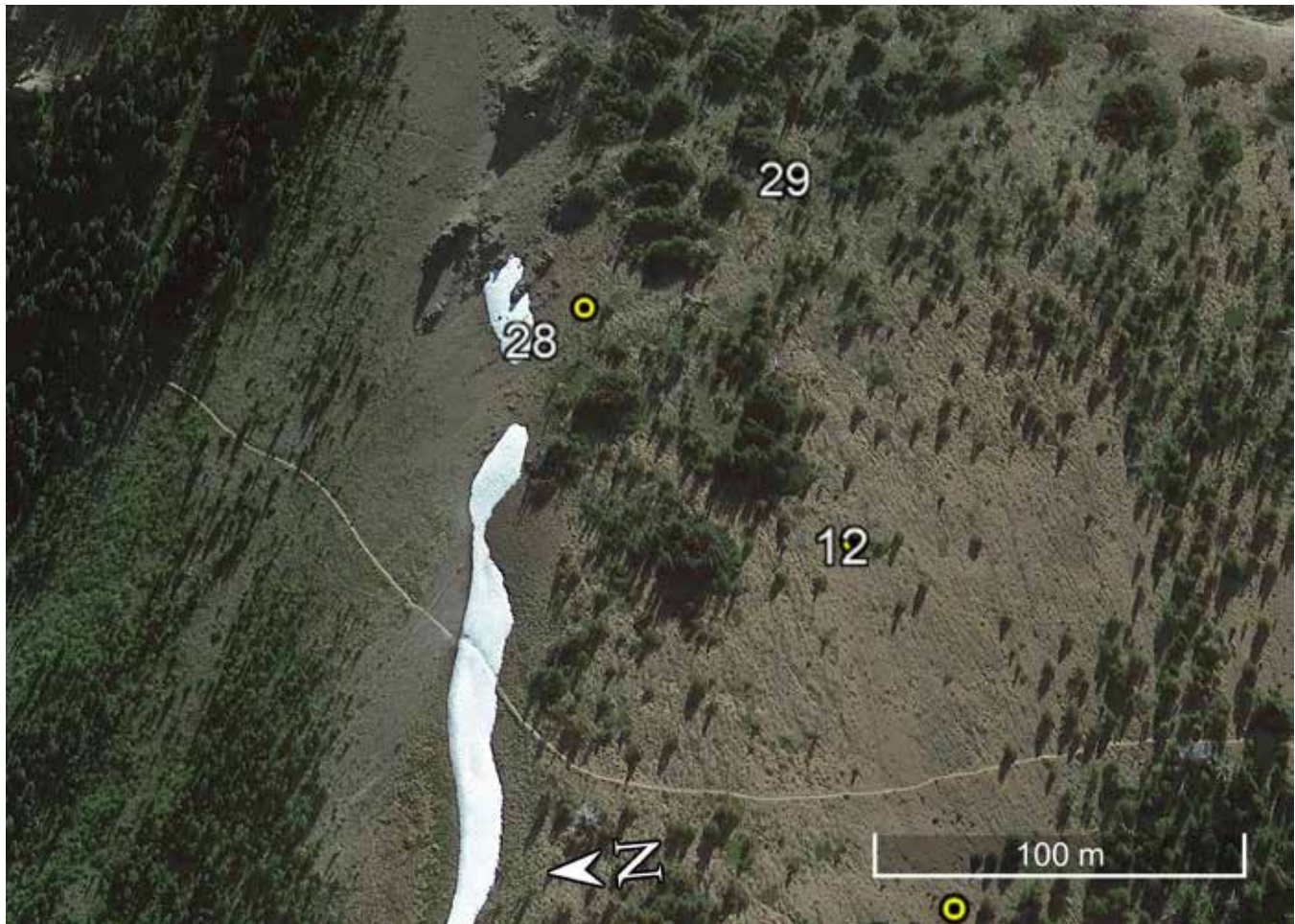


Figure 70—Single trees as opposed to clumps or closed-canopy forest grew on dry, south-facing slopes such as in the vicinity of plot 12 in the Olympic Mountain whitebark pine communities study, and on cold, north-facing slopes, such as the slope north (left) of plot 28. Elsewhere, trees usually grew more densely. Figure 71 shows this phenomenon over a larger area. Google Earth image; July 30, 2017.

dispersed. We believe that these sites will retain much of their previous flora until the over-story canopy closes over them. A case in point is plot 23, our lowest elevation plot, which had 90 percent canopy closure, and we estimated that complete closure is possible based on soil temperature. In the small, remaining canopy gap, there were several species common in alpine communities but not forest communities, including common juniper, Cascade desert-parsley, and pale bellflower. We believe this indicates a more open past community, perhaps during the Little Ice Age. Although Luckman (2000) points out that the Little Ice Age was anything but a climatic monolith, he provides evidence from the Canadian Rockies that the 1200s and early 1300s, and more importantly to current vegetation, the late 1400s through to the mid-1800s, were generally colder than our current climate (Luckman and Wilson 2005).

Topographic relations to the group of potentially cold, root-limiting plots were weak (fig. 71). Few of the plots on or near a ridgeline, including our highest elevation plot, would develop tree-inhibiting soil temperatures under a full canopy. Also, a slight tendency for plots in cold-air drainage topographic situations to have or develop root-limiting soil temperatures was not absolute. The group of cold, potentially root-limiting plots were not distinct from the others in terms of elevation, aspect, or slope steepness, but nevertheless, these plots had significantly lower soil temperatures.

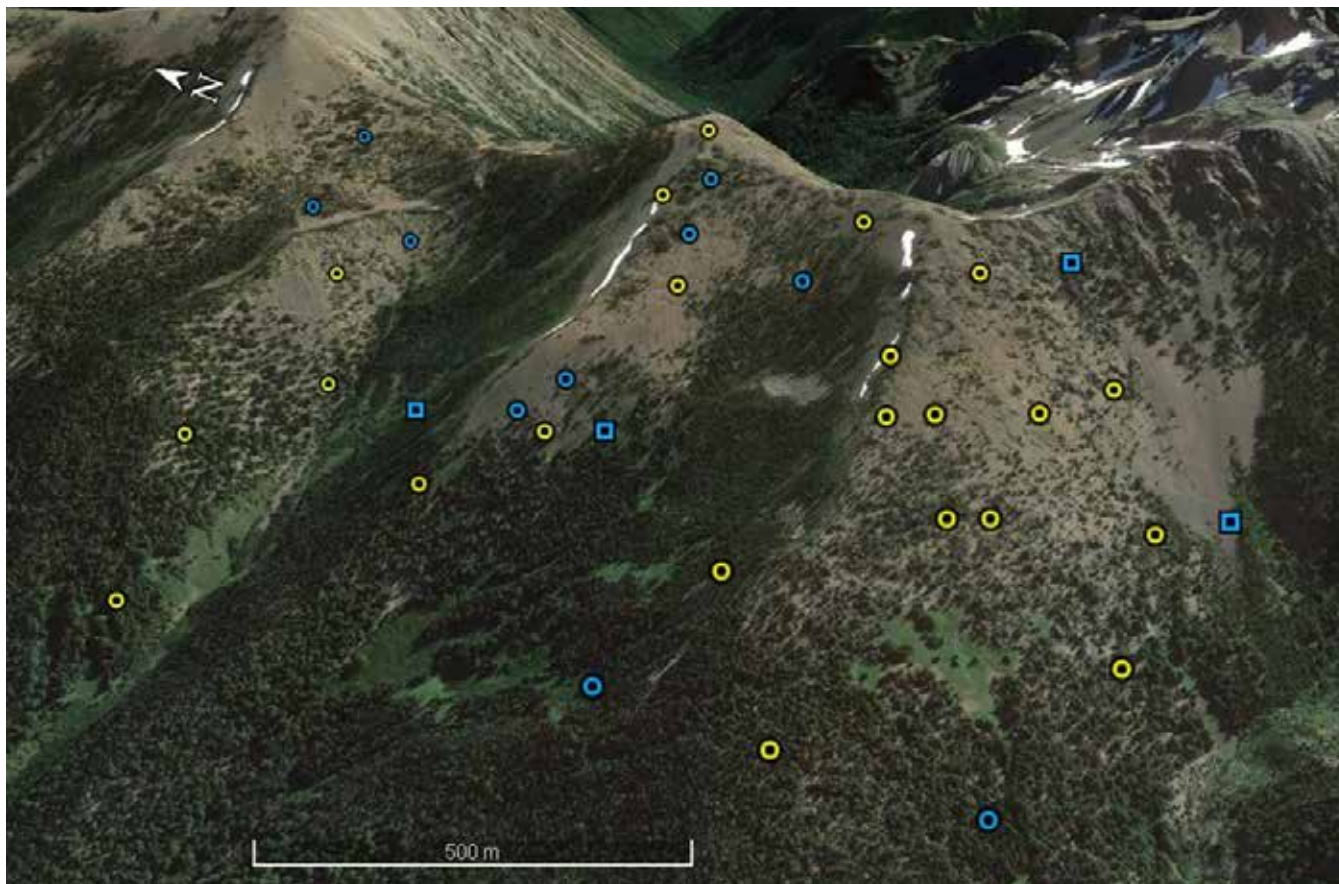


Figure 71—Sample locations of plots in the Olympic Mountain whitebark pine communities study which with 100 percent canopy closure (in blue) would have low enough soil temperatures to inhibit root growth based on soil temperature relationships to estimate thresholds proposed by Körner and Paulsen (2004). Soil temperatures (at 20-cm depth) at plots represented by blue squares would drop below 6.2 °C during the growing season with 100 percent canopy closure. Soil temperatures at plots represented by blue circles would drop below 7.3 °C with 100 percent canopy closure. Plots represented by yellow circles would remain above 7.3 °C, even with 100 percent canopy closure. Google Earth image, July 30, 2017.

Most of the potentially root-limiting plots were near what appeared to be the current, albeit indistinct, tree line, so the Körner and Paulsen (2004) hypothesis was supported in this sense. However, there were many plots with similar vegetation that would apparently not cool to these levels. Explanations for these exceptions could take several forms. It may be that the relationship we calculated for temperature loss due to increasing canopy closure was flawed or too simplistic. Also, solifluction or drought appeared to prohibit establishment in some places. Overall, our analysis considering their theory suggests that our study area straddles or is somewhat below a soil temperature-dependent tree line even if it does not explain the circumstances of every plot. It also suggests that other factors, most probably soil instability and drought, complicate the interpretation and within our study area may be equally if not more important than temperature, at least on south-facing slopes.

By calculating the amount of canopy that would be present at the 7.3 and 6.2 °C thresholds for marginal and probable root growth restriction, we found that the coldest plot (plot 7) could theoretically support 64 percent canopy closure with 7.3 °C soils and 88 percent at 6.2 °C. All the other plots that might be able to reach these thresholds would have even more dense canopy before they reached these temperature thresholds. In viewing figure 71, it is noticeable that the lowest elevation plots that could be cold enough to fall below the root growth threshold already have a considerable overstory canopy with relatively little canopy

opening. Thus, these shady plots are already borderline in this regard. Perhaps, the canopy cannot completely close at these plots, but they already have enough canopy that they cannot be considered alpine.

Thus, assuming the model of Körner and Paulsen (2004) is correct, and the assumptions in our models are reasonable, it appears that soil temperature is only marginally limiting for forest growth in our study area even in the coldest situations and that the large openings currently on these slopes are more likely due to other limitations or perhaps to cumulative limitations including cold soils. The alpine zone, if defined only by soil temperature, lies mostly higher in elevation than the highest elevations in our study area.

In our study area, the occurrence of krummholz tree growth form, which is often associated with alpine vegetation, was clearly associated with windy ridgetops. The best example of this growth form (plot 35, elevation 1742 m) occurred 74 m below less windy areas with well-defined upright tree clump structure (fig. 72). Wind scour was evident on the relatively short, upright stems on this plot. Over Körner and Paulsen's (2004) growing-season, we estimated that 100 percent overstory canopy closure would result in a mean growing-season soil temperature of 7.6 °C, which should be high enough for upright trees to develop a closed canopy, so it appears that this stand is wind and scour limited. Interestingly, our highest elevation stand (plot 30, elevation 1893 m) appeared to have formerly been krummholz in its structure but is currently growing into an upright stand with a continuous canopy, and according to Körner and Paulsen's (2004) criteria, should cool only to a mean growing-season soil temperature of 9.4 °C under 100 percent overstory canopy closure. At ground level, the stems of these trees form an anastomosing (connecting, diverging, and reconnecting) tangle of prostrate growth, but all have now turned up and have grown vertically for up to 7.5 m. Thus, although this stand may have been cold limited during the Little Ice Age, it no longer is, and as a result, the trees are now growing upright. Core sampling of an upright stem at breast height in this stand indicated an age of 188 years; so, these trees were certainly present and at least 1.3 m tall toward the end of the Little Ice Age. The trees on plot 35 were also present during the Little Ice Age. Core sampling from a prostrate stem, but of unknown distance from its germination point, indicated an age of 210 years. Thus, the lower elevation krummholz stand was and still is wind and scour limited regardless of any cold limitation that might have been present in the past. These contrasting krummholz situations indicate the importance of local micro-site conditions to interpretation of stand structure, including structural change as it relates to climate change. Change from krummholz to upright growth form has also been observed in the Sierra Nevada Mountains (Millar et al. 2004) where whitebark pine that entered the 20th century as compact, flat-topped krummholz thickets, often exited the century with a more upright form, similar to what we believe occurred at our higher elevation stand.

If, as our analysis suggests, the soils on many of our nonforested plots are warm enough to support tree growth, then why is there so much nonforest vegetation, including plant communities widely regarded to be of alpine composition in the study area? There appear to be two possible explanations. One explanation is that other environmental factors are limiting tree growth. For example, lack of moisture during the short growing season may limit tree growth on warmer aspects. de Andrés et al. (2015) suggest that this is the case for tree lines in Mediterranean climates. Another possible explanation is that since the Little Ice Age, the environment has warmed faster than many species can migrate. Thus, physiologically limiting cold conditions lie somewhere above them, and given time, they will adjust upward to meet them. These two explanations are not mutually exclusive.



Figure 72—Wind-formed subalpine fir krummholz on an exposed, dry, mid-elevation ridge (the strip of trees that includes plot 35) of the Olympic Mountain whitebark pine communities study. Trees on other study plots on both north- and south-facing slopes in the image are upright and are at similar or higher elevations as plot 35. Google Earth image; July 30, 2017. Inset: Plot 35 from the south with author Timothy B. Harrington. Note the scoured flags (only the downwind branches are left on the stem) protruding above the lower tree foliar skirt in this image. USDA Forest Service photo by James Dollins.

At the time of data collection for this study, 160 years had passed since 1850, the date usually given as the end of the Little Ice Age. This was a period covering 500 to 600 years when at least the northern hemisphere experienced climatic cooling, with the coldest conditions of the last 560 years occurring between 1570 and 1730 and in the 1800s (Bradley and Jonest 1993). The Little Ice Age was not monolithic in time or space (Briffa et al. 1992). Porter (1986) postulated that volcanic aerosols caused negative temperatures, stimulating several glacial advances during the Little Ice Age, and he inferred a decrease in temperature in the range of 0.5 to 1.2 °C during these glacial advances. Briffa et al. (1992) provide evidence that a sharp drop in temperature in 1601 may have originated in this way.

For our purposes, it is important to understand how different the current climate is than what prevailed during the Little Ice Age and during the period around its closing. Eighty-two Olympic National Park glaciers have completely disappeared since 1982, and the remainder have thinned (USDI NPS 2019). The Blue Glacier lost 100 m of length in the 20 years after 1995 but retreated more than 1100 m between 1815 and 1989 (Spicer 1989), suggesting that local warming began before 1850. By using high-elevation tree rings to reconstruct annual temperature at Longmire, Washington, Graumlich and Brubaker (1986) found that the mean annual temperature from 1590 to 1913 was 6.7 °C, while the mean annual temperature from 1914 to 1979 was 7.2 °C.

By using a combination of weather station records and models, Abatzoglou et al. (2014) found that mean annual temperature increased by about 0.68 to 0.88 °C from 1901 to 2012, with corroborating indicators that include a lengthened freeze-free season, a warmer coldest night of the year, and increased growing-season potential evapotranspiration. Previously, Mote (2003) found a similar increase of 0.78 to 0.98 °C over the same time. In the maritime portions of the Pacific Northwest, warming rates were greatest during winter and at lower elevations. His data shows that the Olympic Peninsula largely fits this trend in terms of temperature but had no trend in precipitation (Mote 2003). This implies that drought has become more severe relative to the Little Ice Age climate in the Olympic Mountains.

The warming temperatures have influenced snowpack. Stoelinga et al. (2010) found a 23 percent loss of snowpack in the Cascade Range from 1930 to 2007 that they attributed to warming, as they found no trend in precipitation over the same period. The dates for maximum snowpack and 90 percent snowmelt both shifted 5 days earlier. Peterson et al. (2002) found that growth of subalpine fir in the Olympic Mountains and Cascade Range was negatively correlated with winter precipitation and spring snowpack depth that resulted in shorter growing seasons. Thus, if the snowpack is melting earlier, subalpine fir should benefit. Also, Peterson et al. (1990) found that the only temperature variable with a strong correlation to growth of high-elevation Sierra Nevada whitebark pine or lodgepole pine was spring temperature.

Thus, it appears that the mean annual temperature of our study area has likely increased between 0.5 and 1 °C since the end of the Little Ice Age and that precipitation has changed relatively little. This should favor tree growth, except perhaps on the droughty south-facing slopes. The observed loss of glacial ice in the Olympic Mountains and the loss of snow in the Cascade Range seems largely tied to warming. Depending on the site, earlier snowmelt has the potential to extend the photosynthetic season where sufficient moisture is present, which would benefit trees, but by extending the dry season, potential drought impacts to plant communities could also occur. Peterson et al. (2002) found that on warm, dry sites in the northeast Olympic Mountains where subalpine fir commonly grows with Douglas-fir, subalpine fir growth was negatively correlated with the previous summer's temperature, suggesting a soil moisture limitation on photosynthesis and the following year's growth. Increasing temperatures would presumably make this worse. However, they also found that in wetter sites in the Olympic Mountains and Cascade Range, higher spring temperatures and earlier melting of the snowpack boosted subalpine fir growth. On our study site, it appears that the northern aspects are snow and growing-season limited (so trees would benefit from warming), and the western and southern aspects are soil-moisture limited, so trees may be increasingly challenged there. Peterson et al. (2002) suggest that under a warming climate, subalpine fir on mesic and dry sites will have opposite responses—growing more vigorously on the wetter sites and struggling or dying out on the dry sites.

Because we calculated an overall lapse rate in our study area of -4.93 °C per kilometer gain in elevation, a 0.5 to 1 °C increase in mean annual temperature implies an increase of 100 to 200 m for temperature-dependent features such as the tree line. As individual plants cannot relocate, this implies physiologically based costs and benefits depending on the species. It is quite easy to see that a species growing at its lower elevational range might be challenged, and those at their higher elevational range might benefit, but for those growing in their mid-elevational range, the picture is less clear. All the tree species in

our study are growing in their upper elevational range, so they can be expected to benefit wherever drought is not a factor. According to Albright and Peterson (2013), because of seasonal extension from reduced snowpack, subalpine fir will greatly benefit in the Olympic Peninsula as the decrease in water deficit will not counter the longer growing season. Thus, for a given site, there will be a shift away from the current temperature limitation toward moisture limitation but an overall increase in growth and vigor in all but the lowest elevation trees and those on the warmest and driest sites. We would expect the other tree species in the study area to experience similar benefits, but because subalpine fir is the more shade tolerant of them, we would expect it to be competitive.

Another related factor that could change the distribution of vegetation is CO₂ fertilization, which can counter some of the potential increase in drought limitation caused by a temperature rise without a concurrent increase in precipitation. CO₂ has risen from a preindustrial level of 280 parts per million (ppm) to the current level of 415 ppm. CO₂ affects plant growth both through direct fertilization and through increased water use efficiency. Many laboratory and agricultural field experiments show these effects, but there has been little investigation into the ways natural ecosystems might be affected. Klein et al. (2016) exposed a natural stand of 110-year-old Norway spruce (*Picea abies*) to elevated levels of CO₂ (550 ppm) for 5 years. Although the needles retained their photosynthetic capacity and absorbed up to 37 percent more CO₂ under elevated conditions, they detected no effect on stem or branch growth, litter production, stem or soil CO₂ efflux, fine root production, stomatal responses, or sap flow, and soil moisture remained unaffected. They concluded that the trees were not carbon limited, and further atmospheric CO₂ enrichment would have only subtle effects on growth. However, Gedalof and Berg (2010) analyzed radial tree growth for evidence of increasing growth rates and decreasing sensitivity to drought that could not be accounted for by climate change. About 20 percent of sites globally exhibited increases in growth that could not be attributed to climatic causes, which they attributed to CO₂ fertilization as opposed to increased water use efficiency. They suggested that future forest dynamics may change depending on site conditions and species responses to elevated CO₂ (Gedalof and Berg 2010). Of course, this implies that some change may have already occurred, but we know of no studies that have shown this. It is also possible that species with shorter life spans and faster reproductive rates may respond more quickly. Clearly, more research could help fill such knowledge gaps.

Winter Snow Accumulation

- The permanent winter snowpack developed after the middle of November.
- Snow cover is a strong regulator of soil surface and soil temperatures.
- Soil surface temperatures hovered near 0 °C under deep snow, and daily soil surface temperature fluctuations and soil freezing, which occurred in early November without snow cover, became undetectable as the snow deepened.

Although ephemeral snow showers began in October, the permanent winter snowpack developed after the middle of November. Two of the more important effects of winter snowpack are the supply of water from its melting in spring and its moderation of the subniveal thermal environment. Snow cover is a strong regulator of soil surface and soil temperatures. Our soil surface temperatures hovered near 0 °C under deep snow. Wide daily soil surface temperature fluctuations and soil freezing, which occurred in early November without snow cover, became undetectable with sufficient snow cover. The ability of snow to moderate

soil surface temperatures under even more extreme conditions was shown in a Colorado Engelmann spruce stand where it was found that although temperatures in the top 30 cm of snowpack were as low as -10.5°C , the temperature at the soil surface under 114 cm of snow was only -1°C . Higher up, in exposed tundra, the temperature under 70 cm of snow was still just -4°C (Wardle 1968). The minimum air temperatures in January at the Colorado site ranged from around -20 to -30°C , which are far lower than air temperatures we measured in the Olympic Mountains. However, as spring advanced and the weather warmed, both the spruce and tundra snowpacks became isothermic at 0°C in May.

At our study area, when the snow was shallow, the soil froze shallowly during cold nights or other particularly cold conditions, but this became less frequent as the snowpack deepened and soil freezing eventually ceased altogether on most plots. Shallow snow retains its high thermal emissivity, which increases outgoing longwave radiation, cooling the snow surface, especially at night, and has high albedo, which can reflect warming from the sun. If its insulative properties are also compromised by wind packing or densification from freezing and thawing, shallow snow may enhance soil cooling, unlike deep snow which is an efficient insulator (Zhang et al. 2005). These effects take place at the snow surface, so none of this matters much if the snow is deep enough because of snow's extremely low thermal conductivity. Deep snow rapidly uncouples thermal events taking place at the snow surface from the soil surface.

SNOW ARRIVAL—

- Snow accumulation was determined by aspect and the relation of the landform to the prevailing wind direction as well as by elevation.
- The earliest seasonal snowpack began accumulating on a northern aspect at relatively low elevation for the study area near and on the lee side of a ridgetop.
- The latest seasonal snowpacks accumulated on southwest-facing slopes over a range of elevations.
- Damping of daily soil surface temperature variation indicating snow accumulation did not occur until January 8 on our lowest elevation plot, which was on a southwestern aspect.
- Snow accumulated more at night than in the day.

In our study area, snowfall typically did not occur until October, but snow accumulation that remained for the season did not occur until later in November for most plots and not until December or January for a few. Although elevation was important to when snow accumulation began and how much snow accumulated, the first plot to accumulate a seasonal snowpack was at only 1595-m elevation, but importantly it was close to and on the lee side of a ridgetop, lying nearly perpendicular to the prevailing winds. It also was on a northern aspect and had forest cover that would tend to preserve any snow that fell. This plot was dominated by subalpine fir with a sparse Cascade azalea understory.

Four of the first ten plots to accumulate a seasonal snowpack that remained without interruption until spring melting were in the upper third of elevations, four plots were in the middle third of elevations, and two plots were in the lower third of elevations. Both lower elevation plots and two of the higher elevation plots lay in the lee side of a ridge or slope break. The effectiveness of a simple break in the slope for accumulating snow was illustrated by plot 18 (1741-m elevation), which was on a southwest-facing bench. This plot ranked

fourth in initiation of its seasonal snowpack, but this was only one day behind the plot that was ranked first. The lip of the bench acted similarly to a ridgeline by allowing snow blowing up the slope from the southwest and over the lip to settle on the bench. This accumulation combined with the tendency for the bench to form a frost pocket resulted in the deepest, longest lasting snowpack of any of our plots. As a result, the plant community present on this plot was a black alpine sedge meadow, which is typical of areas of late melting snow (Kuramoto and Bliss 1970).

Of the plots that accumulated snowpack, the latest were all on southwest-facing slopes and over a range of elevations, although the last plot (plot 23) to accumulate snow was, in fact, our lowest elevation plot. The average date of daily temperature suppression on this plot was January 8.

Mean monthly air temperatures from September through December were positively correlated with the arrival date of a continuous seasonal snowpack, which by itself tells us little more than snowpack arrives later in warm places. However, these correlations reflect the importance of microsites to snow accumulation. This is better reflected in the positive correlation between the mean monthly soil surface temperatures in September and October and the arrival date of a continuous seasonal snowpack. Microsites that developed higher soil surface temperatures in fall warmed both the air above and the soil below. The importance of this was shown by the positive correlation between mean monthly soil temperatures in November, December, and January and the arrival date of a continuous snowpack. It is likely that sites with warm soils received snow but did not accumulate it until the soils cooled sufficiently. Nighttime air temperatures were also positively correlated with the arrival date of a snowpack. This is because detectable snow accumulation over bare ground was more likely to occur during lower nighttime temperatures than in the higher temperatures of the day.

SNOW DEPTH—

- We judged relative snow depth by examining the daily fluctuations of 1.5- and 3-m-high air temperatures, but these estimates were affected by snow wells around our sensor trees.
- Snow depth around the tree bole exceeded 1.5 m on about a third of the plots in at least some years for at least a few days.
- Tree wells provided a small insulative effect to uncovered, 1.5-m-high sensors, which recorded 0.5 to 0.8 °C higher temperatures during winter than the 3-m-high sensors.

We were not able to measure snow depths at our study site, but to some extent, we were able to judge them by examining the daily fluctuations of 1.5- and 3-m-high air temperatures. However, these estimates of snow depth were probably affected by the development of tree wells in the snow around our sensor trees, so we assume snow depths farther away from the tree would have been greater than next to the bole where we placed our sensors. Based on continuous daily temperature fluctuation of 1.5-m-high air temperatures as well as their closeness in similarity of record to that of the 3-m-high air temperatures, we conclude that snow depth around the bole exceeded 1.5 m in only 11 of 35 plots for which there was sufficient data to judge, but this did not occur equally in all years. In winter of 2011 to 2012, damping of daily fluctuations in 1.5-m-high air temperatures occurred on 10 plots with an average period of 39 days. In winter of 2012 to 2013, this occurred on nine plots with an

average period of 67 days, and in winter of 2013 to 2014, this occurred on only two plots with an average period of 2 days. As the snow over the 1.5-m-high air temperature sensors deepened, the temperature moderated into the range of -2 to 0 °C, while at the same time, the air temperature measured by the 3-m-high sensor ranged from -16.5 to 13 °C.

This suggests that winters of 2011 to 2012 and 2012 to 2013 were the snowiest, and in 2013 to 2014, the winter was the least snowy, which generally agrees with the surrounding SNOTEL weather station data. Snow depth at the Waterhole SNOTEL weather station site, which has similar vegetation and climate to our study area, ranged from 264 cm in winter of 2013 to 2014 to 396 cm in winter of 2011 to 2012, but SNOTEL equipment failure in winter of 2012 to 2013 prevented a comparison for that year. The nearest SNOTEL weather station site to ours (Dungeness) had its highest accumulation in winter of 2012 to 2013; however, the deepest snow at that site occurred in winter of 2011 to 2012. Both snow depth and total accumulation were greater in winter of 2011 to 2012 at the Mount Crag and Buckinghorse SNOTEL sites.

Although snow did not cover most of the 1.5-m-high air temperature sensors, it did affect their winter temperatures. We found that they were, on average, 0.5 to 0.8 °C warmer during winter than the 3-m-high air temperature sensors, indicating that the 1.5-m-high air temperature sensors received a small insulative effect from their position in the tree well.

Musselman et al. (2008) measured snow depth in and around tree wells under blue spruce (*Picea pungens*) in the subalpine zone of New Mexico and found that average snow depth in open areas was 98 percent greater than in tree wells but varied from 64 percent for trees with 2-m-radius crowns to 200 percent for trees with 3-m-radius crowns. If we assume most of our tree well snow depths averaged 100 to 200 cm and our trees had 3-m-radius crowns, then snow in open areas accumulated to 2 to 4 m in depth according to their findings, which is similar to the Waterhole SNOTEL weather station site, which ranged from 261 cm in winter of 2013 to 2014 to 391 cm in winter of 2011 to 2012. However, our study area has about 18 percent more precipitation according to PRISM, so this may be an underestimate. This, of course, implies that our 3-m-high air temperature sensors were themselves in tree wells, but we know that all but one remained above the snow.

Only on plot 18 was one of our 3-m-high air temperature sensors covered with snow, so we can say with certainty that snow rarely reached as high as 3 m next to the tree boles. Plot 18 was the snowiest site, and the 1.5-m-high air temperature sensor there was covered with snow for 97 days per year on average. The upper sensor at this site was placed at only 2.8 m because the tallest tree was only 2.9 m high. We cannot rule out that the tree was bent under the weight of the snow, decreasing the height of both sensors, but especially the upper one. We suspect that this was the case, as temperatures measured by both sensors resumed daily fluctuation in spring on the same day, suggesting that the tree top was under tension from being bent and rebounded from snow cover on the date that temperature fluctuation resumed. However, in each year, when we returned in summer, the tree was upright and undamaged, so any bending that took place was not severe. We are confident that snow depth exceeded 1.5 m at this plot but cannot say by how much.

SNOWPACK DURATION—

- The duration of the seasonal snowpack was determined by aspect, proximity to a ridgeline perpendicular to the prevailing wind direction, and elevation.
- Aspect is a complex variable with solar exposure and snow redistribution components.
- Night and morning air temperatures were negatively correlated with the duration of the seasonal snowpack, but correlations with daily air temperatures were not significant, suggesting that the duration of the seasonal snowpack is influenced more by nocturnal air temperatures.
- Colder February surfaces and shorter lasting snowpacks occurred in areas where winter thaws reduced or wind eroded the snowpack.
- Melting snow maintained a soil surface temperature of 0 °C, but once the snow was gone, there was an instant return to daily temperature fluctuation.

Our analysis showed that the three factors most important in accounting for the duration of seasonal snowpack were aspect, proximity to a ridgeline generally perpendicular to the direction from which snowbearing storms approached, and elevation, respectively. However, aspect (negative relation), a complex variable with both solar exposure and snow redistribution components, accounted for much more variation (30 percent) than any other variable. Also, the closer a plot was to the lee side of a ridge that was oriented more-or-less perpendicular to the direction of the prevailing winds, the longer the snowpack lasted, and the higher in elevation a plot was, the longer the snowpack lasted (8 and 7 percent variation accounted for, respectively). Even so, the model only accounted for about 45 percent of the variation, leaving 55 percent unexplained. Some of the unexplained variation might simply be due to inadequate measurements. For example, the proximity to the ridgeline was measured from air photos and did not account for local variations in wind direction due to topography, sharpness of the ridge crest, or exact angle of the crest in relation to the wind. However, this would have required a detailed study of windspeeds and directions over many points on the landscape that we were not able to do. Even so, our crude approximation of ridgeline effects was significant. A more sophisticated approach to ridgeline interactions with wind patterns would likely have produced better results, but the interactions of other local topographic and vegetation features with local wind patterns probably also account for a large portion of the unexplained variation.

Night and morning quarter-day air temperatures were negatively correlated with the duration of the seasonal snowpack. The importance of temperatures at these times as opposed to the afternoon suggests that snow accumulation is more likely to occur from the evening through the night and into the morning. There were no significant daily correlations with soil temperature and the duration of the seasonal snowpack, but the soil surface temperature in quarter-day 4 was negatively correlated with the duration of the seasonal snowpack, suggesting that micro-sites with higher evening soil surface temperatures delay formation of snowpack.

Mean monthly air temperatures that correlated with the duration of the seasonal snowpack included only December, January, and May. The importance of May air temperature is obvious, as this is when air temperatures are rapidly warming and when most of the plots melted out. December and January are important because these are the months when areas of slower snow accumulation become covered—the areas of faster snow accumulation having done so in November and early December. Presumably, lower air temperatures in these months allow earlier accumulation.

The only mean monthly soil surface and soil temperatures to correlate with the duration of the seasonal snowpack were in February, April, and May for the soil surface and May and June for the soil. Except for the February correlation, these were negative correlations. However, the soil surface and soil correlations simply reflect postmelting soil and soil surface warming. The earlier the snow melted, the warmer the soils became in these months.

Colder February surfaces indicated shorter lasting snowpacks. This happens because winter thaws or shallow snow cover due to wind-eroded snowpack exposes the surface to greater radiational heat loss. With short winter days and long nights, these soil surface temperatures may drop well below 0 °C under their shallow snow cover. Soils in these shallower-than-average snowpack situations melted out sooner than average in spring because most had southern to western aspects. A deep covering of snow in February will maintain warmer soils, near 0 °C. So, higher soil surface temperatures at this time of year indicated a deeper snowpack and later melting. Whenever the soil froze because of shallow or late arriving snow, if the snowpack later deepened, the soil temperature rose back to the vicinity of 0 °C. This is because of the constant heat flux from deeper soils to the near surface, and because snow keeps heat from releasing to the atmosphere, eventually the energy is consumed, thawing the frozen ground (Zhang et al. 2005). Often, snowpack on our shallower snowpack sites deepened enough in March to return to a steady temperature near 0 °C before melting in April and May.

Because, we did not measure snow depth, we do not know the snow depth required to prevent freezing at the soil surface or at 20-cm depth. Goodrich's (1982) model of the effects of 50 cm of snow on soil temperature produced effects similar to what we observed, suggesting that our observations can be accounted for with less snow than what accumulated at our study area. Also, we detected a damping of daily temperature fluctuations in snow events lasting less than a day, suggesting that even shallow snow cover has a detectable effect. Early in the season, while such events were detectable, we observed both soil freezing (albeit not as severe as during the night in the absence of snow) and snowmelt resulting in loss of the snowpack, which manifested as a temporary return of daily temperature fluctuations. Melting snow maintains a surface temperature of 0 °C regardless of the air temperature above, as long as meltwater seeps into the soil. Zhang et al. (1997) found, as did we, that during spring snowmelt, soil temperature was maintained at 0 °C by meltwater from the snowbank above. However, once the snow was gone, there was an instant return of daily temperature fluctuations. This effect is so sensitive that it has been found to closely agree with the U.S. Department of Commerce, National Oceanic and Atmospheric Administration's, National Weather Service records (Zhang et al. 2005).

SNOWMELT—

- Snowmelt proceeded from low to high elevation and from southwestern to northeastern aspects, the latter being dependent on both temperature and accumulation factors.
- Aspect, elevation, and proximity to a ridgeline oriented perpendicular to the prevailing winds were important in early-season accumulation and late-season loss of snowpack.
- Cold nights were especially important in slowing snowmelt.
- Air temperatures in December and January were important to when a snowpack formed but were negatively correlated with the date of snowmelt.
- Air temperatures in April and May strongly influenced snowmelt on nearly all plots.

In spring, snowmelt proceeded generally but not strictly from low to high elevation. Plot 35 (1742-m elevation), the first plot to lose its seasonal snowpack (March 27), was on a highly exposed west- to southwest-facing ridgetop. On the windward side, the plant community was alpine tundra, and on the ridge and slightly to the leeward side, the community was subalpine fir/krummholz. Wind removes snow from the ridgetop and redeposits it on the lee slope, which is also a nonforest community due to late-melting snow. Thus, the snowpack on this plot did not become as deep as on some other plots, and the exposure to the sun was quite high and direct. The next three plots to lose their snow cover were all on southwestern aspects but included both our lowest elevation plot and a plot higher up in the upper third of elevations.

The first 5 plots to accumulate a seasonal snowpack were among the last 10 plots to have it melt. Thus, aspect, elevation, and proximity to a ridgeline running perpendicular to the approaching storm tracks (or other topographic feature that acted similarly) were important in the early-season accumulation of snow and in late-season loss of the snowpack and thus in the total duration of the seasonal snowpack.

There was a negative correlation between all mean annual quarter-day air temperatures and the date of snowmelt, but the night and morning correlations were stronger than the afternoon and evening correlations. This suggests that cold nights are especially important in preventing snowmelt, possibly by causing free water in the melting snowpack to freeze. Mean monthly air temperatures from all months were also negatively correlated with the date of snowmelt. This would suggest little more than that warm places melt soonest, and places that are warm in one part of the year are likely warm in other parts of the year, except that the strongest correlations occurred in December through January and in April through May. Air temperatures in December through January are especially important in determining how soon the warmest microsites form a snowpack. The earlier the snowpack forms, the greater the subsequent accumulation, effectively pushing back the date of snowmelt. Air temperatures in April through May are largely responsible for melting the snowpack on nearly all the plots, so the higher they are, the earlier the snow melts.

There were also strong negative correlations between all mean annual quarter-day soil temperatures and the date of snowmelt as well as between the mean monthly soil temperatures from April through June. However, soil temperature under the snowpack at this time of year is close to 0 °C and varies only slightly among plots. The correlations with mean monthly April through June temperatures reflect the rise in the mean monthly soil temperature caused by including postmelting soil warming in the calculation.

BIOLOGICAL IMPLICATIONS—

- Our data show gradual tree establishment as the Little Ice Age waned, continuing to the present but with more rapid establishment in moister communities and on northern exposures.
- Wind deepening of snow in our study area resulted in lower summer soil temperatures because of late melting, which limited tree establishment in a black alpine sedge meadow and may contribute to depauperate understories in some subalpine fir stands.
- Although tundra had lower winter soil temperatures from slow snow accumulation, early spring melting caused rapid warming and a higher average soil temperature than in nontundra areas.
- Tundra had only two-thirds as many snow-covered days as nontundra areas.

Arrival and departure dates for snowpack and its depth and duration have important biological implications. As already mentioned, temperatures under the snowpack, although not subject to hard freezing, were also not high enough for active root growth. However, some plant processes are active in these environments. For example, embryo development in white marsh marigold (*Caltha leptosepala*) largely takes place under the snowpack (Forbis and Diggle 2001), and a number of subalpine geophytes, including yellow avalanche-lily (*Erythronium grandiflorum*) emerge through snowbanks in spring (Hamerlynck and Smith 1994). Other organisms, including many fungi (Cripps 2009), and a wide assortment of arthropods (Schmidt and Lockwood 1992) are active in the subniveal environment. Snow mold, which was observed in the study area, is an important decomposer of forest litter and is capable of high rates of growth under snow (Schmidt et al. 2008).

The accumulation of snow is known to be locally influenced by topography and vegetation. For example, individual trees create snow wells (Musselman et al. 2008), and snow can accumulate in forest canopy gaps (Teti 2003); in the lee side of trees (Hiemstra et al. 2002), tree islands (Holtmeier and Broll 1992), and shrubs (Essery and Pomeroy 2004); and on various topographic lows, cols, and lee slopes (Hirashima et al. 2004).

The date of snowmelt was an important determinant of subalpine meadow community composition in the North Cascades of Washington (Evans and Fonda 1990). Meadows that were dominated by green false hellebore (*Veratrum viride*), Sitka valerian, showy sedge (*Carex spectabilis*), broadleaf lupine, American bistort (*Polygonum bistortoides*), Cascade bilberry (*Vaccinium deliciosum*), pink mountainheath (*Phyllodoce empetrifomis*), western moss heather (*Cassiope mertensiana*), partridgefoot (*Luetkea pectinata*), and black alpine sedge emerged from the snowpack at successively later dates (Evans and Fonda 1990). None of these meadow types, as described by Evans and Fonda (1990) grew in our study area except for the black alpine sedge type, because of a drier climate. Broadleaf lupine emerged from the snow in the middle of their sequence but was late in the sequence in our area as most of the surrounding landscape was relatively warmer and drier than our broadleaf lupine habitat. Near Hurricane Ridge in the Olympic Mountains, broadleaf lupine emerged from the snowpack from May 20 through July 28 but grew best where the growing season was 60 to 80 days long (Canaday and Fonda 1974).

The length of the snow-free season is a determinant of plant community type in some subalpine settings, and the fluctuation in duration of snowpack has been shown to affect the ability of trees to invade some meadow types. Franklin et al. (1971) found decreasing rates of tree invasion over a series of communities that were dominated by pink mountainheath, high mountain cinquefoil (*Potentilla flabellifolia*), Sitka valerian, and Roemer's fescue on Mount Rainier in Washington. Of these communities, the longest lasting snowpack occurred in the pink mountainheath type and the shortest in the Roemer's fescue type, so in this case, moisture was more limiting than temperature. In our study area, which is climatically drier than where Franklin et al. (1971) worked, communities resembling Franklin's Roemer's fescue type are found, but neither pink mountainheath or high mountain cinquefoil occurred on our plots.

In most years on Mount Rainier, the growing season on the pink mountainheath type was not long enough to permit tree growth, but snowpack duration was not limiting for tree establishment in the Roemer's fescue type; other factors prevented invasion there, even though tree growth in the few trees that did establish exceeded that of the pink mountainheath type (Franklin et al. 1971). What Franklin et al. (1971) showed was that the tree

invasion in the pink mountainheath type was centered on a period around 1930 that was unusually warm and dry, resulting in reduced snowpacks and longer growing seasons. The implication is that a growing season long enough for tree establishment temporarily opened up in the moist, but snow-limited pink mountainheath type. The Roemer's fescue type, which is drought limited, did not benefit from a longer season. Equivalent kinds of communities are found in the Olympic Mountains, and a similar tree invasion of the pink mountainheath type was documented elsewhere in the Olympic Mountains (Agee and Smith 1984). However, Fonda and Bliss (1969) found a 1953 through 1960 tree invasion of Roemer's fescue/spreading phlox/broadleaf lupine meadow type in the northeastern Olympic Mountains that has not been found elsewhere in the Pacific Northwest. None of these establishment periods are apparent in our data. Rather, our data show gradual establishment as the Little Ice Age waned and continuing to the present. However, establishment has been much more rapid in moister communities, such as the subalpine fir/Cascade azalea plant association.

The subalpine fir/Cascade azalea plant association is typical of northern exposures in our study area, but it is frequently excluded from areas that are nearest to ridge crest locations. Although we did not place any plots in these nonforested areas near ridge crests, we did make observations. Areas immediately below a north-facing ridge crest tended to be zoned from top-down as follows: perennial snowbank, bare soil from late snowbank melting, sparse herbaceous community (including broadleaf lupine, Olympic Mountain ragwort [*Senecio neowebsteri*], Olympic larkspur [*Delphinium glareosum*], yellowdot saxifrage [*Saxifraga bronchialis*], Flett's ragwort [*Packera flettii*], and others), Cascade azalea brush field, then the subalpine fir/Cascade azalea plant association. These treeless snowbank communities showed every indication of having been larger in the past, and the sequence just mentioned appears to be successional in nature. The aforementioned herbaceous community only emerged from the snowbank in late July and early August.

According to Zhang et al. (2005), windblown snow deposited in depressions or on lee slopes can lead to either higher or lower annual soil temperatures. When such snow accumulation occurs in fall or early winter, the snow insulation effect dominates, resulting in higher annual surface temperatures. However, if the snow accumulation becomes too deep, the snow will cause lower surface temperatures through two mechanisms: deep snow will delay soil warming by its late melting and the process of melting consumes a large amount of energy long after other areas are snow free and warming (Zhang et al. 2005).

The dominant effect of wind deepening of snow in our study area was to cool soils through late melting. In the case of plot 7, cooling appears to result both from late melting and late covering. Plot 18 represents a case of depressional deepening of snow where the bench forms a depression relative to the wind direction blowing upslope, and this plot had the lowest mean annual soil temperature of any nonforested or open-canopy plot in our sample (third lowest mean annual soil temperature overall). In most other cases, deepening of snow was the result of lee slope accumulation enhanced by vegetational capture. Plot 32 is a case in point. It had the second lowest mean annual soil temperature of any plot, despite being in the lower part of the middle third of elevations for the study area. We suspect that its depauperate Cascade azalea understory is due in part to the low soil temperature, but its 75-percent canopy closure is also important in this regard. We also had cases where both lower soil temperature from slow accumulation of snow in fall and rapid warming from early melting occurred in the same place—thus a more extreme environment. An example

is the tundra on the windward side of the krummholz plot 35 where wind prevents snow accumulation well into winter, allowing the soil to freeze relatively deeply, but because the snowpack does not become deep, it melts earlier, allowing for rapid warming in spring. These processes seem to be present to varying degrees in other tundra locations, especially those with signs of solifluction. Plots with a strong tundra component had soil temperatures averaging about 1 °C higher than the remaining plots; these warmer plots averaged only two-thirds as many snow-covered days.

IMPLICATIONS OF SNOWPACK REDUCTION FROM CLIMATE CHANGE—

- A reduced snowpack in open areas would likely cause more frequent and deeper soil freezing in winter, but warmer summer soils would result from earlier snowmelt.
- Longer, warmer growing seasons will allow trees to invade upslope wherever enough soil water and stable soil is present.
- Dry, south-facing slopes in our study area may become too extreme for subalpine fir.

The climate has been warming since the Little Ice Age, and indications are that this will continue. Climate change will likely result in warmer winters leading to less snowfall. These changes may lead to decreases in winter soil temperatures and more soil freezing because of lack of an insulating snow cover. However, as already discussed, such areas of shallower snowpacks tend to melt sooner and warm earlier, faster, and more than other soils. Thus, at least in open areas, we would expect a more extreme soil environment. Results from snow manipulation experiments in the Northeastern United States indicate that even mild winters with low snowfall resulted in increased soil freezing (Groffman et al. 2001, Hardy et al. 2001). These results suggest that a climate shift toward less snowfall or a shorter duration of snow on the ground will produce increases in soil freezing in otherwise snowy parts of northern latitudes (Zhang et al. 2005).

Warmer growing seasons will allow trees to invade upslope where they find enough soil water and stable soils. However, the dry, south-facing slopes in our study area may become too extreme for this to occur, at least for subalpine fir. Even though subalpine fir is currently able to invade these slopes, it was far less vigorous than on north-facing slopes. A longer, warmer drought season, possibly coupled with soil churning from winter soil freezing might be sufficient to discourage at least this species from growing on these slopes. This could provide habitat for some tundra species that might otherwise vanish.

Bedrock, Regolith, Soil Texture, Solifluction, and Soil Movement—

- Eighty-eight percent of plots with nonsorted stripe solifluction were associated with basaltic regolith.
- Areas with solifluction occurred on steeper south- or west-facing slopes at higher elevations and had more coarse fragments in the soil than areas without solifluction.
- The mean annual soil temperatures of plots with solifluction did not differ from plots without solifluction, but soil freezing and thawing occurred in at least some years, depending on the annual snowpack.
- About 15 to 20 percent of the area has soil movement, which probably limits tree establishment, especially on south- and west-facing slopes.
- Spreading phlox appeared to be more tolerant of slope instability than many species, providing habitat for other species to colonize.
- Deep, unstable scree deposits of small, loose rock fragments formed on steep slopes underlain by argillite that few plants colonized.

Bedrock can influence vegetation in several ways because of differences in how it weathers and the products into which it weathers. Thus, it can influence soil moisture through the degree and orientation of fracturing and the particle sizes that it tends to form during weathering (discussed in the following section). The decomposition products can also influence the balance of soil nutrients. We did not conduct soil nutrient analyses, but Kuramoto and Bliss (1970) reported on Olympic Mountains soils developed on parent materials similar to those in our study area. They noted that soils were mostly poorly developed, the less-developed soils generally had higher amounts of available nutrients, and pH decreased with depth.

Among the surficial soils of community types resembling ours (a dwarf sedge community similar to our black alpine sedge community, a grass-forb community somewhat similar to our subalpine fir/blue wildrye community type, and a dry grass-forb community of basaltic substrates), Kuramoto and Bliss (1970) reported pHs of 3.8 to 6, organic matter of 3.2 to 5.8 percent, nitrogen of 0.36 to 0.73 percent, phosphorus of 11 to 42.5 parts per million, and potassium of 1.50 to 3.04 milliequivalent/100 g. Total nitrogen in the mineral soil was closely associated with organic material and differed little among community types (Kuramoto and Bliss 1970). The physical properties differed little between soils in their plant communities except for their dry grass-forb community type, which grew on basaltic regolith with a higher coarse fragment content than most other communities, which grew on sedimentary regoliths.

Schreiner (1994) suggested that soil moisture is a primary driver of plant community composition but that slope, substrate characteristics (i.e., particle size and the quantity of bedrock near the surface), and parent material play secondary but crucial roles, although he was unclear about the mechanism. Soil stability has also been implicated as a factor in subalpine and alpine vegetation patterns in the Olympic Mountains (Bell and Bliss 1973, Belsky and del Moral 1982, Pfitsch and Bliss 1985). According to Schreiner (1994), parent material and substrate size may influence slope stability.

In the northeastern Olympic Mountains, solifluction has been observed in several forms. A common form in steeper parts of our study area is what Washburn (1956) referred to as nonsorted stripes, also referred to as solifluction stripes, in which stripes of vegetation alternate with a nonsorted mix of stones and finer rock and soil materials. This kind of solifluction occurred primarily in areas having basaltic regolith in our study area. Bell and Bliss (1973) reported on steep slope movements of rock stripes from Obstruction Point, 22 km northwest of our study area, and Hansen-Bristow and Price (1985) studied turf-banked terraces on gentle topography.

Solifluction is strongly affected by soil moisture content as well as particle size (Goldthwait 1976). Small-pattern solifluction occurs in areas of exposed soil consisting of nonsorted to poorly sorted gravel- to boulder-sized rock fragments suspended in a matrix of mud or sand (called diamicton). This material is subjected to deep annual freeze and thaw (10 to 50 cm or more), has abundant soil moisture, and is in areas with mean annual temperatures of -2 to 5°C (Goldthwait 1976). Because coarse soils have higher thermal conductivity and lower moisture, seasonal temperature fluctuation at depth is much greater than for fine-grained soil (Goodrich 1982). However, the fine soil fraction is important. A fine soil fraction containing 2 percent clay is necessary for solifluction, with 3 to 8 percent most effective (Corte 1961). Some of our plots that showed evidence of solifluction met these conditions.

To form a diamicton, bedrock weathering must produce an abundance of large rock fragments. Our study area is almost equally divided into basalt and sedimentary substrates, which had different weathering patterns (fig. 73). Weathering of the sedimentary rock, which mostly consisted of brittle, black argillite, produced mostly gravel-size splinters and laminar fragments. This material tended to form loose, often poorly vegetated scree slopes on southern and western aspects, which was also observed by Bell and Bliss (1973) near Obstruction Point. However, the basalt weathered into a larger range of durable fragments from gravel to boulders. We found that 88 percent of our plots with nonsorted stripe solifluction were associated with basaltic regolith, indicating strong bedrock control of this process.

We found visual evidence of solifluction on 14 plots, nearly all on south- or west-facing slopes, similar to what Bell and Bliss (1973) found at Obstruction Point. A comparison of our plots with and without solifluction showed that soils with visible signs of solifluction were significantly steeper, higher in elevation, and had more coarse fragments in the soil than those without solifluction, but they were in only marginally colder areas (a mean annual air temperature of 2.4 °C compared to 3 °C, $P = 0.06$), and the mean annual soil temperature for plots with solifluction did not differ from those without, suggesting that thermal conditions suitable for solifluction are widespread in this area but that nonsorted stripes are limited by the presence of diamicton.

Soil temperatures at 11 of the 14 plots with solifluction showed various levels of freezing and fluctuation in November, December, and January in at least 1 of 3 years. Some of these



Figure 73—Regolith types in the Olympic Mountain whitebark pine communities study area. Above the white line, the regolith is dominated by basalt, and below the white line, the regolith is dominated by argillite. Note the rock striping on the basaltic-dominated regolith but not on the argillitic scree. Note also how the basaltic regolith ravel over the argillitic scree, blurring the line between the two. The oval patches of vegetation in argillitic scree (upper left corner) are skirted subalpine fir trees. Google Earth image; July 30, 2017.

plots showed similar temperature fluctuations at other times of winter and spring as well, but such freezing and temperature fluctuations were largely concentrated in fall and early winter. We assume that freezing and temperature fluctuations at shallower depths were more extreme and occurred over a longer period than what we recorded at 20-cm depth. We also assume that if subzero temperatures reached 20-cm depth, freezing actually extended to a deeper depth, but we cannot say how deep. Thus, in all but three cases the visual evidence was supported by soil temperature data.

We have not seen anything in the literature suggesting how often soils must be subjected to such conditions to produce rock stripes. It would appear that in our study area, this is not a consistently annual phenomenon and that when it does occur, it may be of variable intensity. The potential for such frost action seems strongly dependent on the snowpack depth. Thus, a year with less snow or more wind removal might produce stronger solifluction.

It may be that solifluction was more active during the Little Ice Age and that some areas with visible rock stripes are now inactive. This may be the case, for example, with the three plots that did not freeze at 20-cm depth or did so without temperature fluctuation. If this is the case, it must have ceased recently, as there was little lichen growth on the rocks in the stripes that we observed. Trees were establishing in many of the areas with rock stripes, suggesting that at least some areas have become inactive. However, we cannot be certain that all solifluction has ceased on the three plots where we did not find suitable thermal conditions in our 3 years of observation.

Such unstable soils represented a considerable part of the study area. Striping visible on Google Earth imagery occupied 5 to 10 percent of the area. In addition, apparent active scree and talus slopes on western to southern aspects occupied about 10 percent of the study area. Also, 39 percent of our plots had visual evidence of solifluction. Although we cannot be precise, it appeared that soil movement was occurring in at least 15 to 20 percent of the area. This has, no doubt, had a considerable impact on where trees have been able to establish and is perhaps responsible for the counterintuitive observation that the apparent tree line is lower on south- and west-facing slopes than on north-facing slopes, even in similarly steep areas. Many areas on south- and west-facing slopes have soils that are warm enough in the growing season to support root growth but are sparsely populated with trees.

Bell and Bliss (1973) measured rates of rock stripe movement of 3.5 to 4.5 cm per year (faster on steeper slopes). Rock stripe movement was greatest at the center of wide stone stripes and minimal alongside vegetation, and there was no movement of vegetation between the rock stripes (Bell and Bliss 1973). However, we found buried stems and dead seedlings incorporated into some stone stripes, suggesting failed colonization.

Bell and Bliss (1973) found, as did we, that as the slopes became steeper, the stripes tended to become less distinct. We found vegetation clumps were often anchored by spreading phlox that formed elongated clumps in line with the slope (fig. 74). Spreading phlox appeared to act as a stabilizer, providing habitat for other herbaceous species to colonize; this suggests that spreading phlox is more tolerant of these unstable slopes than many other species. The rate of rock movement is probably greater on these slopes, but neither we nor Bell and Bliss (1973) measured it.

Although solifluction has been invoked to explain nonsorted stripes (Washburn 1956), causes of regolith and soil movement on other scree slopes is less clear. As the term “scree” has been used in many ways and is often associated with talus slopes, we will describe our usage here. In our study area, there were large slopes of loose gravel and finer material.

Cliffs above and boulder fields below were often absent. This material is soft underfoot and may slide 50 cm or more when tread upon. People and animals leave obvious trails with a single passage, and animal trampling has been shown to cause significant movement on similar slopes elsewhere (Govers and Poesen 1998). In our study area, these slopes are more likely to be found in areas underlain by argillite than by basalt because of argillite's greater tendency to break down into smaller fragments (e.g., above plots 14 and 25). However, we also found similar materials in the upper portions of talus aprons generated below basalt cliffs (e.g., below plot 6).

Bell and Bliss (1973) and Matsuoka (1994) described movement of similar regolith formed from sedimentary rocks on slopes in the Olympic Mountains and Japan, respectively. Bell and Bliss (1973) found that regolith movement on open scree slopes was up to three times faster than movement in rock stripes (i.e., 10 to 14 cm per year). They observed a period of extreme instability associated with water saturation directly in front of receding snowbanks, suggesting that areas immediately in front of receding snowbanks are especially prone to downslope movement at this time. However, Matsuoka (1994) found that similar steep alpine slopes in Japan moved in response to short-term, frost-heave cycles during fall and spring when not covered with snow and thus exposed to daily freeze-thaw cycles. Longer but stable seasonal freezing that occurred during winter had little effect; rather, up to 30 to 40 frost-heave cycles associated with daily or multiday freezing periods that affected the upper 15 cm of soil generated 23 cm per year of frost creep at the surface, decreasing to negligible amounts at 44-cm depth.

Such soil movement affects the structure, distribution, and composition of vegetation. Rock stripe vegetation consisted mostly of tundra species, often dominated by spreading phlox. It is difficult for trees and shrubs to establish on such actively moving slopes. We observed occasional tree seedlings with curved stem bases and long, buried stems (30 to 40 cm) running upslope to the point of rooting in some of these areas.



Figure 74—An elongated clump of spreading phlox on a slope undergoing solifluction in the Olympic Mountain whitebark pine communities study area. Photo by David H. Peter.

Few plants of any kind colonize the faster moving scree slopes, but we did find Olympic onion (*Allium crenulatum*) growing in this situation. Del Moral (1983) considered Olympic onion talus slopes to be highly disturbed because of soil movement. Such bulbing onions have annual roots and shoots and pass much of the year as dormant bulbs (Kamenetsky and Rabinowitch 2006). Thus, during fall and early winter when most soil movement is occurring, there are no parts subject to damage, and the bulb would simply be transported along with the rest of the soil material. In spring, once the soils warmed enough for new root growth, the soils would be stable. We did not find any shrubs or trees in this situation.

In comparing the canopy cover of plants growing in the three main plant associations or community types where solifluction occurred, with or without solifluction, subalpine fir, shore pine, Douglas-fir, common yarrow, squirrelnose, broadleaf lupine, and Douglas' catchfly had significantly higher canopy cover on plots without solifluction. There were no species with significantly higher canopy cover on solifluction plots. Although not significantly different, whitebark pine, western white pine, common juniper, and spreading phlox had higher canopy cover values on plots without solifluction. Thus, all the tree species that grew on these slopes had lower canopy cover in areas showing signs of solifluction.

Soil Moisture

- Because basalt is harder than argillite, basaltic soils averaged 66 percent coarse fragments, while argillitic soils had only 22 percent, resulting in drier and more variable moisture conditions in basaltic soils.

Previous Olympic Mountains subalpine and alpine investigators have found that soil moisture is a primary environmental factor controlling plant community composition and distribution and that its availability is controlled by multiple factors, including precipitation, date of snowmelt, aspect, and elevation (Belsky and del Moral 1982, Canaday and Fonda 1974, del Moral 1983, Fonda and Bliss 1969, Kuramoto and Bliss 1970, Pfitsch and Bliss 1985).

Daubenmire (1943) showed in greenhouse experiments that although species of warmer climates had higher resistance to heat girdling from surface temperatures, all species he examined had high enough resistance to permit them to grow far outside of their natural range. But with soil moisture, Daubenmire (1943) found 100 percent mortality occurred when 70-day-old subalpine fir seedlings were subjected to 4 days of soil moisture below the wilting coefficient. The same level of mortality for Douglas-fir required 8 days of the same treatment. Thus, species differences in soil water drought tolerances exist within conditions that should be expected in typical seedling root zones and were more likely than surface temperatures to limit subalpine fir.

Basaltic rock weathers to soil much more slowly than argillite. Differential weathering and erosion are the reasons why major mountain peaks in this area are composed of basalt, while lower areas and river valleys lie in argillite and other sedimentary rocks (Tabor 1975). Thus, a large fraction of the soils developed from basaltic regolith in our study area was composed of coarse fragments, which limits the water storage capacity to the fine material between them. Basaltic soils averaged 66 percent coarse fragments while argillitic soils had only 22 percent. However, the soil between the fragments differed little in texture or water content. When a soil-water probe is used, there is an inherent bias in that it cannot pass through and measure the water content of rock. Thus, it can only be inserted into and measure water content of finer soils between large rock fragments and is not able to account

for the low water content of the large volume of rocks. But because of this large difference in coarse fragments, argillitic soils have up to three times more potential to store water than basaltic soils. Fonda and Bliss (1969) suggested that Olympic Mountains stony volcanic soils held less water compared to sedimentary soils. The difference in the standard deviations of summer soil moisture, both among years and within plots, also reflected an important difference in available moisture. Summer soil moisture was not only less but was also much more variable in basaltic soils.

CORRELATION ANALYSIS—

- The strongest correlations between summer soil moisture and temperature were negative correlations with soil surface temperatures in June, suggesting transpiration-driven soil drying.
- The driest soils occurred in open stands with direct, summer, afternoon soil heating, especially on lower elevation, south- and southwest-facing slopes.
- There were many significant negative July, August, and September correlations between soil surface temperatures and summer soil moisture, but none were as strong as in June.
- Depth of snowpack and variables related to snowpack persistence did not correlate with summer soil moisture perhaps because we measured soil moisture from the top 12 cm of soil in July and August, and residual soil moisture from melting snowbanks occurred deeper in the soil at this time.

Our correlation analysis examined the relative importance of air, soil surface, and soil temperatures to surficial summer soil moisture. In total, there were 560 variables examined, of which there were 38 significant correlations with air temperatures, 44 significant correlations with soil surface temperatures, and 47 significant correlations with soil temperatures. All were negative correlations.

Our finding that there were similar numbers of negative correlations between air temperature and summer soil moisture in all months of the year implies that warmer sites dry faster than cooler sites and that sites that are relatively warm in one part of the year tend to be relatively warm in other parts of the year as well (excepting areas with shallow winter snow described above). Warmer sites were lower in elevation, steeper, on southern and southwestern aspects, and had more open canopies.

Negative correlations between soil and soil surface temperatures and summer soil moisture were concentrated in summer months because under winter snow or the influence of fall and spring rains, there is little variation. However, within summer months, there were differences in the distribution and strength of the significant correlations. The single strongest correlation ($r = -0.78$) was with the mean June soil surface temperature in quarter-day 4 followed by the mean daily soil surface temperature in June ($r = -0.68$). Thus, sites with early-summer warming dried the fastest. Soil drying in June may have as much to do with high rates of transpiration from vegetation growing in the warmer soils as it does with direct evaporation from the soil. Transpiration is often the dominant soil drying mechanism when soil water is plentiful, but evaporation increases in relative importance as soils approach critical water potential (Craine and Dyzinski 2013). The next strongest correlation was with the mean September maximum air temperature in quarter-day 4 ($r = -0.68$). As mentioned, the afternoon pulse of heat absorbed at the surface shows up at 20-cm depth in quarter-day 4. Also, shaded soils undergo minimal soil heating, so these quarter-day 4

correlations imply that the driest soils occur in open stands where direct summer afternoon soil heating occurs.

Soil surface and soil temperatures in July and August were also important to soil moisture content. The correlations with these temperatures were not as strong but were more numerous than the June and September correlations. The greatest number of significant soil temperature correlations with summer soil moisture occurred in July, but for soil surface temperatures, this occurred in August. Kuramoto and Bliss (1970) found that most aboveground biomass production in dry and mesic grass and grass-forb Olympic Mountains subalpine meadow plant communities occurred by mid- to late July. Green biomass production declined at the end of July and early August for the remainder of the season, suggesting a drought limitation.

Variables relating to the duration of seasonal snowpack or its persistence in spring did not correlate significantly with summer soil moisture. Although this seems counterintuitive, we point out that our summer soil moistures were derived only from the top 12 cm of soil in July and August, and residual soil moisture from melting snowbanks may be found deeper in the soil at this time. Kuramoto and Bliss (1970) found that available soil moisture at 20- to 25-cm depths lasted 3 to 4 weeks longer than at 0- to 5-cm depths in some plant communities in the Olympic Mountains. Over a larger landscape with greater variation in snow depths and melting dates, snowpack relations may be more apparent. However, one late melting plot (plot 18) had consistently moist soils. This black alpine sedge community also had a more water-retentive soil that was high in organic matter. The accumulation of organic matter suggests a long period of uninterrupted accumulation under cool, moist conditions. Similar organic soil accumulated under a black alpine sedge community in the Olympic Mountains that was investigated by Gavin and Brubaker (1999). By studying accumulated pollen, they found that their site had hosted several different kinds of vegetation in the past, but since the beginning of the Little Ice Age, it had consistently hosted a black alpine sedge community (Gavin and Brubaker 1999) with an O horizon above an A horizon high in organic material.

REGRESSION ANALYSIS—

- Slope steepness, overall microtopography, and aspect together accounted for about half of the variation in summer soil moisture.
- June soil temperature in quarter-day 4, slope steepness, and overall microtopography together accounted for 63 percent of the variation in summer soil moisture.
- Plots with high soil temperatures in quarter-day 4 had open canopies that permitted more soil warming and thus drying.
- Increased convexity and steepness decreased summer soil moisture as did the amount of solar radiation striking the surface.

In addition to temperature and snowpack-related variables, we also examined correlations between summer soil moisture and physical site variables, which indicated that steep, convex, southwestern exposures were driest and suggested relationships that would be better approached with regression analysis.

We modeled summer soil moisture in two ways. In model 1, slope steepness, overall microtopography, and aspect accounted for 51 percent of the variation in summer soil moisture. Thus, purely physical site features accounted for about half of the variation in summer soil moisture. Aspect along with slope steepness determined the potential for soil

warming, while slope steepness and overall microtopography determined how fast water ran off as opposed to infiltrated into the soil. Thus, this model included both factors that determined the ability of water to get into the soil and factors that tended to cause it to evaporate out of the soil, yet a considerable amount of variation in summer soil moisture was not accounted for.

The significance of aspect in this model suggested that solar radiation is important. However, we found little correlation with any of the calculated potential solar radiation values for our plots. Of 42 variables investigated, including diffuse and direct solar radiation and duration of solar radiation for all months of the year and the year in total, the only variables significantly correlated with summer soil moisture were the duration of direct solar radiation in June ($r = 0.49$) and in July ($r = 0.36$). Aspect was negatively correlated with summer soil moisture, implying that warmer aspects would be drier. Although this finding seems logical enough, correlations with direct solar radiation counterintuitively suggested that higher irradiance was associated with more summer soil moisture. We know of no explanation for this, but correlations with ground-level PAR, which was obtained in July and August, also suggested that higher irradiance decreased summer soil moisture, which runs counter to the potential solar radiation findings.

Model 2 accounted for 63 percent of the variation in summer soil moisture. This model included June soil temperature in quarter-day 4, slope steepness, and overall microtopography. Plots with high soil temperatures in quarter-day 4 had open canopies that permitted more soil warming than plots with closed canopies. Thus, these sites dried faster as a result of greater soil heating and their susceptibility to convective air exchange, which reduced the accumulation of humidity from evapotranspiration processes. Ashcroft and Gollan (2013) found that soil drying was highly dependent on the vapor pressure deficit, which would be enhanced in open stands. Slope steepness and convexity have obvious implications for rate of water runoff, causing steeper, convex slopes to be drier.

Two things stand out relative to summer soil moisture: (1) characteristics reducing the surficial residence time of water (convexity and steepness) caused measurable decreases in summer soil moisture, and (2) the amount of solar radiation that strikes the surface in summer decreased summer soil moisture, as shown by the negative relationship with aspect and ground-level PAR. Higher soil temperatures occurred on southwestern aspects in areas with low percentages of canopy closure. Direct measurements of soil surface temperature revealed a stronger relationship between summer soil moisture and June surface temperature in quarter-day 4 because it integrated both aspect and canopy closure relations. Xue et al. (2020) found a similar negative relationship between mean growing-season soil temperature and soil moisture. They, like us, found that soil temperatures did not exhibit an elevational lapse rate, which they attributed to the uneven distribution of soil moisture (Xue et al. 2020).

Biological Relationships

In the following sections, we discuss the relationships between species abundance and environmental parameters that we documented to provide a more robust interpretation of species' requirements and tolerances. We also evaluated these relationships for entire plant communities in our study area.

Correlations Between Species Canopy Covers and Temperature

- Correlations between temperatures and species canopy cover indicated three thermal plant habitat groupings: neutral, warm, and cold.
- Positive correlations between species canopy cover and temperatures (warm habitat group), especially with air and soil temperatures, indicated lower elevation species approaching their higher elevational limits, but positive correlations between species canopy cover and soil surface temperature also indicated a preference for open, sunny conditions facilitated by a tolerance of high soil surface temperature.
- Negative correlations between species canopy cover and temperatures (cold habitat group) generally indicated an intolerance of heat or drought but in some cases indicated competition avoidance facilitated by cold tolerance.
- Subalpine fir was in the neutral habitat group for air and soil surface temperatures, but its positive correlation with cool soil temperatures occurred because soil warming was limited by its shade, meaning this correlation indicated cold soil tolerance and was a consequence of its occupancy.
- Any benefit subalpine fir derives from shade-cooled soils is likely because of the suppression of competing species that require warmer conditions.

The relationship between temperature and species distribution is commonly acknowledged but rarely quantified; however, there are well known physiological reasons why plants are temperature limited. For example, below temperatures of about 5 °C for Engelmann spruce (*Picea engelmannii*) and 6 °C for shore pine, water uptake was severely restricted because of abrupt decreases in root permeability (Kaufmann 1975, Running and Reid 1980). As a result, and perhaps for other reasons as well, trees growing in cold soils may experience water stress, restricted nutrient uptake, decreased photosynthesis, reduced root or shoot growth, and delayed bud burst (Goldstein et al. 1985, Kaufmann 1975, Lopushinsky and Kaufmann 1984, Running and Reid 1980). Aboveground portions of plants are also subject to cold-induced damage, and this too can limit where they can grow. Minore (1979) listed frost tolerance of several Pacific Northwest conifer species as follows: lodgepole pine = western white pine > subalpine fir > Douglas-fir. There is less information on heat tolerance, and as a result, his comparisons in this regard are not helpful for our purposes. However, in terms of mean temperature relations, he lists (from warm to cold) Douglas-fir > subalpine fir = whitebark pine > lodgepole pine. However, it should be pointed out that he makes no distinction between lodgepole pine (*Pinus contorta*) varieties, and in our study area, we have only *Pinus contorta* var. *contorta*, or shore pine. He cautions that such varietal differences can affect species temperature tolerance (Minore 1979). In our study area, subalpine fir grew on colder sites than did shore pine, which may reflect less cold tolerance of shore pine compared to other varieties of lodgepole pine or that frost tolerance is of little concern in our study area, and other factors control the distribution of these two species. Because we did not record low temperatures as extreme as those often recorded in more interior lodgepole pine habitats, we suspect the latter is a satisfactory explanation.

Although plants, especially at higher elevations and latitudes, are often cold limited, the plants themselves may prevent soil warming with their shade. June through September 10-cm-deep soil temperatures under an open, Cascade azalea brush field, ranged from 5 to 9 °C in a British Columbia Engelmann spruce/subalpine fir zone site (Coates et al. 1991). However, when the shrub layer was removed, soil temperatures rose to 10 to 15 °C,

indicating that the shrub layer, even in the absence of an overstory, had a substantial effect on soil temperature. Interestingly, although there was no evidence that the vegetation depleted soil water during the growing season, moderate water stress occurred in Engelmann spruce and lodgepole pine seedlings planted in undisturbed Cascade azalea, most likely because low soil temperatures restricted water uptake (Coates et al. 1991).

In our study, three plots with high percentages of total canopy cover containing various combinations of subalpine fir overstory and Cascade azalea understory had June through September 20-cm-deep soil temperatures averaging 7.5 to 7.9 °C. Thus, we found similar soil temperatures on our Cascade azalea sites to what Coates et al. (1991) found but with varying levels of subalpine fir overstory, suggesting that multilayering of trees and shrubs had little additional effect over a single, dense layer of shrubs.

Ranking our 20 analysis species by the number of significant correlations between canopy covers and 65 temperature variables provided an objective comparison of their relative thermal habitat affinities on the study landscape (fig. 26). Because the air, soil surface, and soil thermal environments affect plants differently, the three rankings are somewhat different. However, there is broad similarity—on average, two and a half of the three lists were in agreement for any species. From this analysis, we identified three thermal habitat groups: warm habitat species were those with positive correlations with temperatures, neutral habitat species were those with no correlations, and cool habitat species were those with negative correlations.

The study area is central to the thermal affinities of neutral habitat species, like broad-leaf lupine and subalpine fir, while warm and cool habitat species were approaching thermal tolerance limitations. Thus, warm habitat species, such as white hawkweed and Douglas-fir, grew only on the warmest microsites of this landscape, while the cool habitat species, such as cliff dwarf-primrose and Cascade azalea, only grew on cold microsites. These relationships are specific to this landscape and its climate, so if we shifted our study location to lower elevations or latitudes, we would expect that some of the species that we found associated with cold environments would entirely disappear from our list, some which had previously been associated with warm environments would appear to be neutral, and species of warmer climes, not present on our current study landscape, would make their appearance among the warm habitat species. This tool could also be useful in assessing individual species response and vulnerability to climate change. For example, with climate warming, white hawkweed and Cascade deserparsley might become neutral habitat species on this landscape, implying that more area should be available, but for Cascade azalea, which is already confined to some of the coldest microsites, the available habitat would shrink.

A more dominant species, Douglas-fir, is also limited to warm microsites, but in this case, snow breakage may also be an important limiting factor. Although snow breakage is related to low temperatures, it is not entirely dependent on them, thus serving as a cautionary note for making interpretations with limited data. We did observe snow breakage of Douglas-fir on a subalpine fir krummholz site, but high winds were also likely contributors to the breakage. What we did not observe were young, supple Douglas-fir seedlings in colder areas, including at lower elevations on north-facing slopes, suggesting that germination is inhibited by cold soils. Although more research is needed to determine the proximal cause(s) of higher elevation limitations for Douglas-fir and other species as well, we believe it is likely that such causes will be closely related to temperature or perhaps combined with it.

The maximum soil surface temperatures that were recorded in open areas were potentially damaging to plants, so we interpret a positive correlation with soil surface temperature as a proxy for an open, sunny condition preference that is facilitated by species tolerance for high surface temperatures.

Douglas-fir, shore pine, white hawkweed, and Cascade deserts parsley all had positive correlations with air, soil surface, and soil temperatures. These shade-intolerant species are specialized for warmer conditions, which are not common in the study area. All four species can be found at much lower elevations, and they occur in the warmest microsites in the study area. Thus, they can be expected to respond positively to climate warming in the study area and probably already have done so. Douglas-fir sample tree ages were negatively correlated with elevation, suggesting upward migration.

Broadleaf lupine was in the neutral habitat group for air, soil surface, and soil temperatures, suggesting that this location is central to its thermal tolerance. Its tendency to grow in open areas on cool aspects and in partially shaded areas on warm aspects suggests an important soil temperature moderation role of trees for this species on the warmest aspects. Given that this species can be found at lower elevations, soil moisture, rather than heat, may be the reason for its presence in the subalpine fir/broadleaf lupine plant association.

Only two species, Cascade azalea and cliff dwarf-primrose, had significant negative correlations with air, soil surface, and soil temperatures. Cascade azalea rapidly disappeared at lower elevations indicating a narrow thermal tolerance with a preference for cool habitats. We found cliff dwarf-primrose only in the open, higher elevations of our study area, but it is occasionally found at lower elevations in rocky or cliff locations where competition from taller plants does not occur. Thus, this species has broad ecological tolerance but is relatively intolerant of competition, especially in the form of shade.

Subalpine fir was in the neutral habitat group for air and soil surface temperatures but was associated with cool soil temperatures as indicated by its negative correlation with soil temperature. During the snow-free season, soil warming was driven by direct radiation of the soil. Thus, this species' own canopy maintained lower surface and soil temperatures, which is also reported for other tree species (Breshears et al. 1998, Körner and Paulsen 2004). Under subalpine fir shade, the soil surface temperature approximated the air temperature, thus the correlations between subalpine fir canopy cover and air and soil surface temperatures were similar. However, because the shade limits soil warming, the association of subalpine fir with cool soils is likely a consequence of its occupancy rather than a needed condition. Indeed, shade-cooled soils limit tree growth at higher elevations (Körner and Paulsen 2004) resulting in an alpine tree line. If subalpine fir derives benefit from the shade-cooled soils beneath its canopy, it is likely because of suppression of competing species, such as Douglas-fir, which require warmer conditions than subalpine fir (Minore 1979).

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND AIR TEMPERATURE—

- Local climate generalists (species that did not have seasonal or daily correlations with air temperature) included subalpine fir, whitebark pine, common juniper, thinleaf huckleberry, broadleaf lupine, and orange agoseris.
- Species limited to warmer areas in this landscape included shore pine and Douglas-fir, and these species may benefit from a warming climate.

- Shade-intolerant species with strong affinity to the coldest areas, including cliff dwarf-primrose, Roemer's fescue, common yarrow, giant red Indian paintbrush, and hookedspur violet, will likely lose ground in a warming climate, which will bring competition with taller, shade-producing species.

Because air temperature is subject to convective mixing, it varies less among microsites than soil or soil surface temperatures. Thus, vegetation patterns and species preferences to air temperature tend to reflect more generalized patterns than with soil surface or soil temperatures. However, in a snow-covered landscape, air temperatures largely lose relevance to species buried under snow.

We viewed species that did not have seasonal or daily correlations with air temperature as climatic generalists within the study area, including subalpine fir, whitebark pine, common juniper, thinleaf huckleberry, broadleaf lupine, and orange agoseris. However, some of these species had various correlations with soil surface or soil temperatures (see below). In contrast, shore pine and Douglas-fir canopy covers were positively correlated with air temperature in every month of the year and in all quarter-days, indicating a strong climatic limitation to warmer areas in this landscape. Although the pattern was somewhat different, western white pine also seemed to be tied to warmer sites. These warm climate specialists have ranges extending to sea level. We would expect these species to have a positive response to climate warming in places similar to our study area and to increase their area of dominance. White hawkweed, Oregon boxleaf, and Cascade desertparsley had similar positive correlations between their canopy covers and air temperature throughout the year, but Oregon boxleaf canopy cover tended to be more strongly correlated with afternoon air temperature, and Cascade desertparsley canopy cover was more strongly correlated with daytime and evening air temperatures. Higher morning temperatures were only important to Cascade desertparsley in spring and fall, suggesting that this species would do better with a longer, warmer growing season.

Species such as cliff dwarf-primrose, which correlated with lower air temperatures at all times of the year and day, but especially at night, will likely lose ground in a warming climate. The preference of this heliophyte for cold environments probably has more to do with avoidance of taller species through its superior tolerance of dry, cold environments. Shade-tolerant Cascade azalea canopy cover was also negatively correlated with air temperature throughout the year and day, but especially in the afternoon. This fits well with the observation that it grew mostly on northern aspects in partially shaded situations.

Roemer's fescue, common yarrow, giant red Indian paintbrush, and probably hookedspur violet canopy covers were all more negatively correlated with nighttime than daytime air temperatures, although there was little seasonality in the correlations. As these are strong heliophytes that also grow in openings at lower elevations, we believe their cold tolerance provides them access to high-elevation, nonforested habitats and does not represent a physiological preference so much as a tolerance. At lower elevations, they are found on rocky south-facing balds, in anthropogenic prairies, or coastal bluffs and beaches. This suggests an enormous ecological amplitude as some of these sites can be warm. Thus, these species are heliophytic generalists seeking out sunny environments from low to high elevations, apparently regardless of air temperature. Such an amplitude suggests the possibility of physiological ecotypes, but to our knowledge this has not been investigated in this area, although many varieties of common yarrow are known, and ecotypes have been

studied in relation to elevation elsewhere (Clausen et al. 1941). Ours was variety *alpicola*. Littleflower penstemon canopy cover had only two negative correlations with March and April air temperatures in quarter-day 1, suggesting that it grows where it is exposed to low nighttime air temperatures as a result of early snowmelt. This suggests a preference for open sites with longer growing seasons that may become quite dry because of early loss of snow.

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND SOIL SURFACE TEMPERATURE—

- Strong positive or negative correlations between species canopy cover and soil surface temperature extremes indicated species that were intolerant of shade but tolerant of extreme conditions that enable them to grow in the open where such conditions occur.
- A preference for warmer winter soil surfaces (e.g., whitebark pine) indicated a preference for a deeper insulative snowpack that also provided growing-season moisture.
- The negative correlation between shade-tolerant Cascade azalea canopy cover and late-morning and early-afternoon summer and fall soil surface temperatures is due to tree shade, which also inhibits less cold-tolerant competitors.
- Cliff dwarf-primrose (and likely other alpine cushion plants) grew where fall and winter soil surfaces were cold, suggesting a tolerance of cold soil and frost heaving that precludes establishment of overtopping competitors.

The soil surface can be subject to large temperature variation, but this is minimized by vegetative cover in summer or snow in winter. Surfaces on relatively barren south- and southwest-facing slopes, however, heat rapidly to high temperatures during summer. Given the potential stress associated with such high soil surface temperatures, a preference for a warm soil surface in summer is likely a proxy for a preference for a generally warm opening. Nevertheless, a species with this preference must be adapted to tolerate these conditions.

Open slopes can be subject to extreme radiative heat loss at night, especially in winter, resulting in frost, frozen soil, and possibly higher daytime temperatures when the roots are frozen. But snow is insulative, so where it is present, the soil surface is warmer than where it is absent. Thus, a preference for warmer winter soil surfaces is a proxy for a preference for a deeper snowpack. In the subalpine and alpine, places that are not covered with snow in winter are subject to deep freezing and also dry faster in spring and summer because there is less snowmelt to wet the soil.

Whitebark pine canopy cover was associated with warmer soil surfaces in February and March. The warmer temperatures referred to are close to 0 °C, and low temperatures, by contrast, are about -2 °C, so it is likely that the difference has to do with the depth of the insulative snowpack. On south- to west-facing exposures where whitebark pine occurs, a deeper snowpack may be critical to a summer moisture supply. Two other species with similar canopy cover associations were orange agoseris and common juniper. White hawkweed, Cascade desertparsley, and shore pine canopy covers were positively correlated with fall or early-winter soil surface and soil temperatures, suggesting a sensitivity to frost heaving or solifluction.

Douglas-fir and Oregon boxleaf canopy covers were both associated with higher night and early-morning soil surface temperatures during summer months. These species are

more common at lower elevations and occur as low as sea level. This suggests a benefit in the study area from warmer nights as well as longer, warmer days (i.e., faster morning warming). However, the higher temperatures may be in part due to reduction of night rera-diation of heat by the overstory canopy (Oregon boxleaf generally grows in at least partial shade). Common yarrow and hookedspur violet had almost the opposite pattern. Both of these species grew in open areas where nighttime radiative heat loss might be expected to be considerable, lowering soil surface temperatures by the early morning. This is probably less a preference for low temperatures than a consequence of growing in open sites, but these conditions may discourage potentially competing species, such as Douglas-fir and Oregon boxleaf, from growing there.

Shore pine and white hawkweed grew more abundantly where soil surfaces were warmer in spring, summer, and fall. White hawkweed tended to grow in places with higher morning temperatures in the late summer and fall, and common juniper appeared to have a prefer-ence for places that warm more in the afternoon, especially in fall. Both suggested a prefer-ence for longer seasons, such as could be found at lower elevations, but both are heliophytes, and lower elevations are mostly forested. However, white hawkweed with its plumose seeds and rapid maturity is a common early-seral species that occurs down to sea level wherever the forest canopy has been removed. It is only where extreme environments preclude arbo-real species that it might be termed a late-successional species. Common juniper, although less common at lower elevations, does occur in dry, rocky situations that create permanent openings, but being a slow-growing species, it cannot exploit most seral situations. Thus, the relatively stable subalpine environment provides its principal habitat.

The negative correlations between Cascade azalea canopy cover and late-morning and early-afternoon summer and fall soil surface temperatures were probably partly due to shade produced by it and its common associate, subalpine fir. But because this species does not occur at lower elevations, like some of the species just mentioned, we assume it derives a benefit from the cool environment where it grows—perhaps this would take the form of decreasing the vigor of potential competitors.

Cliff dwarf-primrose grew more abundantly where soil surfaces were cold in fall and winter, suggesting a strong association with places that have high radiational heat loss and a shallow snowpack. These are places that are entirely open and exposed to enough wind to keep the snowpack to a minimum. We suspect that cliff dwarf-primrose and similar heliophytic cushion plants have wider physiological tolerances, but this harsh environment precludes establishment of potentially overtopping competitors.

Broadleaf lupine canopy cover was negatively correlated with soil surface tempera-tures in April and May from morning through the evening. Warming of the soil surface in April and May represents an early melting of the snowpack. After snowmelt, soil surface temperatures rapidly rise in the daytime. Species such as broadleaf lupine may find it diffi-cult to tolerate excessive summer drought in places that melt out too early. Snowmelt typi-cally occurred on broadleaf lupine plots later than for most other species. As it is insect pollinated, there may also be a pollination advantage to not starting growth too early in the season.

MONTHLY AND QUARTER-DAY CORRELATIONS BETWEEN CANOPY COVER AND SOIL TEMPERATURE—

- For species with canopy covers that were associated with high, summer soil temperatures, much of the study area is too cold to sustain processes such as root growth or water uptake.
- Species with canopy covers that were associated with warm, fall and early-winter soil temperatures need a longer growing season to complete basic life-cycle processes or benefit from an early snowpack, which prevents frost damage or heaving.
- Douglas-fir was at the opposite end of the spectrum from subalpine fir in terms of thermal and moisture correlations, confirming Douglas-fir's competitive advantage on warmer, drier soils and subalpine fir's competitive advantage on cooler, moister soils.
- At lower elevations, subalpine fir's cold tolerance is a competitive advantage on cool sites, but at higher elevations, the cooling of soils in its shade limits its growth potential.

Among the species with canopy covers that were positively correlated with soil temperatures, there were two distinct groups: those with strong summer correlations and those with strong fall and early-winter correlations. Douglas-fir, orange agoseris, common juniper, spreading phlox, giant red Indian paintbrush, and common yarrow canopy covers were positively correlated with summer soil temperatures. Associations with warm summer soil temperatures suggest that much of the study area is simply too cold to sustain basic metabolic processes sufficiently for these species to be competitive. As the temperatures in question are soil temperatures, this may take the form of poor root growth or water uptake. White hawkweed, shore pine, and Cascade desertparsley canopy covers were positively correlated with fall and early-winter soil temperatures. The association with warm fall and early-winter temperatures suggests one of two possibilities. Given the cool summer season, it is possible that a plant such as shore pine needs extra time in the fall to complete basic life-cycle processes, which it would find at lower elevations. For diminutive herbaceous species, such as white hawkweed and Cascade desertparsley, this probably has more to do with the protection afforded by an early snowpack from damaging frost, frost heaving, or solifluction that would occur in the open, higher elevation parts of their range.

Subalpine fir canopy cover had moderate negative correlations with soil temperatures during summer months in all quarter-days. It is tempting to say that it prefers cooler soils, but the relation is more complex. Near its lower elevational extent, it is found primarily in the coldest environments, especially in cold-air drainages or on steep, northern aspects (Arno and Hammerly 1977). It seems likely that cold air and soils in these areas limit the growth of competing species with warm thermal affinities, such as Douglas-fir (Franklin and Dyrness 1988, Waring et al. 1972), creating an opportunity that the more cold-tolerant subalpine fir can exploit. These would also be the areas that satisfy subalpine fir's relatively higher moisture requirements (Waring et al. 1972). In our study area, Douglas-fir was at the opposite end of the spectrum from subalpine fir in terms of thermal and moisture correlations, confirming Douglas-fir's competitive advantage on the warmer, drier soils, and conversely, subalpine fir's competitive advantage on cooler, moister soils.

However, at higher elevations, another dynamic comes into play. In these areas, the competitive species from lower elevations have largely dropped out, leaving subalpine fir nearly unchallenged. However, subalpine fir produces dense shade, which limits soil warming. Thus, although it may begin its growth in sun-warmed soils, as it grows, the soils under its canopy become cooler, and this may limit its growth (Körner and Paulsen 2004). Thus,

far from preferring cold soils at these elevations, subalpine fir prefers to establish in somewhat warmer soils, and the lower temperatures obtained under the canopy are a limiting consequence of its growth. At increasingly higher elevations, this results first in the prevention of closed canopies, thus they grow in clumps or as individual trees, and finally they are prevented from growing at all (Körner and Paulsen 2004).

Another species with a canopy cover that was negatively correlated with soil temperatures was Cascade azalea, which overlaps extensively with subalpine fir in this area. Indeed, it is hard to find Cascade azalea without subalpine fir, and all our Cascade azalea plots also had substantial cover of subalpine fir. However, subalpine fir also occurred in areas without Cascade azalea. As already discussed, subalpine fir maintains lower summer soil temperatures in its shade. Thus, summer soil temperatures were negatively correlated with the amount of subalpine fir that was present. Plots with subalpine fir or Cascade azalea were cooler in all 12 months at 20-cm depth in the soil than plots without them, and plots with Cascade azalea averaged lower soil temperatures than the larger set of subalpine fir plots. Thus, Cascade azalea is more restricted to cool soils than subalpine fir.

Correlations Between Species Canopy Covers and Solar Radiation—

- Because we did not have local seasonal cloud cover data, our potential solar radiation analysis is primarily an evaluation of topographic position, so our results reflect drought stress more than light.
- Orange agoseris, Cascade desertparsley, and Oregon boxleaf canopy covers were positively correlated with fall and winter potential direct solar radiation, suggesting they grow in dry areas that resulted from shallower snowpack and earlier melting.
- Cascade azalea canopy cover was negatively correlated with potential direct solar radiation in every month of the year as well as with duration of direct solar radiation in winter, suggesting it grows where snow accumulation is greatest, spring melting is slow, and evapotranspiration is minimal.
- The negative correlation between thinleaf huckleberry canopy cover and potential direct solar radiation and its duration suggests that it favors cooler slopes in this landscape.

The examination of how species abundances correlate with potential solar radiation is one way to evaluate broad, topographic distributional trends in a mountainous landscape. The use of solar radiation integrates the position in the landscape of the sample unit in relation to the sun throughout the year in a more sophisticated way than can be done with slope steepness, aspect, and elevation. However, without estimates of local seasonal cloud cover, it remains an evaluation of topographic position, not of actual radiation. In fact, the results of the analysis seem to have more to do with drought stress than with light. As would be expected, there are strong similarities in the results obtained with direct solar radiation and duration of direct solar radiation. For these variables, the position of the sun in relation to the plot location and the horizon is especially important.

Orange agoseris, Cascade desertparsley, and Oregon boxleaf canopy covers were positively correlated with fall and winter potential direct solar radiation. For Oregon boxleaf, the correlations between its canopy cover and potential direct solar radiation extended into the early spring as well. What is interesting about these correlations is that they all occurred when these species were under a deep blanket of snow. Correlations between species canopy covers and duration of direct solar radiation were fewer but formed a similar pattern. Orange

agoseris, Cascade desertparsley, and Oregon boxleaf occurred more often where the snow melted earlier in the season and species canopy covers were all negatively correlated with summer soil moisture (see below). It is possible that because of higher levels of winter solar radiation, areas where these species grow are subject to relatively more winter thawing and sublimation, resulting in less accumulation of snow and, by extension, earlier melting and more soil drought in summer. Confirming this hypothesis would require winter measurements of snow accumulation and loss over these species to compare to similar measurements where these species do not grow.

Cascade azalea canopy cover was negatively correlated with potential direct solar radiation in every month of the year as well as with duration of direct solar radiation in winter. As already discussed, Cascade azalea was also associated with sites that had cool air, soil surfaces, and soils, and grew in late-snow-melting sites. Its canopy cover was also positively correlated with summer soil moisture (see below). Thus, Cascade azalea appears to be relatively drought intolerant, and avoidance of drought is achieved by growing on sites that have the greatest chance of accumulating snow through the season, releasing it slowly, and reducing evaporation to a minimum. As precipitation varies little over the site, this is achieved topographically. This is nearly the opposite pattern as that shown by orange agoseris, Cascade desertparsley, and Oregon boxleaf, and we never found these species growing with Cascade azalea.

Western white pine was the only other species with a canopy cover that was correlated with potential direct solar radiation or duration of direct solar radiation; its canopy cover was negatively correlated with potential direct solar radiation in spring and late summer. In nearly every other respect, this species is found in neutral habitats. It was generally associated with higher air temperatures but was in the neutral habitat group for soil surface and soil temperatures. Yet, western white pine was associated with what should be somewhat cooler sites based on potential direct solar radiation. It was in the middle of the ranking of species by date of snowmelt and its canopy cover was not significantly correlated with summer soil moisture. We believe that in the study area, this species favors the warmer parts of cooler aspects but should be considered neutral overall.

Thinleaf huckleberry was found only in the lower third of elevations in our study area, so the negative correlation between its canopy cover and both radiation parameters (potential direct solar radiation and duration of direct solar radiation) suggests that it favors relatively cooler, lower slopes. Thinleaf huckleberry also tended to grow in areas of late melting spring snow, and its canopy cover was weakly positively correlated with summer soil moisture. It did not grow abundantly in our study area, and in our experience, it was a poor producer of fruit. This suggests that thinleaf huckleberry finds only marginal habitat in this area because of droughty conditions.

Effects of Snowpack

- Spring melting of the snowpack took place from the end of March through June.
- The order in which species locations melted out follows closely our findings from temperature, moisture, and solar radiation analyses.
- Douglas-fir grew in areas of early snowmelt, snowmelt was earlier where whitebark pine grew than where subalpine fir grew, and Cascade azalea grew where snowmelt was latest.

The composition of vegetation is sensitive to snowpack-mediated changes in soil moisture (Schworer et al. 2016) and the length of the growing season. A modeling exercise that assumed all precipitation came as rain lowered the Olympic Mountains rain shadow tree line by 300 m because of drought compared to a model that accurately accounted for snow precipitation (Schworer et al. 2016). Although we could not directly relate snowpack to summer soil moisture, we were able to show preferences of species or communities to both. Spring melting of the snowpack in our study area took place from the end of March through June, depending on the plot. The order in which species locations melted out follows closely our findings from temperature, moisture, and solar radiation analyses. For example, more Douglas-fir, orange agoseris, Cascade desertparsley, and Oregon boxleaf grew in places where snowmelt occurred relatively early, which were also warm, dry places with high levels of winter solar radiation. White hawkweed grew in places with higher air, soil surface, and soil temperatures, which were also areas of early snowmelt. Although the differences in canopy covers of other species by month of snowmelt were not significant, they seemed consistent with our other findings. For example, more subalpine fir grew in areas where snowmelt occurred later than whitebark pine, and more subalpine fir grew on northern aspects than whitebark pine. Shore pine, which grew primarily on warm, dry slopes lower in the study area appeared to favor areas where snowmelt occurred earlier more than most other species. The latest snowmelt conditions among our selected species occurred in areas where Cascade azalea grew, and the canopy cover of this species was strongly associated with cool, moist soils and northern aspects. However, many other species where canopy cover was not significantly associated with month of snowmelt were neutral in terms of affinities to air, soil surface, or soil temperatures.

Relationships Between Species Canopy Cover and Summer Soil Moisture and Temperature

- Our ranking of species correlations with summer soil moisture appeared to apply generally to the northeast Olympic Mountains.
- The negative correlation between summer soil moisture and species richness was likely a result of higher tree and shrub dominance on moist sites and the restriction of species that are not tolerant of shade and cold soils.
- A negative correlation between the age of the oldest whitebark pine trees and summer soil moisture probably reflected competitive exclusion of whitebark pine by subalpine fir on moister sites during post-Little Ice Age upslope tree migration.
- Correlations suggested the following relative local affinities: warm and dry for whitebark pine, warm and mesic for Douglas-fir, cool and mesic for western white pine and shore pine, and cold and mesic for subalpine fir.

We collected our summer soil moisture data in July and August over 5 years from the upper 12 cm of soil. At these times, such shallow soils had already dried considerably. Measurements taken somewhat earlier or deeper might have yielded more significant results. Nevertheless, the species that were negatively correlated with summer soil moisture were the same ones as those associated with warm sites or sites with higher levels of solar radiation, especially in winter months (table A2.12).

The ranking of species from dry to wet (fig. 33) was specific to our study area but appeared to apply generally to the northeast Olympic Mountains. The larger number of dry correlations than moist correlations reflects the prevailing droughtiness of our predominantly

south- and west-facing study area as well as the low species richness of predominantly forested north-facing slopes. In a progressively drier or wetter area, the rankings would shift and, depending on the bias of the sample area, might have more or fewer moist correlations. However, total species canopy cover would likely remain significantly correlated with summer soil moisture because it is a summation and is thus relative to whatever dataset is being analyzed. Throughout this region, moist forest sites are more productive than dry forest sites (Henderson et al. 1989). Thus, the species toward the moist end of the distribution (positively correlated) in figure 33 may be viewed as indicators of higher productivity within our study area and other similar areas. In comparing Olympic Mountains rain shadow alpine meadow communities, Kuramoto and Bliss (1970) also found productivity was positively related to soil moisture. We add one important caveat to this finding, and that is that productivity decreases at higher, colder elevations. Thus, a moist, high-elevation site may not be more productive than a dry, lower elevation site.

It is interesting that the combined species canopy cover of alternate hosts for white pine blister rust falls in the middle of the distribution of the 19 species in figure 33. This suggests that, in aggregate, these species are neutral in that they favor neither dry nor wet sites. We would expect from this that they are widespread, common species, which is supported by our observations in the wider area above the zone of continuous forest canopy as well as by the presence of one or more of these species on 94 percent of our plots.

There was a tendency for species that had stronger positive correlations with potential solar radiation or temperatures to be associated with drier soils (tables A2.12 and A2.13). Although this is not unexpected, species that were negatively correlated with temperature or potential solar radiation tended to have nonsignificant, weak, positive correlations with summer soil moisture. However, many of them expressed a strong affinity for cool sites, especially thinleaf huckleberry, Cascade azalea, and cliff dwarf-primrose, and several others to a lesser extent. The conclusion we draw for these species is that they occupy a broad spectrum of summer soil moistures, compensating drought with lower temperatures, while avoiding the driest soils. Most species in the mid-range of the moisture ranking appear to prefer cooler sites as well.

The negative correlation between summer soil moisture and species richness appears to be due to increased tree and shrub dominance, which occurs with more moisture and limits the number of species to those that can tolerate deep shade and in this case, cold soils (Huston 1979). A stronger negative correlation between the age of the oldest whitebark pine trees and summer soil moisture probably reflects competitive exclusion by subalpine fir on moister sites during post-Little Ice Age upslope migration. Franklin et al. (1971) found faster subalpine fir invasion occurred in moister plant communities than in drier plant communities on Mount Rainier. Also, lower humidities on the driest sites could discourage white pine blister rust infection, allowing old whitebark pines to survive longer on dry than on moist sites.

Arraying the species by their correlations between canopy cover and summer soil moistures and temperatures provides a clear view of their relative niche spaces (fig. 34). In interpreting this diagram, we need to be mindful of keeping the concepts of correlation and causation separate. However, plotting these many independent correlations together revealed broad relationships among species that were supported by our other analyses and field observations. Many of the significant correlations were of moderate strength, but given the modest sample sizes, they were likely nevertheless meaningful. We used statistical

significance of the correlation coefficients to define nine generalized niche spaces. These spaces are demarcated with sharp lines, but the correct view would be that of a continuum across the lines. Although we have demarcated broad niche areas, the location of most species appears relevant even at a much finer scale. Thus, within the central cool and mesic area, Cascade azalea does grow better on cooler, moister sites than shore pine or Roemer's fescue, as is shown by their relative positions.

The central part of the diagram in figure 34 (cool and mesic) is the area where neither the correlation between canopy cover and soil temperature nor its correlation with summer soil moisture were statistically significant. These species did not express a strong affinity to the summer soil moistures or soil temperatures that would be considered extreme, marginal, or atypical for this area. This niche area included most of the species in our sample and should be viewed as modal for this landscape. Some of the more important species were shore pine, thinleaf huckleberry, broadleaf lupine, and Roemer's fescue. Cascade azalea was also in this area but was marginal with the cold and mesic area, which included subalpine fir. This was a mixed group, as it straddled the area where the forest canopy was breaking up from the forests below to alpine above. Twenty-two of the species were typical of lower elevations, including 6 of the 13 heliophytes, which were common in the lowland, anthropogenic Puget Sound Basin prairies. There were also nine species more typical of montane forests and openings and nine species that were clearly subalpine or alpine.

Outside of the cool and mesic modal area, we found species such as Douglas-fir, white hawkweed, and spreading phlox growing in relatively warmer areas but in a similar range of summer soil moistures (warm and mesic). There were 10 species in this space, including 6 that were typical of lowland habitats, 2 that were of montane and higher habitats, and 2 that were of subalpine or alpine habitats.

Species such as subalpine fir, heartleaf arnica, and sickletop lousewort occurred in relatively colder areas but of similar summer soil moisture (cold and mesic). Interestingly, when subalpine fir invades a new area, the soils would be warmer until the canopy shaded them (Körner and Paulsen 2004). Thus, this species may belong in the cool and mesic space, as that was where its seedlings were more likely to be successful. Heartleaf arnica, which is often found growing in the shade of subalpine fir, may be an opportunistic follower, finding less soil moisture stress in its shade. There were only six species in this space—four typical of montane forests and two subalpine or alpine species. This area represented a space that was too cold for any lowland plants to survive.

We had only one species, roughfruit berry (*Rubus lasiococcus*), in the cold and moist space. This is another shade-tolerant species that follows subalpine fir, seeking its shade. Within our study area, it was found at the lower elevations, indicating the profound effect that dense tree shade had on soil temperatures. We might expect some wet snowbank plant communities to fall into this category as well as high-elevation riparian areas, but we had only one snowbank plot and no riparian plots in our sample. Had we sampled east- and northeast-facing slopes, this area might have been more populated.

The cool and moist space included only two species, common alplily (*Lloydia serotina*) and spiked woodrush (*Luzula spicata*), both of which are strictly subalpine or alpine. Common alplily was always found with spreading phlox but only in the highest elevations and the coolest aspects on which spreading phlox was found.

The cool and dry space had species typical of lowland and montane areas, including Oregon boxleaf, red fescue (*Festuca rubra*), Saskatoon serviceberry (*Amelanchier alnifolia*),

and Cascade wallflower (*Erysimum arenicola*). Two of these, Oregon boxleaf and Saskatoon serviceberry are shade tolerant, but at this elevation, they are found mainly in sun or light shade, possibly because of an intolerance of the cold soils found in shade.

The warm and dry space included predominantly heliophytic plants, such as Cascade deserparsley and common juniper. Two of the species in this space, silverleaf phacelia (*Phacelia hastata*) and Columbia lily (*Lillium columbianum*), can be found at low elevations in openings; four species occur in montane and higher openings; and two species, white sagebrush and whitebark pine, are subalpine or alpine.

There were also two spaces with no species, representing unsampled areas. The cold and dry space in this area would be found on steeper, north- and east-facing, upper slopes. The warm and moist space would be found in riparian areas on south- and west-facing slopes, and although we had two plots that bordered these conditions, we had none that were actually in them. These areas were present, but our interest was in upland areas in the vicinity of a whitebark pine population, so we did not sample them.

Plant Association and Community Type Floristic Relations

- The ordination supported the plant associations and community types that we identified (fig. 35), and the overstory canopy (especially subalpine fir) reflected or drove plant association or community type composition along with summer soil moisture and soil temperature.
- The strongest correlated ordination axis variables were subalpine fir and whitebark pine canopy covers (in opposite directions); total overstory canopy closure, which was more or less opposite from measures of PAR (ground level and 1.3-m height); maximum tree diameter at breast height (mostly with axis 1); and maximum September air temperature in quarter-day 2, which closely paralleled whitebark pine canopy cover.
- Trees were increasing in number across most of the study area, suggesting that cold soils were generally not limiting, but above the study area, forest canopies opened around 1800 m on northeastern exposures, and few trees existed above 1900 m on any aspect, suggesting that strong cold soil limitations occurred there.
- Most open areas in the study area were likely due to soil drought combined with cool soils and short growing seasons that provided suboptimal growing conditions, or in some cases, these areas may exist as a result of solifluction.

We used ordination to provide an independent evaluation of the floristic-based plant association and community type plot groupings and to reveal overall patterns of vegetation response to environmental gradients. The names of plant associations and community types that we used were partly based on existing literature and partly on our field observations and are not intended to serve as a formal classification. However, the ordination did support our plant associations and community types. Detailed descriptions of each plant association and community type are provided in the results section and discussed more fully in appendix 3.

Ordination axis 1 (fig. 35) accounted for 40 percent of the variance in the distance matrix and appeared to be closely associated with the amount of overstory canopy. Plots lower on the axis were nonforested, and those higher on the axis had higher levels of overstory canopy closure and lower levels of PAR (ground level and 1.3-m height). Also, the species progression along ordination axis 1 was from low-growing species associated with open

areas to trees and understory plants associated with montane forests. The diameter at breast height of the largest tree also increased with ordination axis 1, suggesting a productivity-age gradient. This axis was positively correlated with several winter and spring air temperatures and negatively correlated with elevation and the duration of the seasonal snowpack. In all, this axis sums up an alpine to montane forest transition.

Ordination axis 2 (fig. 35) accounted for 22 percent of the variance in the distance matrix. It was strongly correlated with subalpine fir canopy cover, which had profound effects on species composition. There were also several negative correlations with fall through spring maximum air, soil surface, and soil temperatures. A negative correlation with aspect was key to understanding these temperature correlations. These correlations collectively suggested a gradient from exposed, south- and west-facing sites that accumulated less snow and experienced more thermal extremes in winter and spring to more northerly subalpine fir-forested sites that accumulated more snow and, although generally cold, experienced less temperature fluctuation. Plots lower on the axis also developed higher summer soil temperatures and were generally drier than those higher on the axis, but they were a mix of high-elevation plots that developed high soil temperatures because of their open, southern and western aspects and forested, low-elevation plots that were warm because of both elevation and aspect. This mix sorted out along ordination axis 1. Plots higher on axis 2 were cool, but the relationship was not entirely straightforward because although subalpine fir appeared to establish best on cool aspects, their dense, mature canopy limited soil warming. Thus, ordination axis 2 was a complex temperature gradient that favored subalpine fir dominance.

Ordination axis 3 (fig. 35) accounted for 25 percent of the variance in the distance matrix. The most striking thing about ordination axis 3 was that the subalpine fir/common juniper plant association, which included a tree component but was largely open, was well separated from the nonforested spreading phlox community type even though there were some strong floristic similarities between them. The strongest correlation with ordination axis 3 was with summer soil moisture ($r = -0.46$) followed by the maximum June air temperature in quarter-day 3 ($r = 0.42$) and is thus a gradient from cool and moist to warm and dry at higher axis positions. There were also several positive correlations with minimum air temperatures in winter and spring, and maximum air temperatures in summer, supporting the temperature gradient. A positive correlation with overstory canopy cover and a negative correlation with elevation suggest decreasing canopy cover with increasing elevation, as would be expected. Plots lower on the axis were open, higher elevation, relatively cool and moist sites, and those higher on the axis were warmer and drier sites with more trees. Thus, the separation of subalpine fir/common juniper plant association from the spreading phlox community type indicates that the latter type was of cooler, moister, higher elevation sites with less overstory canopy. In other species-specific analyses of common juniper and spreading phlox, common juniper was consistently more strongly associated with warm, dry sites than spreading phlox.

The plots in the major plant associations or community types were ordered along a diagonal vector of about 45°, originating at the intersection of ordination axes 1 and 2. Near the intersection of the axes was the spreading phlox community followed with overlap by the subalpine fir/common juniper plant association. This overlap was real and observable in the field where these two types were often intricately mosaiced over the landscape and shared many species. Although overlapping on ordination axes 1 and 2, they were separated on

axis 3, which suggested that the spreading phlox community occurred in cooler and moister environments than the subalpine fir/common juniper plant association, and this is further supported by other analyses. As indicated by the joint plots, these types were low in productivity, had low percentages of canopy closure, and had small tree sizes but were high in ground-level PAR. They were also associated with lower amounts of subalpine fir and higher amounts of whitebark pine than plots beyond the ordination centroid on the diagonal axis. These two communities were also the principal communities undergoing solifluction now or in the recent past.

Next on the diagonal was the subalpine fir/broadleaf lupine plant association, which did not overlap with the previously mentioned types in ordination space. The ordination centroid was located between the subalpine fir/common juniper and subalpine fir/broadleaf lupine plant associations. The latter type was a moister, more productive type, and this has also been suggested by others (del Moral 1983). However, this was only indirectly indicated by the joint plots, which suggested higher levels of tree canopy cover, especially subalpine fir canopy cover, and larger diameter at breast height of trees for subalpine fir/broadleaf lupine plant association. The krummholz and talus plots were loosely associated with this group because of floristic similarity, but they were obviously different in important ways, including their low productivity. Farther out on the diagonal were the cool, moist subalpine fir/Cascade azalea plots. These were at the opposite end of the spectrum from the spreading phlox community and were associated with high percentages of canopy closure, low ground-level PAR, and high subalpine fir canopy cover. Whereas the spreading phlox community occurred in warm, dry summer soils, the soils in the subalpine fir/Cascade azalea plant association were cool and moist, partly because of tree shade. Subalpine fir canopy cover was negatively correlated with soil temperature in all quarters of the day during summer months. Among the 20 species that we examined closely, it was second only to cliff dwarf-primrose in the number of significant negative correlations with annual, seasonal, and daily soil temperatures. Also, subalpine fir canopy cover was positively correlated with summer soil moisture and typically occupied areas of later melting snow, thus subalpine fir favors cold, mesic sites in our study area and promotes these conditions with its shade. The ability of this species to grow densely on moister sites and reduce the soil temperatures relative to open areas with its shade has profound implications for which species can associate with it as the canopy grows.

Plots 22 and 23 were the farthest from the centroid on ordination axis 1 but were relatively close to it on ordination axis 2 and were separate from all others. These two low-elevation plots were distinguished floristically by having a mostly montane forest flora that was dominated by Douglas-fir. These warm, low-elevation plots were associated with larger stem diameters at breast height indicating not just older trees but also more productive sites.

Of 209 temperature, moisture, physical site, and vegetation variables investigated with the PC-ORD joint plot program, the highest ordination axis correlations were with vegetation variables, including canopy covers for subalpine fir and whitebark pine (in opposite directions), overstory canopy closure, and maximum diameter at breast height of trees on the plot. Only 1 of the 192 temperature variables, maximum September air temperature in quarter-day 2, had a correlation of similar strength. However, it is notable because the joint plot indicates this variable closely parallels whitebark pine and is opposite from subalpine fir, further suggesting that subalpine fir competes better in cooler habitats than whitebark pine.

Our analysis showed that a subalpine fir overstory can maintain soil temperatures that are 3.8 to 7 °C lower than in open areas from June through August. However, in cooler environments at higher elevations, shade-cooled soils can limit tree growth, resulting in the formation of the alpine tree line (Körner and Paulsen 2004). When mean growing-season soil temperatures approach 6.7 °C, trees can no longer grow close enough together to produce a closed canopy, so subalpine parklands and the alpine tree line form (Körner and Paulsen 2004). We estimated that in the highest parts of our study area, soils under tree shade approached this limiting level. However, we also found that trees were increasing in number over most of the study area. We assume that in most of the study area, soil temperatures were not limiting subalpine fir, thus most of the study area was located below this physiological barrier. Examination of aerial photography outside of our study area showed few trees existed above 1900-m elevation on any aspect and that forest canopies were breaking up around 1800 m on northeastern exposures. Thus, the higher elevations of our study area appeared to be transitional to the thermally defined open alpine flora. Most of the open areas in our study area were more likely due to soil drought and solifluction, but the effects of these stressors were, no doubt, amplified by cool soils and short growing seasons that provided less-than-optimal growing conditions for many species.

Near the intersection of ordination axes 1 and 2, the spreading phlox community closely aligned with the maximum September air temperature in quarter-day 2 because of its high level of solar exposure. Subalpine fir canopy cover increased with higher values of axes 1 and 2 over the entire ordination. Whitebark pine canopy cover increased opposite subalpine fir but only to the transition into the spreading phlox community where it dropped off. In ordination space, whitebark pine was confined between inhospitable alpine areas where it is physiologically excluded, and equally inhospitable areas because of competition from subalpine fir where it might otherwise be able to grow; it was only successful in the warmer, drier space in between.

Plant Association or Community Type Ordination and Descriptions

- The all plots and species ordination provided similar plot groupings as the subset joint plot ordination, suggesting that the relationships found for the subset ordination apply to the entire dataset.
- Plant association or community type composition is a sensitive environmental indicator, but during times of rapid climate change, species not normally found together may be juxtaposed because of differential migration and extinction, so the current plant composition reflects both past climate and present climate.
- Subalpine fir restricted understory species diversity with low soil temperature and light caused by its high percentage of canopy closure, while whitebark pine, which grew in warmer, drier, open woodlands, enhanced understory species diversity by providing a mix of open and shaded environments.
- Diverse woodland structure of whitebark pine stands resulted from the harshness of the environment, white pine blister rust, and stand history, as these stands were emerging from the colder period of the Little Ice Age.

Just as individual species are useful indicators of local environments, whole plant associations or community types are sensitive indicators of landscape-level processes and changes. During times of change, juxtaposition of species not normally found together will occur because of differences in their rates of migration and local extinction. For these

reasons, it is important to provide detailed descriptions of the vegetation, and ordinations of plant associations or community types are useful for communicating this information. However, we had robust environmental data for only a 26-plot subset of our vegetation sample and so could not do a single ordination with joint plot calculations that included all plots. To this end, we repeated the ordination with all plots and species. This ordination provided similar groupings of plots as the joint plot ordination, so we have confidence that the relationships that we found and discussed for the joint plot ordination apply equally well to the entire dataset. Also, the ordination supported our plant association or community type plot grouping and confirms the utility of the plant association classification of Henderson et al. (1989) to this area, suggesting inference derived from our case study extends to a larger area.

By including all the plots, this ordination showed the outlier nature of some of the plots, allowing an objective evaluation of their value in the overall dataset. For example, late melting snowbank microsites, such as the black alpine sedge community at plot 18, provided little value to understanding landscape-level principles within the study area but reminded us of an important level of landscape complexity; although minor in extent, this community type was nevertheless widespread in its distribution over many landscapes. Similar black alpine sedge communities are widespread in the Olympic Mountains but occupy only small areas (Kuramoto and Bliss 1970), and they have been reported from subalpine and alpine regions of coastal southern British Columbia (Brooke 1965, Peterson 1965) and the North Cascades of Washington (del Moral 1979, Douglas 1972, Evans and Fonda 1990).

Subalpine fir is a keystone species in this landscape. It was present in nearly every plant association or community and codominated or dominated much of the landscape. Low soil temperatures and light levels in its understory greatly restricted the number and kind of understory species that were present to the few that were both shade tolerant and cold soil tolerant. This, in turn, restricted the amount of canopy cover they could produce because of restrictions on their productivity. Whitebark pine was mostly a codominant species on warmer and drier sites. Nowhere in the study area did it form a closed-canopy stand, although it was sometimes the only tree species present. The presence of only open woodland or savanna-like canopies of whitebark pine was due in part to the effects of white pine blister rust, partly due to the harshness of the environment, and perhaps also partly due to stand history, as these stands were emerging from the colder period of the Little Ice Age. However, subalpine fir was present and increasing in most of these areas.

The nonarborescent flora included many dry, subalpine meadow and alpine tundra species, yet trees were growing throughout the area. At our highest elevation plot (plot 30), a stand that started as krummholz subalpine fir, had begun growing vertically with no apparent abrasion on their growing tips. A distinctly nontundra flora, including broadleaf lupine, sickletop lousewort, heartleaf arnica, and a species of *Mitella* (miterwort), grew in the shelter of these trees. Our lowest elevation plot (plot 23) included a stand that was dominated by 85-percent cover of Douglas-fir, with such lowland species as Cascade barberry, western swordfern (*Polystichum munitum*), sidebells wintergreen (*Orthilia secunda*), and common snowberry in the understory, and there was a canopy gap with common juniper, white hawkweed, kinnikinnick, Columbian lewisia (*Lewisia columbiana*), and Cascade desertparsley. The canopy gap showed every sign of closing over, and the heliophytic gap species had thin foliage and were unhealthy looking. Although one subalpine fir and several Douglas-fir were older than 100 years (oldest around 200 years), most of the trees in this

plot entered the stand in the past 100 years. Clearly there was a floral change occurring here associated with increasing shade that juxtaposed species rarely found together. Similar change was visible at our highest plot and on many plots in between. Thus, the current plant composition and configuration of vegetation reflected a past climate to some degree. As more change is likely, our descriptions of current composition and environment represent benchmarks for evaluation of future change.

Species Richness—

- Species richness was greater on droughty, open sites with warm days and cold nights, including steep, dry, rocky, warm southwestern exposures with a mix of large canopy gaps and tree shade.
- Dense, homogeneous stands of subalpine fir cast deep shade that excluded heliophytes and maintained root-inhibiting, low soil temperature that further limited understory species diversity.
- Higher species richness associated with white pine blister rust reflects the open environments where whitebark pine and white pine blister rust alternate host species typically grow, but white pine blister rust mortality may also cause richness-enhancing canopy gaps.

Species richness was negatively correlated with summer soil moisture and was positively correlated with indicators that suggest drought, including coarse fragment content, slope steepness, and aspect. Correlations between species richness and maximum air temperatures in fall and early spring were positive, but those with minimum air temperatures in spring, summer, and fall were negative, suggesting that species richness was greater on open sites that were warm by day but cold at night. Similarly, species richness correlations with soil and soil surface temperatures were mostly positive with maximum temperatures in summer, as is expected in open sites. Thus, species diversity tended to be higher on steep, dry, rocky, open, warm, southwestern exposures. These kinds of sites tended to have open overstory canopies, and species richness was positively correlated with several measures of light and was negatively correlated with overstory canopy closure. The positive correlation with the standard deviation of ground-level PAR points to an association between species richness and open stands with a mix of large canopy gaps and shade. As was discussed in the temperature section, a high standard deviation of ground-level PAR enhanced daytime surficial warmth by allowing solar radiation to heat the soil, while decreasing convective winds that remove that heat, but nighttime reradiation of heat from the gaps can also be high. In contrast, subalpine fir tended to grow densely and cast deep shade that maintained cool daytime soil temperatures and low species diversity. Thus, the correlations with soil temperature that suggested low species diversity in cool, shady areas may be attributed partly to the effects of subcanopy cold soil on root growth, partly to the light competition, and partly to the greater variety of niches available in stands that have both sun and shade.

Species richness was also positively correlated with white pine blister rust severity, which reflected the fact that whitebark pine tended to grow mainly in open, southwest-facing stands, and these stands tended to harbor several alternate host species for white pine blister rust. It is also the case that white pine blister rust caused openings in these stands by killing whitebark pine trees, which helped to maintain the conditions suitable for high species diversity.

Tree Growth and Age

- Subalpine fir and whitebark pine seedlings in open-canopy plots grew at similar rates.
- Canopy gaps are required for the release of shade-grown subalpine fir.
- Whitebark pine diameter at breast height growth curves for trees age <90 years differed from those that were age ≥90 years, which is roughly when we think white pine blister rust arrived.
- Younger whitebark pines grew in diameter slower than older trees but faster than when the older trees were young and the climate was cooler.

Subalpine fir and whitebark pine seedlings in open-canopy plots grew at similar rates. We estimated attainment of 1.3-m height in 44 years for whitebark pine and 43 years for subalpine fir seedlings in open-canopy areas and 92 years for subalpine fir in closed-canopy areas. The slow growth of subalpine fir in closed-canopy areas suggests that the opening of a canopy gap would be required for their recruitment into a mature stand. Laroque et al. (2001) reported that several species, including mountain hemlock and subalpine fir, required 37 years to reach breast height in moist, southern Vancouver Island subalpine meadows.

To relate age to stand structure, we first had to estimate ages for most of the trees, as it was not possible to determine all their ages from core samples or stem sections. This was accomplished by deriving relationships between age and tree diameter at breast height. Linear relationships for subalpine fir and Douglas-fir were strong (both with $r^2 = 0.8$). The relationship for whitebark pine was weaker, but by dividing the data at 90 years, two moderate-to-strong relationships were achieved. The division at 90 years is near the likely arrival date of white pine blister rust that resulted in high mortality of the original population and a marked change in age structure by the mid-1920s (see history section below). Thus, the older curve captured the remnant population of trees that established before the coming of the white pine blister rust and have survived to the present, and the younger curve captured the progeny of these and other trees that have grown their entire lives in the presence of the disease and a warmer climate. The diameter growth of the older trees was more rapid than that of the younger trees; however, the curve shape implies that in their youth, growth must have been much slower for the older trees. This implies that young trees now grow more rapidly than young trees did in the past, which may be because of the current warmer climate. However, the sample size of the older trees was small, so we advise caution in extrapolating these results.

Basal Area Relationships

- Subalpine fir basal area was positively correlated with age and was negatively correlated with growing-season soil temperature, reflecting the cool, moist sites where it grows best and shade-limited soil temperature.
- Whitebark pine basal area was positively correlated with slope steepness and was negatively correlated with summer soil moisture, reflecting its dry, open core habitat and exclusion by subalpine fir from moister sites.
- Total tree basal area increased with cooler soils, especially at lower elevations, which partly reflected better summer soil moisture conditions but also reflected maintenance of cooler soils by shade.

The amount of basal area a stand has accumulated relates both to the age of the stand and site productivity. We found a moderately strong correlation between total basal area and age

of the oldest tree on the plot ($r = 0.61$), which was driven largely by the basal area accumulation in subalpine fir ($r = 0.64$, for whitebark pine $r = 0.14$). Also, for subalpine fir but not for whitebark pine, the basal area correlations with growing-season soil temperatures were negative. This is a reflection of cooler, moister soils and thus higher site quality of the areas that are dominated by subalpine fir. However, as previously discussed, the density of subalpine fir shade made possible by the moister conditions of these sites also promoted lower growing-season soil temperatures. Whitebark pine basal area had only a few weak correlations with environmental variables. The only significant correlations we found were a positive correlation with slope steepness and a negative correlation with summer soil moisture, which are related, as we have previously shown. This is evidence that whitebark pine can tolerate some of the harshest sites in the area, and together with the subalpine fir correlations suggests that whitebark pine may be competitively restricted to them.

Our regression analysis suggested that total tree basal area increased in areas with cooler soils, especially at lower elevations. To some degree, this probably reflected better summer soil moisture conditions in these areas, but shade produced in more productive stands helps maintain cooler growing-season soils compared to less productive stands where the sun penetrates to the ground level, causing them to warm. Thus, more work is needed to sort out the degree of cause and effect. Summer soil moisture, as we measured it, was not significantly correlated with total basal area or with subalpine fir basal area but was negatively correlated with whitebark pine basal area. However, the inescapable conclusion that can be drawn from this and other analyses that we have done is that the principal or at least the core habitat of whitebark pine in this area was droughtier than that of subalpine fir. Others suggest replacement of whitebark pine by subalpine fir is likely on all but the driest sites (Arno and Hoff 1990, Keane 2001), which makes these dry sites especially important to the long-term survival of the species. Although whitebark pine grows largest on cooler, moister sites (Arno and Hoff 1990), those sites are not currently available to the species in our study area, and a wildfire would be required to make them available.

Stand Structure by Age Class, Elevation, and Aspect for Trees ≥ 1.3 m Tall—

- The age-class distribution of subalpine fir implied a successional young, rapidly reproducing population of trees, with mature trees that were mostly <100 years old.
- Whitebark pine had an especially young age-class distribution because with the passage of time, the probability that a tree will be infected and succumb to white pine blister rust increases.
- Subalpine fir and whitebark pine were increasing in tundra-like plant communities, suggesting upslope migration and that alpine conditions as defined by tree-limiting, low, soil temperatures are now at higher elevations than our study area.
- Most low-elevation tree basal area derived from trees that germinated during or immediately after the Little Ice Age, while most mid- and higher elevation basal area derived from trees that germinated in the past 40 to 100 years.
- Within the study area, forest will eventually dominate wherever sufficient soil and water exist, while only meadow and tundra species capable of surviving in the warmest and driest openings will remain.

Surveys of known stands of whitebark pine in the Olympic Mountains found the species present on all aspects but more commonly on aspects ranging from 135 to 225° and rarely on east- or north-facing slopes (Shoal and Aubry 2004). However, it was not dominant on all

aspects and elevations where it was found. In our study area, subalpine fir was the dominant forest species on all aspects at mid- to high elevations, with the exception of mid-elevation, southwestern aspects where whitebark pine was dominant. Subalpine fir was also an important species on aspects in the lower third of elevations, with exception of southwestern aspects where Douglas-fir, whitebark pine, and sometimes shore pine typically codominated.

The overall shape of the age-class distribution implied a successional young, rapidly reproducing population of trees, with most mature trees <100 years old. The subalpine fir population was the largest and fastest reproducing, but most other species had similar reproductive curve shapes. Because of white pine blister rust, whitebark and western white pines have experienced far greater mortality at younger ages than any other species. However, many individuals from both species survive long enough to reproduce in open areas. The size- and age-class distributions of whitebark pine were strikingly youthful, which is also the case in Olympic National Park (Jules et al. 2020), and this is likely because of cumulatively greater white pine blister rust infection probability with age. All species except shore pine were increasing in density, but subalpine fir and whitebark pine were the main species increasing in open, subalpine environments with tundra-like plant communities, suggesting an upslope migration. It is not clear why the shore pine population was static, but our sample of it was quite small ($n = 8$).

Trees were not reinvading previously occupied forest habitat. There was little evidence of wildfire, even at the lowest elevations, and there were few snags and little down wood, especially at higher elevations. Most snags and dead wood are easily attributed to recent mortality, mostly from white pine blister rust in the case of whitebark pine and western white pine, or from stem exclusion stage mortality (Oliver and Larson 1996) or snow breakage in the case of dense subalpine fir. We also observed krummholz form subalpine fir that appeared to be growing into tree form, a phenomenon also observed in the Sierra Nevada (Millar et al. 2004) and in the Rocky Mountains (Weisberg and Baker 1995), apparently related to warming climate.

Because recruitment occurred earlier at lower elevations, lower elevation trees were larger than those at higher elevations, which was reflected in greater stand basal area at lower elevations. More than half of the basal area at low elevations derived from Little Ice Age or immediate post-Little Ice Age cohorts, while 65 to 75 percent of the basal area in mid- and higher elevations derived from trees established in just the past 40 to 100 years. The stands of larger, low-elevation trees with their more continuous canopies, suppressed reproduction. Thus, only 55 percent of lower elevation trees established between 20 and 60 years ago, but in the more open, mid- and higher elevations, more than 80 percent of the trees established in the same period.

About 5 percent of lower elevation trees pre-date 1850, but only 1 percent or less of mid- and higher elevation trees do so. Thus, in the 1800s, trees were sparse at lower elevations but extremely sparse at higher elevations. All of this led to a significant negative correlation between age and elevation for subalpine fir and Douglas-fir. The Little Ice Age climate was regionally cooler by 0.5 to 1 °C (Luckman and Wilson 2005), which translates to a 100 to 200 m lower tree line according to our lapse rates, bringing the zone where the continuous forest canopy begins to break up at the level of our lowest plots. Similar rising tree lines and tree invasion of subalpine meadows and snowfields have been observed in many parts of the Pacific Northwest (Brink 1959, Douglas 1972, Fonda and Bliss 1969, Franklin et al. 1971, Kuramoto and Bliss 1970, Laroque 2001, Rochefort et al. 1994). Most of the literature reports

waves of invading trees during favorable species-specific periods of weather. Millar et al. (2004) related infilling of subalpine meadows and snowfields by whitebark pine and lodgepole pine in the Sierra Nevada Mountains to 20th century variations in the Pacific Decadal Oscillation, and Peterson et al. (2002) found subalpine fir growth patterns in the Olympic Mountains were related to low-frequency variation in spring snowpack and summer soil moisture, also driven by the Pacific Decadal Oscillation.

Our impression from these data is that the lower elevations in our study area were subalpine parkland during the Little Ice Age, representing the location of the tree line at that time. Currently, establishment is taking place at all elevations, suggesting that the potential modern tree line is higher in elevation than where it appears to be today (fig. 75). By potential tree line, we mean the location of the physiological temperature boundary that would restrict tree growth. Indeed, our soil temperature data, interpreted through Körner and Paulsen's (2004) hypothesis, would indicate that the highest ridges in our study area are largely available to tree growth. This would account for the indistinct nature of the current tree line and suggests that the openness of south-facing slopes is driven by drought more than temperature. Peterson et al. (2002) found that annual growth of subalpine fir in drier, northeastern Olympic sites appeared to be limited by summer soil water availability. By using dendrochronological methods, they found that tree growth was negatively correlated with spring temperature and was positively correlated with early summer precipitation, suggesting a delay in snowmelt can reduce the severity and duration of summer drought and favor growth. Warm, dry summers reduced growth the following year, probably by reducing

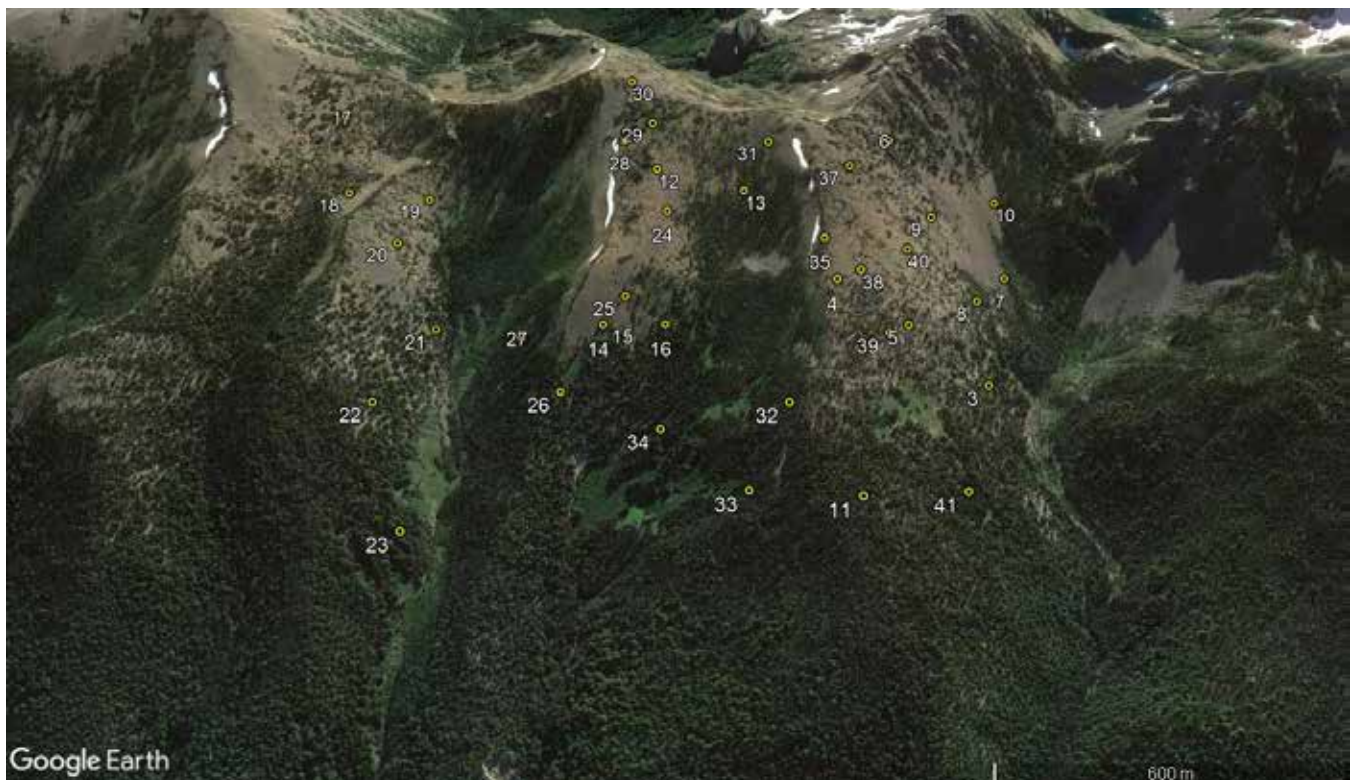


Figure 75—The Olympic Mountain whitebark pine communities study area from the west showing study plot locations. Note the strong north-south dichotomy in vegetation of the ridges and the indistinct nature of the tree line. Also, note that forests extend to higher elevations on north-facing slopes than on south-facing slopes. In terms of elevation, plot 22 is slightly more than 100 m higher than plot 23 (lower left portion of the plots). Both plots lie in the lower third of elevations. Google Earth image; July 30, 2017.

the availability of stored carbohydrates for spring shoot growth (Fritts 1976, Fritts and Swetnam 1989). Similar climate-growth relationships have been reported for subalpine fir in the more continental climate of the Rocky Mountains (Colenutt and Luckman 1991, Villalba et al. 1994).

The physiological temperature boundary for root growth may now be as high or higher than our highest elevation plots, even though trees have yet to fill in much of the intervening space. The fact that none of our plots currently have growing-season soil temperatures that would limit root growth suggests that cold soils do not limit tree establishment anywhere in our study area. This is supported by our estimates that root growth-limiting temperatures would only be attained with a relatively dense canopy, and then, not everywhere. Thus, it is only a matter of time before trees occupy most slope space to the tops of the ridges in this area wherever sufficient soil and water exist.

Over time, only meadow and tundra species that can tolerate shade or the warmest and driest slope conditions will continue to find habitat in this area, given its current conditions. Wershow and DeChaine (2018) found that a habitat contraction of 86 to 99 percent was likely for five Olympic Mountains endemic species: Olympic bellflower (*Campanula piperi*), Flett's fleabane (*Erigeron flettii*), Olympic Mountain ragwort, featherleaf kittentails (*Synthyris pinnatifida*), and Olympic violet (*Viola flettii*), by the 2080s, based on climate projected habitat models. These species occurred in the general study area and three (Olympic bellflower, Flett's fleabane, and Olympic Mountain ragwort) occurred on one or more of our plots. Solifluction could continue to limit tree growth in places, but if estimations of mean annual temperatures rising by 3 °C in the Pacific Northwest by the 2080s (Mote and Salathe 2010) are accurate, this phenomenon may cease. Our ability to understand what habitat may continue to be available is hampered by our lack of understanding of the physiological drought tolerances of most of the flora, including tree seedlings; insufficient measurements of drought conditions throughout the growing season in various open habitats; and our current inability to predict the effects of changing climate on soil drought in these habitats.

Habitat Relationships for Seedlings (Reproduction)

- Subalpine fir had high reproductive vigor on cooler aspects, but its reproduction was better represented than any other species throughout the study area.
- There was more whitebark pine mortality from white pine blister rust than from all causes in subalpine fir, even though there were fewer whitebark pine trees.
- It is likely that subalpine fir will replace whitebark pine in most of the study area, albeit more slowly on warm, dry sites than on cool, moist sites.
- Whitebark pine regeneration was more abundant in areas with high soil and air temperatures, especially where the late summer was warmer.
- Subalpine fir regeneration was more abundant where soil and air temperatures were low, especially in shady, well-established stands providing the means to exploit canopy gaps as they develop.

Seedlings (trees <1.3 m tall, which we refer to as reproduction) decreased in density with elevation, but the differences by elevation band were not significant. Subalpine fir reproduction was more numerous than any other species on all aspects in our study area but was by far the most numerous on northwestern aspects. Thus, subalpine fir showed more reproductive vigor on cooler aspects, yet its reproduction was better represented than any other species on any aspect in the study area. Given that this was the most shade-tolerant species

in the area, it would seem to be on a trajectory toward dominance on all but the driest micro-sites. Of course, this could not always have been the case, or all slopes in the study area would already be forested with subalpine fir. Thus, change is implied, and the two most obvious sources of change are the climatic emergence from the Little Ice Age and the introduction of white pine blister rust.

We observed white pine blister rust on all sizes of whitebark pine, including reproduction-size trees, and there was significantly more mortality in whitebark pine than from all causes in subalpine fir, even though there were far fewer live whitebark pine trees. Thus, it is likely that over time, subalpine fir will largely replace whitebark pine throughout the study area, albeit more slowly on warm, dry, sites than on cool, moist sites, as suggested by others (Arno and Hoff 1990, Keane 2001). In British Columbia, Clason et al. (2014) found that xeric whitebark pine sites were becoming more like nearby mesic sites without whitebark pine in terms of overstory but not understory composition over a period of 21 to 29 years. As whitebark pine trees died from white pine blister rust, they were replaced by subalpine fir and mountain hemlock. However, Amberson et al. (2018) found no evidence of replacement of whitebark pine by subalpine fir or Engelmann spruce in the Cascade Range of Washington over a 22-year period, even though the abundance of whitebark pine declined because of white pine blister rust, beetles, and fire. However, they allow that 22 years may not be long enough to detect this change because of slow stand-development rates.

Our correlation analysis suggested a distinct difference in habitat preferences between regeneration of whitebark pine and subalpine fir in terms of temperature. Whitebark pine seedlings grew more abundantly on warm sites, both in terms of growing-season soil and air temperatures, and on sites with late-summer warmth in particular. However, subalpine fir regeneration was negatively correlated with measures of growing-season soil and air temperature; positively correlated with canopy closure, tree density, and stand basal area; and negatively correlated with ground-level PAR. Most subalpine fir regeneration occurred in dense, cool, shady subcanopies of well-established stands. In such stands, much of the subalpine fir regeneration will be unsuccessful without overstory mortality, but their generous presence in these habitats indicates an extreme tolerance of shade and cool, summer soils, providing them the ability to exploit canopy gaps as they develop. Many of these soils were only slightly above Körner and Paulsen's 6.7 °C seasonal physiological threshold for tree root growth. However, should a canopy gap open, the soils would warm in that area. Thus, this species stores much of its reproduction under its canopy, which ensures continued dominance once it occupies a site. A catastrophic disturbance, such as fire, would be required to reopen the site. However, it is important to note that subalpine fir's regeneration was also more widespread than any other species. It is a reproductive generalist, but it has a distinct advantage in cool, shady situations unequaled by any other tree species in this ecosystem.

Standing Dead Trees (Snags ≥ 1.3 m Tall)

- White pine blister rust was the only cause of death determined with certainty for both whitebark and western white pines, and these species are dying at about twice the rate of subalpine fir.
- There was little mountain pine beetle evidence, possibly because the pine populations are not large enough to support large outbreaks.

- Even though whitebark pines commonly live to reproductive age, it is unlikely that large trees, capable of competing with invading subalpine fir that might sustain the species between disturbances, could be numerous in the future because of white pine blister rust mortality.
- In mid-elevation, west-northwestern aspect areas, subalpine fir was dominant, but dead whitebark pine trees were numerous, suggesting high white pine blister rust virulence and that this was important whitebark pine habitat in the recent past.

White pine blister rust was the only cause of death that we were able to determine with certainty for both whitebark and western white pines, suggesting that this disease is by far the most important agent of mortality for these species. The primary insect that kills whitebark pine trees is mountain pine beetle (Arno and Hoff 1990). These beetles, which can be problematic elsewhere, are estimated to become more problematic with climatic warming (Logan and Powell 2001). We observed evidence of their presence in the study area, but they are not currently a problem, possibly because the pine populations are not large enough to support large outbreaks. In surveys of the surrounding area conducted in 2002 and 2003, only 0.4 percent of whitebark pine tree clumps were noted as having mountain pine beetle damage (Shoal and Aubry 2004). All the attacks were on pole- or mature-sized trees. Even without significant mountain pine beetle damage, white and whitebark pines are dying at about twice the rate of subalpine fir.

Most mortality is currently among trees 0- to 30-cm d.b.h. About half of all dead trees in these size classes were whitebark pines; but this species composed much less than half of all live trees. However, the percentage of trees that were killed increased with the size of the trees, suggesting that the longer a whitebark pine tree lived, the greater the probability it would succumb to white pine blister rust. Although trees commonly live to reproductive age, it seems unlikely that large trees, capable of competing with invading subalpine fir and that might sustain the species between disturbances, could be numerous in the future. Thus, it appears that subalpine fir will increase in density throughout most of the study area at the expense of whitebark pine.

In the mid-elevation, west-northwest part of the study area, subalpine fir was clearly the dominant species, but dead whitebark pine was far more numerous than either live whitebark pine or live subalpine fir, suggesting displacement of whitebark pine. The ratios of live to dead whitebark pine were 5 to 22 times higher than in other parts of the study area compared with the west-northwestern aspects at mid-elevations. This suggests higher virulence for the white pine blister rust in mid-elevation, west-northwestern aspect environments and that this was important whitebark pine habitat in the recent past.

Coarse Woody Debris

- Most CWD was on west-northwestern and southwestern aspects reflecting the preferred habitat of whitebark pine and high rates of white pine blister rust mortality, but almost no whitebark pine CWD was found on northwestern aspects, suggesting whitebark pine has not been a significant part of the flora on cooler aspects.
- More and larger CWD occurred at lower elevations than at higher elevations because of the longer history of forest occupancy and greater productivity at lower elevations as well as the higher rate of decomposition of the smaller pieces that are typically produced at higher elevations.

- Most CWD of decay classes 4 and 5 was on southwestern aspects where it tended to be larger and more decomposed than CWD on northwestern aspects, suggesting whitebark pine occupied southwestern aspects before subalpine fir occupation of northwestern aspects.
- Density-dependent mortality was largely restricted to young stands of subalpine fir on lower to mid-elevation, northern aspects where the pieces tended to be small.

CWD plays important roles in biodiversity, regeneration, nutrient cycling, and carbon storage (Franklin et al. 1987, Gray and Spies 1997, Harmon et al. 1986, Laiho and Prescott 2004, Luyssaert et al. 2008). Given the high soil surface temperatures recorded on our southerly exposures, the role of CWD in providing shaded germination microsites for trees and other plants could be important to tree establishment (Gray and Spies 1997). A similar argument could be made for the role of CWD in providing an erosion check on steep, unstable slopes (Franklin et al. 1987, Maser and Trappe 1984). Given the low soil temperatures in dense, subalpine fir subcanopy soils, raised, decomposing logs may offer warmer germination sites for seedlings growing in those circumstances. The use of these substrates by tree and shrub germinants is well known in other forested situations (Maser and Trappe 1984). Unfortunately, these were not ideas that we were able to investigate, but they deserve attention in future studies.

Most CWD was on west-northwestern and southwestern aspects. This reflects the preferred habitat of whitebark pine and high rates of white pine blister rust mortality. We found almost no whitebark pine CWD on northwestern aspects, suggesting that whitebark pine has not been a significant part of the flora on those cooler aspects. Some CWD was on west-northwestern aspects derived from young stands of dense, stem-exclusion stage subalpine fir as well.

Both the number and size of CWD pieces were larger at lower elevations, resulting in much more CWD biomass than at higher elevations. Takeda and Takahashi (2020) also found that piece size and biomass of CWD decreased with elevation in the subalpine. They found that CWD biomass decreased faster than aboveground live biomass, which they attributed to greater decomposition rates of the smaller pieces being produced at higher elevations. We agree that this is likely but also point out that in our case, there has been a longer history of forest occupancy at lower elevation as well.

More of the CWD in advanced states of decay (classes 4 and 5) came from mid- to higher elevations. Of the wood that we could identify there, most was whitebark pine, and we suspect that much of the unidentified wood was too. Thus, much of the CWD at these elevations was not of recent origin, which may indicate heavy whitebark pine mortality shortly after the arrival of the white pine blister rust. The abundance of dead, standing trees and CWD probably reflects establishment of early post-Little Ice Age whitebark pine, followed by the introduction of white pine blister rust in the early 1900s (Lachmund 1926).

There were fewer whitebark pine trees at low elevations on west-northwestern aspects, as subalpine fir tended to dominate these areas. However, the population on southwestern aspects was relatively large and had a large proportion of dead trees. This area may have been an important Little Ice Age habitat for whitebark pine as suggested by larger CWD piece sizes. Other species of trees, including Douglas-fir and subalpine fir, were also present on these low, southwest-facing slopes but contributed little CWD. We found little CWD from any species in high elevations, but all that could be identified was either from whitebark pine or subalpine fir.

Although there was relatively little CWD in decay classes 4 and 5, much of it was on southwestern aspects, and there it tended to be larger and more decomposed than CWD on northwestern aspects. This suggests that southwestern aspects were occupied by whitebark pine ahead of the subalpine fir occupation of northern aspects but may also relate to faster decomposition on the warmer, southwest-facing slopes. Density-dependent mortality was largely restricted to subalpine fir forests on the lower to mid-elevation, northerly slopes. This wood accounts for most of the decay class 2 CWD pieces and derives both from recent competitive thinning and snow breakage. As these are relatively young stands, the pieces tended to be small.

Surficial Soil Organic Layer Depth

- Litter was deepest in low- to mid-elevation forests on cool, moist north-facing slopes (e.g., subalpine fir/Cascade azalea plant association); shallowest in dry, mid- to higher elevation alpine tundra (e.g., spreading phlox community type); and especially shallow on unstable soils.
- Sixty-one percent of litter depth variation was accounted for by summer soil moisture and total stand basal area, suggesting the importance of site productivity and decomposition rates.
- Surficial soil organic matter density in forest stands increased with snow accumulation and compaction.
- Temperatures that we measured under the snowpack were suitable for significant litter decomposition, according to work by others.

We did not quantitatively distinguish between the different organic layers often referred to by soil scientists and here lump them all under the term “litter.” Litter was the prevalent form of soil organic matter on the drier sites as well as the colder open sites, but other more decomposed forms of organic material were common in wetter and more forested sites. Thus, we are limited in what we can say about the surficial organic layers as we measured only the depth and made only cursory observations about other qualities. However, we observed large differences on different sites that warrant comment. The main factors determining litter depth most often given in the literature are productivity (amount of litter produced), litter quality (e.g., coniferous needles vs. herbaceous leaves), and rate of decomposition, which is influenced by temperature, moisture, and litter quality. In general, decomposition increases with temperature but only when sufficient moisture is available (Gavazov 2010).

At our study site, litter depth increased with summer soil moisture and total plot basal area. In this context, both these variables can be thought of as proxies for productivity. However, we also found negative correlations between litter depth and several soil temperature variables, which can be thought of as proxies for decomposition. However, care must be taken in this interpretation as higher soil temperatures tended to occur in areas that were dry and open because of low productivity and few trees. Thus, in our study area, the litter layer tended to be deepest in low- to mid-elevation forests on cool, moist north-facing slopes and shallowest on dry, mid- to higher elevation, spreading phlox community types on southern aspects, especially on unstable soils. A linear model including summer soil moisture and total basal area accounted for 61 percent of litter depth variation. Even so, our third deepest litter layer was on one of the least productive plots—a black alpine sedge meadow. However, this was one of the wettest plots and had the longest lasting snowpack. Litter production may have been low, but wet, cold conditions largely preserved it.

Our deepest litter layer was not included in the model as we had no moisture or snow data for it. However, it still fit the relationship well, being on a wet site, on a northern aspect, at lower elevation in the study area, with a conifer overstory. There was only a weak correlation between litter depth and the age of the oldest tree on the plot, which we used as a stand age proxy. This probably relates to the generally young age of most of the stands and the tendency for the oldest trees to represent an age class of what were probably scattered lone trees in the late Little Ice Age environment.

In the Austrian Alps, soil organic matter increased with elevation from 900 to 1500 m before decreasing with additional elevation to 1900 m (Djukic et al. 2010). Over the same range of elevation, temperature decreased while precipitation and snow cover increased. Djukic et al. (2010) hypothesized that a combination of factors caused the change in soil organic matter accumulation above 1500-m elevation. Decreasing temperatures may have reduced decomposition rates with elevation gain up to 1500 m, allowing for accumulation of soil organic matter, but eventually also caused net primary productivity to decline enough to reduce litter production and soil organic matter (Djukic et al. 2010). However, the vegetation also changed from coniferous forest lower down to *Vaccinium* (bilberry) shrubland where the soil organic matter was deepest, to higher elevation grassland where soil organic matter decreased, and along with these changes, litter quality changed as well (Djukic et al. 2010). There were similar changes in vegetation, productivity, snowpack, and temperature at our study area with elevation. However, the dominant pattern that we saw was decreasing litter with elevation, although other factors were important. This trend needs to be qualified, however. As earlier stated, we measured depth and not biomass, and the litter in forest stands nearer the tree line was denser than it was farther downslope as a result of snow compaction, thus we cannot rule out a pattern in our forest stands similar to what Djukic et al. (2010) found in the Austrian Alps. We should note too, that our study did not sample elevations as low as 900 m as was done in their study.

Although montane, especially alpine, growing seasons are short, decomposition continues under the snowpack because of the unique $\sim 0^{\circ}\text{C}$ temperature regime (Gavazov 2010). Our temperature data showed this temperature regime throughout our study area. Even in places where snow arrived later or built up more slowly, frozen soils warmed to $\sim 0^{\circ}\text{C}$ temperatures once the snowpack became deep enough. In this protected environment, films of liquid water on soil particles support a diverse cold-adapted fungus dominated microbial community (Ley et al. 2004). This community reached its annual peak in biomass under the snow (Schadt et al. 2003) and was active from 3 to -5°C (Gavazov 2010). Because of starvation and intolerance of higher temperatures in spring, nitrogen was released from the dying microbes and taken up by plants. The fungal community was then replaced by a bacterial summer microbial community that tolerated temperatures between 5 and 20°C (Gavazov 2010, Lipson et al. 2000). Such subnivean litter decomposition has been reported in the Washington Cascades (Edmonds 1980) and in Colorado (Seastedt and Walker 2001).

In Colorado, decomposition was fastest around the time of snowmelt, and variation in melting of the alpine snowpack established a temperature-moisture gradient that controlled litter decomposition, with moisture being the stronger determinant (Seastedt and Walker 2001). As temperatures warmed, the soils dried, greatly reducing decomposition in summer. Thus, wet alpine habitats had higher surface decay rates than drier habitats, even though drier areas had longer snow-free seasons and higher surface temperatures.

In the Washington Cascade Range, Edmonds (1980) also found that forest litter decomposition was more related to moisture than temperature. However, in winter, decomposition was faster under the snow in the Pacific silver fir zone where the litter temperature remained at a constant 0.5 °C, than it was at lower elevations where lack of snow cover permitted greater temperature fluctuation and frequent daily freezing of the litter (Edmonds 1980). He also found that decomposition continued through summer in stands over a range of elevations but slowed considerably and in proportion to litter moisture content. It seems likely that this is a good model for the relationships of our north-facing subalpine fir forests compared to lower elevation, mixed-species forests and woodlands in our study area. In the subalpine fir forests, there was a long-lasting snowpack, under which temperatures hovered near 0 °C through winter and remained moist for some time after the snow melted. In mixed-species forests and woodlands, especially at lower elevations, summer drying occurred earlier and was more intense. Also, there was more soil freezing in the fall associated with late-arriving snow and a slower deepening of snowpack in these lower elevation plots. However, the litter was denser, and in most cases, it was deeper in subalpine fir forests than in lower elevation, mixed-species forests and woodlands because of the large difference in productivity.

Litter quality is also important. For example, red alder (*Alnus rubra*) leaves decomposed faster than Douglas-fir needles, which decomposed faster than western hemlock (*Tsuga heterophylla*) and silver fir needles (Edmonds 1980). Similarly, Kuramoto and Bliss (1970) found faster litter decomposition in Olympic Mountains grass-forb subalpine meadows than in grass-dominated meadows, as the forbs had softer leaves than grasses. But decomposition was slowest in moist forb meadows that were dominated by *Saussurea* and *Senecio* because of their large, hard stems. Thus, large differences in litter structure and chemistry can be as important as moisture. Their meadows had higher coverage of grasses and forbs than most of our nonforest plant communities, suggesting moister conditions and different litter structure and chemistry than we had.

At our study area, another important factor appeared to be slope instability. We found almost no organic matter on steep, southwest-facing, nonforest plots with actively moving loose, sandy, gravelly soils. Steeper slopes are often drier as they shed water more quickly, and if positioned on south- or west-facing slopes, they are also warmer. When coupled with unstable soils, little can grow on these slopes, sometimes reducing productivity to near zero. Soil movement on such slopes tends to mix organic matter that falls on them into the soil as opposed to allowing surficial accumulation, but it also reduces vegetation cover and production. Plots with rock stripe solifluction had little to no litter in the rock stripes and shallow layers between them.

In contrast, we found the deepest layers in older forests with cool, moist soils where production was higher. In these areas, the layers were not only deeper but denser and can be described as mors. Mors form in coniferous forests under less-than-ideal circumstances for decomposition, so a portion of the litter is decomposed into humus, which is more stable and slowly accumulates (Prescott et al. 2000). Our deepest organic layer was a mor on a productive, lower elevation, subalpine fir-forested plot (plot 34), in an area with many emerging seeps. It was also in a low-lying area that received cold-air drainage. Thus, litter production was high, and the cool, damp understory conditions favored humus production.

A combination of low temperatures during most of the year, high soil moisture, and softer, more decomposable litter in the black alpine sedge meadow (plot 18) also produced

a humified organic layer. This soil was under snow longer than any other soil in the study and had the second lowest temperature in June (2.6 °C), but it warmed rapidly to an average temperature of 12.8 °C in August, which was slightly lower than the August site average of 14.2 °C (SD = 3 °C). Litter production was almost entirely herbaceous, and it is also likely that fine root turnover contributed substantially to the organic layer. The loose litter layer was shallow, but the 5-cm-dense humic organic soil layer, was the third deepest organic layer that we measured, and it was also one of the densest. Black alpine sedge meadows are typical of late-melting, moist sites (Kuramoto and Bliss 1970). This location was on a bench facing the prevailing winds and accumulated snow blown off the slopes below it. As a result, this plot was the latest to melt out, usually in late June or July, and because of its bench topography, it also accumulated runoff from above. Thus, the soils were moist well into the growing season.

The explanation for the depth of this litter layer on a relatively unproductive site may be that this site has been accumulating organic matter far longer than the forest sites. Gavin and Brubaker (1999) found that a similar black alpine sedge meadow in the Royal Basin (at a nearly identical elevation and a mere 6 km west of our study area) had been accumulating black alpine sedge material for at least 1,500 years and had been accumulating organic material from other drier, nonforest communities for at least 6,000 years. Most of the forests in the study area are newer than the Little Ice Age, which ended around the year 1850 and have achieved forest density even more recently. At most of those sites, the previous plant community was probably a dry tundra type, or in colder sites, perhaps only a snowbank was present.

There was a general trend toward deeper litter layers in older and more productive forests with dense canopies. For example, our lowest elevation plot (Douglas-fir/Cascade barberry community type) where some trees were more than 200 years old, and which had a summed canopy cover of 211 percent, had the second deepest litter layer, even though it was on a moderately steep, southwest-facing slope. Its productivity derived partly from its lower slope position, which received topographic moisture enhancement. Spring water was moving down the slope just off the plot, and no doubt there was enhanced subsurface flow under part of the plot. Although moisture explains much of the increased productivity, this warmer, low-elevation plot was more productive and had a deeper litter layer than cooler and younger but equally moist forest plots at higher elevations.

Among the four plant associations or community types with enough data to compare statistically, we found the least litter in the spreading phlox community. This is a dry, alpine tundra type and produces little biomass and is subject to solifluction. At the same time, its surficial soils warm considerably during its short growing season, becoming quite dry. Of forest communities represented by more than one plot, the one averaging the deepest and densest soil litter layer was the subalpine fir/Cascade azalea plant association. This plant association is found on cool, moist north-facing slopes and has a forest overstory of subalpine fir. Snow tends not to melt during winter thaws on these slopes, and so it accumulates to deeper depths. The weight of the snow compresses the litter considerably and this may, by excluding oxygen, reduce decomposition. In any case, our measured soil temperatures in this community type indicated that it had one of the coldest soils.

It should not be surprising that stands with higher basal areas resulted in higher accumulations of litter. However, this relation is not simple. Places with higher basal areas are

moister sites and are mostly on cooler aspects. However, if soil moisture is topographically augmented, then stands with high basal areas can be found on warm aspects as well. In any case, the shade produced by the canopy maintains cooler soils, which decreases decomposition.

Foliar Nitrogen and Carbon

- Our measured foliar nitrogen levels do not suggest limitation.
- Whitebark pine and subalpine fir had similar foliar nitrogen and foliar carbon, suggesting similar nutrient foraging and allocation.
- Foliar nitrogen, but not foliar carbon, was negatively correlated with warmer aspects, resulting in higher carbon-to-nitrogen ratios in warm areas.
- Whitebark pine foliar nitrogen increased with summer soil moisture, suggesting drought limitation of nutrient foraging.
- When larger, older trees were present and when overstory canopy closure increased, foliar nitrogen decreased, possibly because of higher levels of nutrient competition in denser forests.

Foliar nitrogen from whitebark pines at our study area was comparable to, if not somewhat higher than, what was reported for whitebark pines in Montana (Sala et al. 2012) and was somewhat higher than what Moore et al. (2004) reported as typical for Douglas-fir, grand fir, ponderosa pine, and lodgepole pine in Montana. We found no literature suggesting what levels of nitrogen might be considered limiting in whitebark pine, but elevated nitrogen levels may increase susceptibility in pines and currants to infection by white pine blister rust (McDonald and Dekker-Robertson 1998, Van Arsdell 1972, Zambino 2010).

Moore et al. (2004) provided cumulative nitrogen distributions for ponderosa pine, lodgepole pine, and grand fir in the area encompassing western Montana to eastern Oregon and Washington. Our whitebark pine and subalpine fir mean foliar nitrogen levels of 1.3 percent fall in the 60 to 70 percentile range for ponderosa pine, 90 to 95 percentile range for lodgepole pine, and 95 and 100 percentile range for grand fir. Our subalpine fir foliar nitrogen level was considerably higher than that found in subalpine fir trees in central Utah (which ranged from 0.83 to 0.91 percent) (Rhodes et al. 2016). Thus, nitrogen does not appear to be low relative to other areas where such measurements have been taken.

Körner (1998) proposed that the breakup of forest at the tree line is due to cold-induced growth limitation rather than production of assimilates (i.e., not limited by photosynthesis or carbon balance). This suggests that higher levels of nonstructural carbohydrates, lipids, and leaf nitrogen should occur in tree line trees as a result of there being no growth dilution (growth dilution occurs when increased plant growth leads to a dilution of certain compounds within the plant) than in lower, warmer, areas where trees grow faster. Our generally high levels of foliar nitrogen may reflect this, but we found a negative correlation between foliar nitrogen and temperature, which did not seem to be in line with Körner's (1998) hypothesis on nitrogen.

Our measurement of foliar carbon as opposed to nonstructural carbohydrates make evaluating Körner's (1998) carbon hypothesis difficult. We found no difference in total foliar carbon between warm and cool parts of the study area. However, Bansal and Germino (2008) found that nonstructural carbohydrates in needles and roots of subalpine fir and Douglas-fir were greater in seedlings grown at the cooler, upper tree line than seedlings grown at the warmer lower edge of the tree line. The mechanism that they suggest is that although

photosynthesis was 13 to 15 percent less at the upper tree line edge because of temperature limitations, this was more than offset by respiration that was 35 to 39 percent less.

Bansal and Germino (2008) also found that summer nonstructural carbohydrate levels fluctuated with the highest levels in August and the lowest in September. Perhaps more importantly, there was little difference between their carbohydrate values from high- and low-elevation sites in September, which is when our measurements of foliar carbon were taken.

The nearly identical foliar carbon and foliar nitrogen in whitebark pine and subalpine fir and the positive correlation of both between these two species suggests similarities in nutrient foraging and allocation strategies. In both species, foliar nitrogen was negatively correlated with warmer aspects and the mean of the 10 maximum air temperatures recorded. However, foliar carbon did not change with these conditions, so the reduction in nitrogen in warm relative to cool areas caused an increase in the carbon-to-nitrogen ratio of warm areas.

As nitrogen foraging by roots depends on available soil water, this suggests that moisture limitations in warm, dry parts of the study area may influence foliar nitrogen uptake in both species. As has already been shown, subalpine fir was far more common on moister sites, which helps explain why its foliar nitrogen was not correlated with several soil moisture indicators. However, whitebark pine grew mostly in droughty areas, and its foliar nitrogen was positively correlated with several soil moisture indicators (12-cm-deep summer soil moisture, duration of the seasonal snowpack, soil freezing). The duration of the seasonal snowpack and soil freezing reflect later melting of the snowpack and thus higher soil moisture during warmer parts of the growing season. The negative correlation between whitebark foliar nitrogen and slope reflects the droughty nature of steeper slopes. Thus, all these variables point to a positive relationship between whitebark foliar nitrogen and soil moisture. Because we do not see comparable correlations with subalpine fir, we conclude that the whitebark pine population faces greater nutrient foraging limitations than does subalpine fir because of drier soils.

Interestingly, although foliar carbon between the two species was strongly correlated and at similar levels, none of the environmental factors that carbon was correlated with were the same between the two species. In whitebark pine, foliar carbon was positively correlated with direct solar radiation in June, which may reflect how rapidly a site warms after snowmelt. We did not find a directly comparable reduction of nitrogen reflecting carbon dilution to this variable, but we found a generally negative response of foliar nitrogen to other summer drought indicators.

Subalpine fir foliar carbon was positively correlated with minimum air temperature (i.e., more carbon with higher minimums). It was also negatively correlated with elevation (i.e., less carbon at higher and cooler sites). Thus, for both species, although in different ways, there is the suggestion that warmer environments promote higher foliar carbon. In view of Körner's hypothesis and the findings of Bansal and Germino (2008), this suggests that structural carbohydrates are sufficiently more abundant in warm than in cool areas, so as to mask the reverse trend in nonstructural carbohydrates suggested by these researchers.

Finally, several indicators of forest maturity and tree size suggest that both species have lower foliar nitrogen in mature forests with larger trees. Thus, when larger, older trees were present or when overstory canopy closure was greater, foliar nitrogen content decreased. This could be attributed to the higher levels of nutrient competition that trees encounter in these denser forests. However, Rhodes et al. (2016) found no relationship between foliar nitrogen and stand structure or species composition in Utah mixed aspen and subalpine fir forests.

White Pine Blister Rust Infection of Whitebark Pine

- Olympic Peninsula whitebark pines may have been infected by white pine blister rust between 1917 and 1922, although the first published report was in 1943 (Bedwell and Childs 1943) when 92 percent of trees were already infected.
- Most plots had one or more alternate hosts for white pine blister rust present suggesting highly localized sources of infection throughout the study area.
- The number and severity of infections were greater in warm areas, reflecting where whitebark pines grow and suggesting the fungus benefits from warmth.
- White pine blister rust severity was positively correlated with the percentage of night temperatures between 9 and 15 °C (best for germination and germ tube growth) only in October, possibly because the humid conditions needed for fungal germination were favorable then.
- Mean monthly air temperatures conducive to mycelial growth (15.5 to 21 °C) occurred only at lower elevations in July and August.
- Summer soil and soil surface temperature correlations with white pine blister rust severity suggested the most severe infections occurred where canopies were open and on temperature-enhancing topographic positions.
- Topography controls the presence or absence of whitebark pine habitat, but stand structure is more important for controlling near-ground temperatures, which correlated with the frequency and severity of white pine blister rust infections.

As has already been discussed, mature whitebark and western white pines are dying at about twice the rate of mature subalpine firs. Also, we found that subalpine fir was reproducing faster on all aspects and elevations than whitebark pine, and there were significantly more dead whitebark pines than subalpine firs despite whitebark pine having a much smaller population. Although we could not identify the cause of death in many cases, when we were able to make this determination for western white and whitebark pines, the cause was always white pine blister rust. Shoal and Aubry (2004) also mention difficulty in attributing fatality to white pine blister rust but were also of the opinion that most of the whitebark pine mortality in the Olympic Mountains population was due to white pine blister rust. There was little evidence of mountain pine beetle kill, which was also found at Mount Rainier in the North Cascades (Rocheft 2008).

Because white pine blister rust enters through the stomata, it usually kills the tree from the top down, girdling the branch tips, reducing cone production, and thus reproductive capacity (Hoff 1992, Keane et al. 2017). One of the most important effects of white pine blister rust is the reduction of regeneration, which alters natural succession (Kinloch 2003). With sufficient population decline, the surviving trees, even if some measure of rust resistance develops, may produce insufficient seed to overcome seed predation by squirrels and nutcrackers. Thus, the local population could go extinct and any resistance that might have developed would not be passed on (McKinney and Tomback 2007).

White pine blister rust is a fungal pathogen of five-needle pines in the subgenus *strobus* (Geils et al. 2010). It is native from central Siberia to the Pacific Ocean and south to the Himalayas where it coevolved with the native pines for about 23,000,000 years (Hummer 2000), and as a result, the pines that it infects there have developed resistance and are not seriously harmed. In 1705, eastern white pine (*Pinus strobus*) was imported to Europe from North America to be grown for ship masts, and by the 1800s, it was being grown widely

across Europe (Hummer 2000). White pine blister rust was first reported infecting eastern white pine in western Russia in 1856, and by the early 1900s, it was infecting eastern white pines throughout Europe (Hummer 2000). In the 1890s, it crossed the Atlantic on eastern white pine seedlings being shipped for reforestation, and the disease spread rapidly through the Eastern United States and Canada in the early 1900s (Hummer 2000).

White pine blister rust was first introduced on the west coast of North America in 1910 from infected French-grown eastern white pine nursery stock that was planted in Vancouver, British Columbia, (Lachmund 1926) and spread rapidly from there to western white pine and other native five-needle pines throughout the Western United States. However, Hunt (2009) suggests that there must have been multiple introductions to several locations in the Pacific Northwest to explain its rapid and in some cases apparently upwind spread, although there is apparently no corroborating molecular or genetic evidence for this. In 1913, white pine blister rust was found in western white pine trees in the vicinity of Vancouver, British Columbia, and by 1917, it had been found 400 km east, 240 km north, and 160 km south (in northern Puget Sound). By 1922, white pine blister rust had been found as far south as the Columbia River at Ilwaco (Lachmund 1926). Thus, it is possible that Olympic Peninsula whitebark pines were infected between 1917 and 1922.

The first west coast observation of a whitebark pine infection was by the British Columbia Office of Forest Pathology on trees in the Birkenhead River area in 1926 (Childs et al. 1938). In the United States, the first published observation of whitebark pine infection was in 1936 on Mount Hood in Oregon and on Mount Adams, Mount Rainier, and on the Okanogan-Wenatchee National Forest at Hyas Lake (all in Washington) (Childs et al. 1938). These authors mention that others had observed infected whitebark pines near Mount Hood as early as 1931 as well as on the St. Joe National Forest in Idaho around that time (Childs et al. 1938). The first published report for whitebark pine infection in the Olympic Mountains came in 1943 (Bedwell and Childs 1943). These authors mention a survey conducted at Marmot Pass between 1937 and 1939 that found 92 percent of whitebark pines and 69 percent of western white pines were infected. This survey was conducted in a portion of our current study area.

Until 2006, it was widely assumed that currants and gooseberries were the only alternate hosts of white pine blister rust. Virtually all currants and gooseberries were thought to be susceptible, which spurred widespread efforts through the middle parts of the 1900s to control the disease by eradication of currant and gooseberry plants—an effort that failed and was abandoned in the 1960s (Benedict 1981, Maloy 1997). Although several species of currants occur near the study area, the only species that was closely associated with whitebark pine trees was prickly currant, which was found with low covers on four plots. However, it occurred in a variety of situations, from forest plots with no whitebark pine to mostly open subalpine plots with only a few whitebark pines. In the latter situation, prickly currant grew as a diminutive plant, perhaps 10 cm tall, closely associated with the shade of a whitebark pine tree. The other species of currant recorded during our study was mapleleaf currant growing on one of the subalpine fir/Cascade azalea plots (plot 36) with no whitebark pine present. Shoal and Aubry (2004) also noted both species of currants in the area along with sticky currant (*Ribes viscosissimum*).

McDonald et al. (2006) showed that white pine blister rust could successfully use sickle-top lousewort and giant red Indian paintbrush as alternate hosts in natural ecosystems, both of which are common in our study area. This supported and extended previous work

by Hiratsuka and Maruyama (1976), who first showed that giant red Indian paintbrush could function as an alternate host in a greenhouse study. Mulvey and Hansen (2011) expanded the list of alternate host species. They found naturally occurring infections at several locations in the Cascade Range on wavyleaf Indian paintbrush (*Castilleja applegatei*), giant red Indian paintbrush, mountain Indian paintbrush, as well as sickletop lousewort. They were also able to induce infections either in the field or laboratory in cobwebby Indian paintbrush (*Castilleja arachnoidea*), bracted lousewort (*Pedicularis bracteosa*), and elephanthead lousewort (*Pedicularis groenlandica*), suggesting a possible role for these species. They did not observe infections in harsh Indian paintbrush and did not try to experimentally inoculate it. Harsh Indian paintbrush is common in our study area and widely common on the Olympic Peninsula. In Asia, there are still other species of paintbrush and lousewort that are alternate hosts for white pine blister rust (Mulvey and Hansen 2011). Given the number of paintbrush species that can be infected, it is quite possible that harsh Indian paintbrush could also be an alternate host.

Mulvey and Hansen (2011) concluded that sickletop lousewort, which held its foliage later into the season than paintbrush species and produced infection-amplifying urediniospores (unlike paintbrush species), was the most effective host at the sites that they studied. They observed telia production from mid-August through mid-September on sickletop lousewort. Early foliar senescence of paintbrush due to drought and aphids cut short the production of basidiospores by early September, and paintbrush rarely produced urediniospores. Although paintbrush produced telia and basidiospores without having produced urediniospores, they could not amplify the infection in this way. Also, sickletop lousewort often occurred in the shade, which they speculate provided better conditions for infection than in full sun, which is where paintbrush is more typically found (Mulvey and Hansen 2011).

The ability of white pine blister rust to use species of lousewort and paintbrush helps to explain the rapid spread of the disease, and the failure of the currant and gooseberry eradication campaign. At our study area, most plots, including 94 percent of the plots with whitebark pine, had one or more alternate host species present. The most common of these was giant red Indian paintbrush followed by sickletop lousewort and prickly currant. This suggests that the source of infection for the trees in the study area is highly localized.

Aeciospores produced on the pine trees that infect alternate hosts are responsible for long-distance transmission. Mulvey and Hansen (2011) found that these spores were being produced on whitebark pines in the Cascade Range from late June through late August, encompassing a period from when snow was still melting and before budbreak for many herbaceous species, through senescence of many herbaceous species. These spores are small, thick walled, and durable. Aeciospores have apparently traveled as far as 300 km (Fujioka 1992) to 500 km (Mielke 1943) and possibly even 1000 km (Kinloch 2003) where they have succeeded in starting new infections in alternate hosts and introduced new infections from them in pines. Thus, on the Olympic Peninsula, all alternate hosts between, within, and around the fragmented Olympic subpopulations of whitebark pine are easily within range, depending only on wind direction.

Germination of the aeciospore on the alternate host's leaves requires conditions of high humidity, such as might occur under nighttime dew deposition. Mulvey and Hansen (2011) found that infection of the alternate host species lagged aeciospore dispersal by several weeks, suggesting that unfavorable infection conditions during summer might lengthen the incubation period. Once the alternate host species is infected, the fungus amplifies the

infection with urediniospores in some, but not all, alternate hosts. Urediniospores only infect other alternate host leaves in the vicinity.

In late summer or fall, or during cool, moist conditions of at least 2 days, basidiospores capable of infecting pines are produced on the undersides of alternate host leaves. If successfully transferred by the wind, and provided they have suitable conditions for their germination, they infect susceptible pines through their stomata (Hoff 1992, Kinloch 2003, Lachmund 1926). However, these spores are fragile and typically only travel distances of up to about 274 m (Lachmund 1926). Basidiospores are vulnerable to desiccation and sunlight, so from the time of production to the time of infection, cool, moist conditions must prevail. Although they do not travel as far as the aeciospores (Kinloch 2003), under exceptional conditions with cool, moist, turbulent winds, they have been transported as far as 27 km (Van Arsdell 1965). Most whitebark pine trees in the Olympic Mountains lie within 20 km of each other, so it is at least theoretically possible given appropriate moisture and wind conditions for basidiospores to be transported from an alternate host to virtually any tree in the population. Although this seems unlikely from what we know of the fragility of these spores, it cannot be ruled out given our poor knowledge of micrometeorology of the area. Also, the alternate host species are well distributed throughout the Olympic Mountains, making it a certainty that one or more will always be near a whitebark pine tree.

Whitebark pine is highly susceptible to white pine blister rust (Bedwell and Childs 1943, Bingham 1972, Childs et al. 1938), and to date, only limited resistance has developed. Resistance can be arrived at in several ways, such as preventing the germ tube from penetrating stomata, rapid shedding of infected needles, production of fungicidal compounds, and canker compartmentalization or tolerance, but with varying efficacy (Hoff et al. 1980, Mahalovich 2013, Zambino and McDonald 2004). Several estimates of resistance in whitebark pine have been made: Hoff et al. (1980) estimated 33 percent, while Mahalovich et al. (2006) estimated 47 percent. Twenty-five percent of seedlings that were inoculated at 3 years of age from six national forests, mostly in eastern Washington and Oregon, were still alive at 5 years of age (Snieszko et al. 2007).

Hoff et al. (1994) suggested that natural selection explained higher levels of resistance observed in stands with high white pine blister rust mortality. It has been observed that white pine blister rust resistance decreased from Washington to Wyoming in a southeasterly direction (Mahalovich et al. 2006), and Snieszko et al. (2007) also found that seedlings from northern Oregon and Washington forests had greater resistance than did seedlings farther south in those states. These northern areas have had a longer history of infection and thus probably more mortality. Perhaps white pine blister rust resistance is greater in northern stands, but Shoal and Aubry (2006) still found greater levels of rust infection in more northerly Washington Cascade Range stands than farther south in Oregon. They suggest that this was because of environmental factors, including decreasing precipitation (Shoal and Aubry 2006). None of these studies included Olympic Peninsula trees.

Greater white pine blister rust mortality in the north may have selected for higher white pine blister rust resistance east of the Cascade Range crest, but infection rates are high in areas west of the Cascade Range crest, even though disease residence has been long, and mortality has been high. Perhaps this is because environmental conditions are much more conducive to infection west of the Cascade Range crest than east of it. Shoal and Aubry (2004) observed much less white pine blister rust infection in the Okanagan-Wenatchee National Forest in the Cascade Range rain shadow than in the Mount Baker-Snoqualmie

National Forest, which occupies the much wetter windward slopes west of the Cascade Range crest. They also noted an association of high levels of infection with proximity to steep, wooded drainages, implying that the wooded drainages harbored more currants. Rochefort (2008) made a somewhat contrary observation on Mount Rainier where infection, although present in all stands that were surveyed, increased from west to east and from lower to higher elevations.

However, Olympic Peninsula whitebark pine trees do not follow the north to south resistance trend just discussed. Preliminary data from the Forest Service (USDA FS 2015) suggests that seedlings grown from Olympic National Forest parent trees have some of the lowest white pine blister rust resistance in Oregon or Washington. They ranked white pine blister rust symptoms on inoculated seedlings into six levels (A through F). An “A” rating indicated ≤ 40 percent of seedlings had stem symptoms, and an “F” rating indicated > 95 percent of seedlings had stem symptoms. Seedlings were grown from seeds collected from 483 parent trees from 15 national forests in Oregon and Washington. Overall, the percentage of seedlings in the A through F ratings were, respectively, 14, 12, 14, 28, 8, and 24. The corresponding data for the Olympic National Forest were 0, 0, 8, 20, 16, and 56 (from 25 parent trees) (USDA FS 2015).

Why Olympic Peninsula whitebark pine trees have such low resistance is not clear; however, they are a small, fragmented population that is isolated from other populations by the Puget Sound and the Strait of Juan de Fuca. Being the westernmost population, they are both remote and upwind from other regional populations. Aubry and Rochefort (2008) found that although other populations of whitebark pine in Oregon and Washington had generally similar genetic diversity to what has been found in the rest of the species range, the Olympic Mountains population was distinct and had less genetic diversity than in the rest of Oregon and Washington. Although lower genetic diversity might be a contributing cause to lower resistance, it is not necessarily the case. Regardless, natural selection for more resistant trees may be taking place, but because the original population first exposed to the fungus was not sampled for rust resistance, we cannot answer that question. Also, the genetic diversity testing that was done does not speak directly to the kind or abundance of genes that could potentially convey resistance—only that there is lower overall genetic diversity in the Olympic Mountains than elsewhere. Finally, resistance may play out somewhat differently in older trees than the seedlings that were tested. Clearly, more work is needed.

Our analysis showed that infected live trees, especially those with more serious infections, were larger and older than uninfected trees. Rochefort (2008) also made this observation on Mount Rainier and suggested that the longer exposure time to the fungus by older trees accounts for their higher infection rate, which we agree with. However, this could also be construed as evidence of developing white pine blister rust resistance (i.e., younger trees are more resistant), but we think, based on the low rust resistance of tested seedlings (Bower 2021), that this is not likely. Rather, we believe the most likely explanation is that older trees have had more time to become infected, and small, infected trees die and decompose more rapidly than large, infected trees, skewing the observations further. Infections on younger trees are initiated closer to the bole because of their smaller size, so they tend to be lethal in a shorter time. However, many young trees are surviving to reproductive age, implying that further selection is possible. This leaves us with the especially difficult-to-answer questions of whether the current level of reproduction is adequate, and if not, how much time remains for a solution to be found. This is a question that is not currently answerable.

Topography, stand conditions, and local wind currents have been shown to be important to local infection patterns. In British Columbia, cankers near the ground in western white pine trees were usually caused by inoculum produced on alternate hosts within the stand, although cankers higher in the tree resulted from inoculum picked up by turbulent air currents and carried greater distances (Hunt 1983). Dense stands on flat topography had fewer cankers, and the cankers tended to be lower in the crown because air circulation was minimal under these conditions. Trees growing in more open stands on slopes, such as those in our study area, had more cankers, including some high in the crown because these trees had greater crown exposure and greater air circulation (Hunt 1982, 1983). It has also been observed that more cankers are found on the side of the tree facing prevailing winds or evening air drainage off adjacent mountains (Hunt 1983). Hunt (1983) concluded that the highest hazard for infection exists in open-grown trees on sloped topography, which are precisely the conditions where most whitebark pines grow in our study area.

In mountainous terrain, such as our study area, summer and fall rain can increase soil moisture and relative humidity near the ground; subsequent calm, clear nights allow radiant heat loss and the downslope flow of cool, moist air that carries basidiospores, initiates germination, and causes infection (Kimmey and Wagener 1961, Zambino 2010). However, transmission may also occur in more complex ways. Van Arsdell (1967) found that nighttime cold-air drainage from surrounding hills flowed into valley swamps infested with currants, forcing swamp air upward and back over to the tops of the hills, carrying basidiospores and infecting the hilltop trees. Thus, the trees closest to the swamp were often spared infection, and the trees farthest away on the hilltops were badly infected. In our study area, most currants tended to be in lower, moister valleys, but paintbrush and lousewort were at all elevations and near all whitebark pines. Thus, cool, moist air currents operating in any direction, including cold-air drainage, are likely to pick up and move basidiospores. However, cold-air drainage would likely concentrate basidiospores picked up while flowing over the slope into lower slope positions, which together with occasional valley fogs provide desirable conditions for spore germination and infection. In our study area, lower slope trees tended to be larger, older, and often severely infected.

The tendency of whitebark pine stems to occur in clumps complicates both field sampling and potentially the interpretation of sampling results. The more closely related the stems are, the more likely they will have a similar level of white pine blister rust resistance. In our sample, 487 stems were present in 228 clumps of 1 to 6 stems. Weaver and Jacobs (1990) found that depending on the stand, whitebark pines had multiple stems in 8 to 79 percent of trees and that clumps could have from 1 to 11 stems. This is important because multistemmed clumps arise in different ways, so the individual stems may be genetically identical, as in the case of layering or low branching, or may exhibit varying levels of genetic difference when they arise from seed caching (Arno and Hoff 1990, Weaver and Jacobs 1990). When Clark's nutcrackers cache multiple seeds, the seeds are likely to have come from the same tree, thus are siblings, half siblings, or selfed, but the seeds may also have come from more than one tree and are more distantly related (Rogers et al. 1999, Tomback 2001). Because of dormancy-induced delayed seed germination, seeds in a cache may germinate over several years, resulting in stems of several sizes and ages (McCaughey and Tomback 2001). Still other clumps may result from the

tendency of Clark's nutcrackers to cache seeds near the base of existing trees (Hutchins and Lanner 1982). Thus, these clumps could consist of unrelated trees of different ages. Single-stemmed trees also arise in different ways, such as when Clark's nutcrackers cache single seeds or when multiple stems are reduced by competition (Weaver and Jacobs 1990) or disease to a single stem.

We found that white pine blister rust infected 16 percent of stems and 31 percent of clumps. As we found 2.14 stems per clump, this is the expected difference if we assume little difference in resistance among the stems in each clump. There was also little difference in the mean white pine blister rust infection severity code, which was 2.26 for individual stems and 2.29 for clumps. Thus, we conclude that the two sampling methods yielded comparable results.

By using a transect method to sample whitebark pine clumps in an area that largely overlapped our study area, Shoal and Aubry (2004) sampled 255 whitebark pine clumps with 866 stems (3.4 stems per clump). They found that 20.8 percent of the clumps were infected with a mean white pine blister rust infection severity code of 3.2. They also sampled whitebark pine populations on three other national forests: Mount Baker-Snoqualmie, Wenatchee, and Okanogan (the Wenatchee and Okanogan National Forests now merged into the Okanogan-Wenatchee National Forest). The four forests had a mean of 2.5 stems per clump, a mean of 27.8 percent of clumps infected, and a mean white pine blister rust infection severity code of 3.1.

Although the difference between Shoal and Aubry's (2004) Olympic Peninsula findings and ours is not large, it also cannot be ignored. Shoal and Aubry's (2004) protocol focused sampling in the areas with the most whitebark pine, and thus was not random as was ours, which may account for some of the difference in findings. Also, Shoal and Aubry (2004) sampled in a different year than we did. This could result in a substantial difference in the number of recent infections as these are visible mostly as flags of dead branch tips, which show up clearly only for a short time. After the needles or branch tips fall, these kinds of infections are much harder to see from a distance. It is possible that we recorded more of these, lowering our mean white pine blister rust infection severity code. In fact, we recorded a large difference in white pine blister rust severity code 1 infections in different years, finding 43 percent of trees with such infections during the first plot measurements (2007 through 2010) and only 2 percent in 2013 and 2016 (plot remeasurements). Perhaps we undercounted white pine blister rust infection severity code 1 infections in 2013 and 2016, but it seems as likely that the number of new infections varies in different years.

According to Shoal and Aubry (2004), a mean white pine blister rust infection severity code of 3.1 means that most of these trees will die or be top killed, adding that, "An isolated population like that in the Olympics, with few cone-bearing trees, could be especially at risk if younger trees are damaged or killed by disease before reaching cone-bearing age."

There were many significant positive correlations between the white pine blister rust indicators and summer soil and soil surface temperatures. The mix of significant air, soil surface, and soil temperature correlations varied by indicator, but the same overall pattern emerged with each. Thus, the number and severity of infections were associated with warm areas. To some extent, this is expected because most whitebark pines grew in the warmer areas. This is reflected in the positive correlation between all three of the white

pine blister rust indicators and whitebark pine canopy cover. However, while this would help explain why there were more infected trees present (because there are more trees to become infected), it does not explain why the infections that were present were more severe on warmer sites, unless it is the case that the fungus grows faster in warmer environments. If white pine blister rust infection virulence is temperature dependent in this environment, then a warming climatic trend could exacerbate future infestations.

Because the basidiospores are sensitive to light and require high humidity to germinate (Kinloch 2003), most germination occurs at night (Van Arsdell 1967). Basidiospore germination and germ tube growth are temperature dependent. Hansen and Patton (1975) found near 100 percent germination at temperatures between 5 and 24 °C; however, germ tube elongation was more vigorous between 9 and 15 °C. As it is the germ tube that grows through the stomata to cause the infection, the latter temperatures are important.

Night temperatures between 9 and 15 °C were most common during July and August and decreased each month thereafter until November, when they were extremely rare. However, the mean white pine blister rust infection severity code was positively correlated with the percentage of night temperatures in this range only in October. In July and August, the correlations were negative. Thus, the places with the most October night temperatures in this range were the most likely to have severe infections. Fall rains and heavy cloud cover increase at this time of year, raising humidity. At the nearby Dungeness SNOTEL weather station, the average number of days with at least 2.5 mm of precipitation, based on the years 2010 through 2016, increased from 4 days in July and August to 7 days in September and 12 days in October. Thus, October has nights when temperatures and humidity are suitable for germination and germ tube development and could be one of the most important months for infection.

Mulvey and Hansen (2011) found that warmer, drier climates of the central Oregon eastern Cascade slopes appeared to limit the ability of Indian paintbrush and possibly of some species of lousewort to act as alternate hosts because the foliage of these species senesced before infections could mature. They also found that powdery mildew and aphid infections of paintbrush species and bracted lousewort limited their ability to produce basidiospores at some sites, but that sickletop lousewort growing in shade retained its foliage late into the season. They acknowledged that these limitations might play out differently in other years or climates.

We did not observe such foliar senescence in the Olympic Mountains in August or early September, which suggests that in the Olympic Mountains, Indian paintbrush and sickletop lousewort foliage is available later in the season for basidiospore development than in the eastern Cascades. Thus, it is possible that alternate host foliage is available for basidiospore production for as long as the season is warm enough for completion of the white pine blister rust life cycle.

Killing of alternate host foliage by frost could prevent basidiospore production but does not appear to be a barrier in the Olympic Mountains. The average whitebark pine plot minimum air temperature did not fall to freezing until October 27, and at the nearby Dungeness SNOTEL weather station, the minimum daily temperature in October recorded between 2010 and 2016 dropped to ≤ 0 °C an average of two times in October, usually toward the end of the month. It appears that climatic conditions in the study area are not a barrier to infection in October and may even promote times during both day and night when infection could occur.

Once infection has occurred, the growth of the mycelium is also temperature sensitive. Harvey and Grasham (1969) grew white pine blister rust on western white pine callus tissue in a laboratory setting, varying daytime temperatures between 10 and 27 °C, while holding night temperatures at 4 °C. The mycelium grew best with daytime temperatures of 15.5 to 21 °C, did not grow at all at 10 °C, and died when subjected to 30 days at 27 °C, as did the callus tissue it was growing on. Based on our data, mean monthly air temperatures between 15.5 and 21 °C occurred only in the months of July and August and even then, only at the lowest elevations, suggesting this is where postinfection mycelial growth would be fastest. This is another reason why lower elevation infections could be more severe. Our mean monthly air temperatures were below 10 °C from October through June, suggesting little mycelial growth could take place then.

The increased number of significant soil surface and soil temperature correlations with white pine blister rust severity indicators in summer suggests that the plots with the most severe levels of infections have more open canopies and are on topographic positions that permit more soil heating than other sites in which whitebark pine is found. This is supported by the positive correlations between all three white pine blister rust severity variables and ground-level PAR. The complete lack of any significant correlations with our three measures of potential solar radiation suggests that the stand structure is more important than topography within the study area. This is not surprising as the area in which whitebark pine grows in this part of the Olympic Mountains is rather homogeneous on steep, south- to west-facing slopes. Thus, topography appears to control the presence or absence of whitebark pine habitat, but within that constraint, stand structure is more important for controlling near-ground air temperatures, soil surface temperatures, and soil temperatures, which were correlated with the frequency and severity of white pine blister rust infections. These relationships could change in different parts of the whitebark pine range depending on how the local climate interacts with the local topography. The Olympic Mountains population is an outlier population growing in a highly maritime climate, albeit in a local rain shadow.

The complexity of these relationships is illustrated by the positive correlations between all three white pine blister rust severity indicators and the standard deviation of ground-level PAR, despite a seemingly incongruous positive correlation with whitebark pine canopy cover. But whitebark pine is often not the only tree species present that influences ground-level PAR. Stands with the most whitebark pine had highly variable open canopies, but where it grew mixed with subalpine fir, there was less whitebark pine and a more uniformly closed canopy.

The correlations between the white pine blister rust severity indicators and higher standard deviation of ground-level PAR help to explain two more correlations: the positive correlations between the white pine blister rust indicators and canopy cover of alternate host species and species richness. Neither paintbrush nor sickletop lousewort grow well in heavy shade, and the mix of shade and sun characteristic of these stands provides a variety of habitats for many more species than simply shade or sun would provide. Also, areas with warm, open canopy gaps lose soil moisture more rapidly, explaining the negative correlation between the number of infected trees and summer soil moisture.

Thus, infection-prone sites were open woodlands, principally composed of whitebark pine, with a diverse understory that included alternate host species. These areas were on

lower slopes where cold-air drainage likely concentrated basidiospores and caused frequent night and morning conditions of high humidity and fog conducive to basidiospore germination and infection (Hansen and Patton 1975). Also, cloudy, rainy events in summer and the fall lasting several days were not uncommon. Single exposures of 12 to 24 hours of suitably damp weather are sufficient for infection to occur (Hirt 1939, 1942). Open stands on south- and southwest-facing slopes warmed in summer afternoons, producing higher bole and branch temperatures conducive to mycelial growth. These higher temperatures were facilitated by direct solar heating of the soil and soil surface in large canopy gaps. Wind interference caused by scattered trees facilitates such heating by reducing air exchange and thus heat removal. These warm, dry sites reduce the competitiveness of subalpine fir, permitting the more drought-tolerant whitebark pine a competitive edge but also maintaining more open canopies and drier soils. Thus, the number of infected trees was negatively correlated with summer soil moisture, and the severity of infection was positively correlated with slope steepness, another indicator of drought. The droughty conditions resulted in whitebark pine dominance and open canopies that created the mix of sun and shade, resulting in higher species diversity, including the abundance of alternate host species.

The second highest number of whitebark pine trees and snags combined occurred on mid-elevation, west-northwestern aspects in our study area. The ratio of live-to-dead whitebark pine trees was 5 to 22 times higher elsewhere when compared to mid-elevation, west-northwestern aspects. Superficially, this might be construed to suggest higher vigor for the white pine blister rust in mid-elevation, west-northwestern environments; however, a young and vigorous population of subalpine fir now dominates this area, suggesting post-Little Ice Age invasion. Subalpine fir has likely contributed to the low ratio of live-to-dead whitebark pines by preventing whitebark pine regeneration. We cannot evaluate northwestern aspects where subalpine fir dominated to the exclusion of whitebark pine, but this may be the trajectory on which west-northwestern stands are now.

Given the toll taken on whitebark pine by white pine blister rust, its apparent low resistance even after a history of exposure and the almost universal encroachment on its habitat by subalpine fir, the outlook for whitebark pine in this area does not look bright. However, such an outlook assumes static conditions in terms of further disturbance. Subalpine fir encroachment in drier areas is slow, and in those areas, whitebark pines continue to reproduce. If whitebark pines remain sufficiently free of subalpine fir in the drier areas, a breeding population appears to be secure. A wildfire in the study area under these conditions would disproportionately affect subalpine fir, because there is insufficient fuel to carry a hot fire in the driest parts of the whitebark pine habitat. Thus, many whitebark pines would be expected to survive. However, much of the subalpine fir grows in dense stands, which would carry a crown fire resulting in little subalpine fir survival. Thus, a fire would open habitat for whitebark pine reproduction that is currently not available on moister sites. According to Tomback et al. (1990), whitebark pine gains advantage over subalpine fir in large burns or where wind-dispersed seeds are disfavored by contrary wind patterns because Clark's nutcrackers carry seeds farther than wind can carry other seeds, and they often carry them upwind. Nutcrackers favor such burned-over, open areas for cache sites, and whitebark pine can become a long-lived seral species on these sites (Arno and Hoff 1990).

However, without such disturbance this picture might change as subalpine fir trees gradually establish on the dry, central habitat of whitebark pine in the study area. Although the

process is slow, subalpine fir will gradually supply additional fuel continuity, making hotter crown fires possible on these slopes and leaving the whitebark pine trees increasingly vulnerable. In this scenario, a wildfire might kill enough whitebark pine to make this area unattractive to Clark's nutcrackers, sealing the fate of whatever scattered trees might remain. Regrowth on south- to west-facing slopes is slow because of the extreme change in soil surface temperatures, rapid evaporation of soil moisture, and extreme maximum and minimum air temperatures—conditions that are challenging to tree seedlings (Fonda and Bliss 1969).

Whitebark pines are found in other parts of the Olympic Mountains rain shadow, and dispersal back to this location by Clark's nutcrackers would be possible, assuming those populations were not affected by fire at the same time. All other known whitebark pine locations on the Olympic Peninsula are within 20 km of our study area, with some much closer. Clark's nutcrackers disperse whitebark pine seeds up to 12.5 km from the tree (Tomback 1978) and perhaps farther. Vander Wall and Balda (1977) found that Clark's nutcrackers transported pinyon seeds as far as 22 km. These distances are much greater than wind can disperse seeds of other conifer species (McCaughy et al. 1986). Given the fragmentation of the landscape due to high, rocky, alpine ridgelines, a fire that would burn all the Olympic Peninsula populations is not likely, so it is possible that individual populations affected by fire could be naturally restocked over a long period.

In the past, whitebark pine gained competitive advantage over other species during forest succession by being long lived and hardy. Thus, it survived long periods of reproductively inhospitable climate. It has sufficient nutrition in its large seeds to both satisfy its seed predator/disperser and give it a rapid early start in life. Large seeds provide a distinct advantage on harsh sites where establishing a large water and nutrient harvesting root system as rapidly as possible is important (Baker 1972).

However, white pine blister rust decreases both the longevity of the tree and its reproduction, negating an important advantage this species has over subalpine fir. For example, an old tree growing on a fire-protected, rocky outcrop might survive several wildfires, contributing to the repopulation of an area several times. Without that longevity, such a tree may not even be present when the next fire occurs. Because whitebark pine is a keystone species, its fundamental contribution to ecosystem resilience would be lost, and the entire system's stability would be compromised.

Because of the harshness of many sites on which whitebark pine grows, seedlings may not be recruited in many years. Also, large seed crops are produced at irregular intervals interspersed with smaller crops and crop failures (Arno and Hoff 1990). Because of its longevity, this has not been a problem. A resident population of trees will supply seeds periodically until a suitable year for establishment occurs. Yet, land managers cannot economically duplicate this service on these harsh sites, as it is unlikely a manager would plant year after year until a suitable year arrived. However, if more amenable sites are opened by fire, better success by managers might be expected, and those trees would then be available to supply this service for poorer sites for many more years. If resistant trees could be established on the harsher, less fire-prone sites, these sites could again become the nucleus of long-term whitebark pine survival.

Whitebark pine grows largest and produces the most seed on the best sites, but this is also where it encounters the most competition from subalpine fir and where it is most

vulnerable to wildfire. In the dry, Olympic Mountains rain shadow, these habitats have relatively heavy snow cover, which moderates air and soil temperatures and provides moisture as it melts, providing better conditions for tree seedling establishment (Kuramoto and Bliss 1970). Where fire has opened north- to east-facing slopes, rapid colonization by subalpine fir occurs (Kuramoto and Bliss 1970), so the window for whitebark pine establishment is narrow.

In our study area, subalpine fir has largely prevented whitebark pine from regenerating on the better sites, and so white pine blister rust is progressively eliminating whitebark pine from these areas as it is no longer able to reproduce there. Thus, an important amount of seed production has been eliminated until resistance strengthens and fire returns. As Keane et al. (2012) point out, fire, whitebark pine, and the Clark's nutcracker form an ecological triangle wherein fire opens new, high-quality habitat that is attractive for Clark's nutcracker caching and conducive to whitebark pine establishment. The whitebark pine seeds that are not retrieved by Clark's nutcrackers grow into mature trees before later seral species can establish from windblown seeds, and because of their longevity, whitebark pines have in the past produced seed from these locations for centuries. However, white pine blister rust has seriously damaged one leg of this triangle, as the residence time and reproductive capacity of trees established in these places is greatly diminished.

In our study area, there is a noticeably greater density of whitebark pine trees that have established since about 1925 than before that time. We believe that this can be partly attributed to massive mortality of the original population of trees around 1920. The denser, younger population may have benefited from the growing space opened by this mortality but may also have higher resistance than the trees that died in the initial infestation, including whatever regeneration was present at that time. However, resistance tests on 25 Olympic Mountains trees showed almost no resistance at all (Bower 2021), and these trees are experiencing various levels of disease throughout much of their lives, which may be why they are growing more slowly in diameter than the older trees. As previously discussed, we found it necessary to split the data into two groups at 90 years of age to calculate the age-diameter at breast height relationship for this species. The curve for the older trees not only indicated a higher rate of diameter growth, but it also had a higher r^2 . Thus, younger trees were, on average, slower growing and were more variable in that growth, as might be expected if some experience more severe disease than others. The older trees experienced disease-free growth for much of their life spans, and because infections occurred closer to the bole in younger trees, those infections tended to be more severe. King (2004, 2005) showed a marked increase in diameter growth suppressions in whitebark pine trees from several Washington State national forests, including the Olympic National Forest, beginning in the 1920s and continuing to the present.

Fire and Establishment History

- There was no evidence of past fire on any of our plots, suggesting that our study area lay mostly above the Little Ice Age tree line and lacked the fuels needed to carry a fire.
- We found small amounts of charcoal on the bark of a few older Douglas-fir trees near the lower edge of the study area, suggesting a low-intensity fire that failed to open new growing space.
- Gradual tree establishment in an upslope direction began in the 1800s, suggesting a response to a changing climate as opposed to any single stand-initiating event.

- Widely scattered whitebark pine trees that were present at high elevations long before the end of the Little Ice Age, such as the Charlia Pass krummholz tree, which dated to around 1384, were an important seed source for new trees as the climate warmed.

The most complete fire history of the Olympic Peninsula to date was set out by Henderson et al. (1989). They suggest that much of the Olympic Peninsula, including nearby lower elevations and possibly the study area, burned under high east winds in each of three large burning periods centered around 1308, 1508, and 1701. Although fires during these periods left most of the alpine core and western side of the peninsula unburned, most of the rest of the peninsula was affected. The age data supporting their fire history comes from numerous core samples and field counts of tree rings on harvested Douglas-fir stumps collected mostly in the 1980s during a period of rapid harvesting of old-growth trees. One of the areas on the Olympic National Forest where Henderson et al. (1989) found trees dating to the 1508 burning period was in the Tunnel Creek drainage, 6 km to the southeast of our study area. We observed an age class of Douglas-fir trees that was much older than any on our plots along the Dungeness River trail within 2 km of the study area that may date to one or both of their last two burning periods.

The history of the later 1800s and 1900s was facilitated with air photo interpretations of various published accounts and records from the Olympic National Forest dating back to 1906, in addition to core samples and stump ring counts (Henderson et al. 1989). The post-Euro-American settlement fire history of the eastern side of the Olympic Peninsula is considerable and is described in Henderson et al. (1989), with some additional detail provided in Henderson and Peter (1983). They documented areas burned, mainly in the low- to mid-montane parts along the north and east sides of the Olympic National Forest and often associated with timber harvesting activities. However, the postsettlement fires that they identified did not affect our study area, nor do the records of the Olympic National Forest, which date back to 1906, indicate any fires in our study area. Henderson et al. (1989) also noted widespread fires in the 1860s in both Oregon and Washington, and in their earlier report to the Olympic National Forest, they noted an age class dating to the 1860s in the upper Big Quilcene drainage, just east of Marmot Pass near our study area (Henderson and Peter 1983). They show this same age class in the upper Tunnel Creek drainage and on the divide with the Dosewallips River near Harrison Lake, all near our study area. Fires also burned into the Dungeness Valley from the Sequim foothills in 1890 and 1891 but apparently did not burn into the upper Dungeness River valley where our study area is located (Henderson and Peter 1983).

Pickford et al. (1980) determined that although 63 percent of the fires in Olympic National Park were human caused, lightning fires accounted for 81 percent of the 2402 ha burned from 1916 through 1975. Lightning-caused fires occurred in fewer than one-third of the previous 60 years, and 94 percent of the burned area burned in just 4 years. They found that 51 percent of the fires occurred above 1220 m, and all but one of the fires larger than 40 ha occurred in the rain shadow of the Olympic Mountains (Pickford et al. 1980). Most lightning strikes did not result in fire because most occurred in moist areas of Olympic Peninsula or under moist weather conditions (Pickford et al. 1977). The probability of a lightning fire occurring exceeded 50 percent only when the strike was preceded by 18 days without measurable rain, and appreciable spread increased greatly under east-wind weather

conditions (Pickford et al. 1977). Thus, although lightning-started fires in the higher elevations of the Olympic Mountains rain shadow account for most of the fires and area burned in Olympic National Park, most strikes resulted in small or no fires. The subalpine areas where most of the lightning strikes occurred had a low rate of spread (Pickford et al. 1977) due to patchy, low fuel loading and interspersed meadow and rock. They note, however, that the likelihood of fire crowning (wind driven fire that moves between treetops) in the trees found in these areas is high because of the long tree crowns (Pickford et al. 1977).

Two relevant fire history studies have been conducted in the nearby Olympic National Park. Wetzel and Fonda (2000) conducted a detailed study of the Morse Creek drainage 26 km to the northwest of our study area. Their study was based on extensive increment coring of Douglas-fir trees. They found few fire scars; however, they found many tree-ring width release patterns that they were able to relate to tree age cohorts. Among their sample was one Douglas-fir tree that germinated around 1280 with a release in 1320 that falls within the 1308 burning period of Henderson et al. (1989). They also found evidence for a series of fires extending from 1687 through 1720 that correspond to the 1701 burning period suggested by Henderson et al. (1989) and documented an intensive post-Euro-American settlement fire history.

A 440-year fire history study from the Elwha River valley, 30 km northwest of our study site, which is a similar Olympic Mountains rain shadow valley to the Dungeness River valley, found a 140-year natural fire rotation and a 127-year mean fire return interval, which they consider to be conservative values (Wendel and Zabowski 2010). Fires were more common at lower elevations, on southern aspects, and in Douglas-fir forest types. They estimated a mean fire return interval for the subalpine fir zone of 210 years, which compares favorably to the 208 years of Henderson et al. (1989). Mean fire return intervals on southern aspects ranged from 85 years below 500 m to 197 years above 1300-m elevation, and on north-facing slopes from 160 years below 500 m to 232 years above 500-m elevation. Thus, they found a sharp decrease in fire frequency with elevation, and their highest sampled elevations were still lower than our lowest elevations. Given the similarity and proximity of our study areas, we would expect to find fire frequencies similar to or less frequent than 197 years on south-facing slopes and 232 years on north-facing slopes at our lowest elevation plots. However, they also found an increase in fires during the settlement period to a mean fire return interval of 53 years. In this respect, our sites differ considerably. Euro-American settlers, who apparently ignited the additional fires, had moved into the Elwha River valley bottom in the vicinity of their study, which was not the case for our study area.

Our major finding regarding fire history was that there was no evidence of past fire on any of our plots. Given the long and widespread fire history documented by others in the region, this finding begs an explanation. Outside of our plots, in the lowest portion of the study area, we found small amounts of charcoal on the bark of a few larger Douglas-fir trees, some of which also had what appeared to be scars that had healed over. However, we were not successful in finding an unequivocal fire scar on any core sample that we took from these trees, and the pitch rings and ring patterns could not be matched to initiation of a tree cohort. Thus, the fire that caused the charred bark must have been a low-intensity surface fire that failed to open new growing space. Such a fire may have been more intense at lower elevations, but if so, it burned out in the light fuels of the Little Ice Age or post-Little Ice

Age tree line, which was then apparently located at the bottom of our study area. Further fire history work is needed in this part of the Olympic Peninsula to ascertain the nature of the Little Ice Age fire regime, how it may have subsequently changed, and what that means going forward. However, fires that occur now will be able to burn through subalpine fir to some of the higher ridgetops in our study area.

The presence of shore pine growing in the vicinity of our charred Douglas-fir trees may be further evidence of a fire. However, their age structure is atypical for a stand establishing after a fire, and rather suggests a gradual invasion, such as would be expected if new growing space became gradually available at the end of the Little Ice Age. Aside from one large Douglas-fir tree of uncertain age (possibly 200 to 328 years old), the oldest Douglas-fir that we aged dated to 1797. This was pre-dated by the oldest shore pine that we aged, which dated to 1788, and we found a lower slope whitebark pine that dated to 1774. Thus, a fire could have burned into the lower parts of the study area and died out for lack of fuel in the late 1700s; however, Wetzel and Fonda (2000) found that the period of 1760 to 1840 had few fires in their study area. Perhaps, it is more likely that a lightning strike ignited a small, local fire sometime in the 1800s or early 1900s that charred the bark of a few trees but caused little mortality.

Wetzel and Fonda (2000) found a marked increase in fires between 1850 and 1859, signaling what they describe as a dramatic climate shift from the Little Ice Age, which produced fewer fires, to the modern climate. Although we did not find evidence of fires, Douglas-fir establishment increased between the late 1850s and the 1870s as the modern climate established. Also, subalpine fir establishment gradually accelerated during this period, and western white pine seems to have entered the area in the later 1800s. Unlike in areas recently subjected to stand-replacing wildfires, shore pine appears to have established gradually (fig. 67).

With the absence of charred remains in any of our plots, together with an age structure that suggests trees were mostly absent on the middle and upper slopes of our study area in the 1800s and earlier, we argue that our study area lay mostly above the Little Ice Age tree line and lacked the fuels needed to carry a fire. Many older Douglas-fir trees have a “wolfy” structure—with many large, lower limbs, suggesting that they grew in the open throughout their lives. Such low limbs could carry a ground fire into their crowns, suggesting that fire has been absent during their lifetime. A pattern of gradual, continuous tree establishment beginning in the 1800s was present in all the tree species, suggesting a gradual response to a changing climate as opposed to any single stand-initiating event. Tree establishment has been infilling and proceeding in a generally upslope direction. Our lowest elevation and now mostly forested plot (plot 23) had several shrub and herbaceous species that are more typical of open, subalpine environments surviving tenuously in a small and shrinking canopy gap, suggesting that this location was more open in the recent past. The ending of the Little Ice Age appears to have made more habitat available to trees, while reducing habitat for subalpine shrubs and herbs. Elsewhere, revisitation studies of historical sites have clearly shown tree line, alpine, and nival species migrating to higher locations in response to climate warming (Grabherr et al. 1994, Kullman 2002, Meshinev et al. 2000, Motta and Nola 2001, Pauli et al. 2001).

Whitebark pine was present at the highest elevations in the study area long before the end of the Little Ice Age. These were widely scattered trees growing in sparse, rocky alpine vegetation that is resistant to burning. These old, high-elevation trees would have had a huge impact in their lifespan on recruitment of new trees in a large radius around them via Clark's nutcracker dispersal of their seeds. One of these trees of krummholz form from Charlia Pass dated to around 1384 (fig. 76). This tree, which was not on a plot, was the highest elevation tree that we core sampled (1936 m). The most notable feature of this tree's chronology was the increase in decadal basal area increments that began around 1860 and continued to around 1990. This was a continuation but also an acceleration of a long-term trend. Although the most recent decadal basal area increment was less than the highest increment, it was still among the highest increments in the tree's life. Thus, this core chronicles post-Little Ice Age warming, which has benefited its diameter growth. Although it would be careless to extrapolate a compression wood chronology of a single tree to the population, this finding is compatible with our observation of increasing tree density over the same time frame. Carlson et al. (2017) offer a mechanism for the increasing whitebark pine ring widths associated with the warming climate in Pacific Northwest maritime climates. Based on whitebark pines growing in the southern Coast Mountains of British Columbia, they found that larger growth rings resulted from reduction of autumn snowfall in the previous year. They hypothesize that this benefits tree growth through seasonal extension and increased storage of photosynthate. They suggest that a warmer climate and reduced snowpack benefits the growth of maritime whitebark pine (Carlson et al. 2017). We see no reason why this shouldn't already be happening, and indeed they found that the correlation of wider growth ring widths with reduced autumn snow had held for at least 91 years (Carlson et al. 2017).

Finding a tree so much older than any other that we encountered in the study area raises the interesting question as to whether some sites are physically more likely to produce old trees than others. There were three considerations that suggest a high degree of soil stability that may contribute to longevity. First, the tree was growing on a gentle slope where soil erosion and movement would be expected to be minimal (fig. 76). Second, it was growing slightly downwind from a gap where snow would be expected to accumulate and protect the ground from solifluction. Third, it is also likely that the soils here were shallow, so the tree may have penetrated bedrock fractures with its roots, providing especially good anchorage. These observations suggest that other, steeper sites may simply erode too rapidly to allow trees of this age to occur. Also, at lower elevations, forest fires may limit longevity of thin-barked trees, such as whitebark pine. But in extreme subalpine sites, such as this one, this would not be an issue, and the low profile of the krummholz growth form would not lend itself to being struck by lightning.

Subalpine fir krummholz can also be found in the area and was probably present before the end of the Little Ice Age. However, we were not able to obtain ages from these trees that we felt closely approximated their true age, but none appear to approach the age of the krummholz whitebark pine tree just mentioned. There appears to be an upward migration into new habitat by the upright form of this species, as well as release of older krummholz form trees in the higher parts of our study area. Judging from where we saw most of the



Figure 76—A krummholz whitebark pine tree that was about 636 years old growing on Charlia Pass. Note the scoured upright branches on the tree and the subalpine fir krummholz in the background. The people are Beth Willhite (left) and Robin Shoal. USDA Forest Service photo by David H. Peter.

subalpine fir and from the pattern of snowbank melting, it appears that much of the new habitat that this species is occupying is in former perennial snowfields on cooler aspects.

Historically, fire in the study area has been minimal, affecting only the lowest elevations and even there does not appear to have been stand-replacing. It is not likely that the 1701 fire suggested by Henderson et al. (1989) affected the study area, considering that the lower portions of the area were likely subalpine in nature with relatively sparse woody fuels and trees, and the mid- to higher elevations in the study area were likely alpine in nature with no trees other than scattered krummholz interspersed with rock and snowfields. Currently, subalpine fir forests provide continuous fuels on cooler aspects of the study area to more than 1800-m elevation, and the warmer aspects, although much more open, are gradually infilling. In the latter case, continuous tree canopies are present from 1500- and 1600-m elevation. Thus, it is now the case that fire can cross ridges of those heights and move from valley to valley in places where this was not possible in the past, making larger, more continuous burns possible.

Conclusions

We studied whitebark pine-dominated plant communities in the northeastern Olympic Mountains rain shadow in relation to temperature, moisture, soil instability, climate change, and white pine blister rust. We compiled a 3-year air, soil surface, and soil temperature record over a dissected west-facing ridge, spanning elevations from 1420 to 1893 m. We describe a subalpine gradient with mean annual air temperatures ranging from 1.1 to 4.1 °C and frost-free intervals from 48 to 132 days. We presented plant community information, including tree growth and age, species canopy cover, and the effects of white pine blister rust on whitebark pine.

Physical Environment

Environmental extremes often influence the distribution of vegetation over the landscape as much or more than the typical or average conditions. With our network of temperature sensors, we were able to document both extreme and average thermal conditions within our study area. The lowest air temperatures occurred from December through February, with February being the coldest month, but they were broadly distributed over the sample area at a time when snow covered most of the land surface, suggesting that although low temperatures are likely a limiting factor for cold-sensitive vegetation in a general sense, they would not differentially affect plant communities within the study area. The lowest air temperatures were in the morning hours in topographic lows or on exposed ridges and upper slopes where nocturnal thermal reradiation was greatest.

Where deep seasonal snowpacks developed, the lowest soil surface and soil temperatures occurred in November, as low, winter air temperatures arrived before the deep snowpack. After November, low soil surface temperature measurements tapered off as snowpack insulation increased. However, the overall lowest soil temperatures occurred in December and January where snow removal by wind or snowmelt occurred. These areas were close to ridgetops on windward western to southwestern exposures and tended to show signs of solifluction (i.e., gradual movement downhill of surface soils).

Solifluction caused by alternate soil freezing and thawing appeared to inhibit plant establishment. Most plots with evidence of solifluction were on south- or west-facing slopes, and nonsorted rock stripe solifluction was associated with basaltic regolith. Plots with such stripe solifluction were steeper, higher in elevation, and had more coarse fragments than those without. A snowpack was slow to form on solifluction plots, as they often warmed enough in the afternoon to melt the snow and thaw the soil. Thus, our soil temperatures showed various levels of freezing and fluctuation from November through January. About 15 to 20 percent of the study area had tree-limiting, nonsorted rock stripes, or apparently active scree and talus slopes that were partly responsible for a lower tree line on south- and west-facing slopes than on north-facing slopes. Solifluction did not occur on the coldest slopes because snow rapidly accumulated there, insulating the soil from wide swings in temperature so cycles of repeated freezing and thawing did not occur.

Tree Interaction with Temperature

During the growing season, soil and soil surface temperatures were higher in areas with open tree canopies than in forest and varied more from afternoon highs because of direct solar exposure to nighttime lows due to radiative heat loss. From mid-July through mid-August,

afternoon surface temperatures on open, southern exposures reached biologically damaging levels (57 to 59 °C), possibly inhibiting tree seedling establishment and maintaining the openness of southern aspects in the study area. Our analysis indicated that the warmest soils occurred on southwestern aspects with about 50 percent tree cover. Where tree spacing allows sunlight to strike the ground but obstructs wind removal of heated air, daily maximum temperatures may be elevated (Daubenmire 1974, Day 1946, Smith 1926). However, judging from the nearly complete canopy closure on south-facing slopes at lower elevations, it seems unlikely that this will be sufficient to maintain the open condition of these slopes as climate warming progresses. If this is the case, the entire species assemblage that is currently present in the openings will have progressively smaller land areas at increasingly higher elevations available to them.

High percentages of canopy closure reduced the number of days that the soil temperature was above 9 °C, below which root growth is diminished (Alvarez-Uria and Körner 2007). This restriction on root growth, which occurred mainly on northern aspects, might explain the depauperate understories that we observed there and the low species diversity under dense subalpine fir overstories as much or more than light competition. Thus, shade had powerful indirect and direct roles in driving ecological outcomes and succession.

Lapse Rates

In addition to elevation, air temperature lapse rate varied by canopy closure, season, and time of day. Our overall air temperature lapse rate of 4.94 °C per kilometer gain in elevation trends toward flatter maritime rates. However, when dissected into areas of closed and open canopies, we found steeper air temperature lapse rates for both canopy conditions that were similar in October but differed greatly in May. In spring, tree canopies shielded the snowpack from solar radiation and retained snow-cooled air. Thus, when the lower elevations were snow-free but upper elevations were not, large differences in subcanopy temperatures occurred, resulting in a steep air temperature lapse rate. After the snow melted over the entire slope, the air temperature lapse rates in closed-canopy areas became similar to or flatter than those in open-canopy areas. The usefulness of these air temperature lapse rates depends on the questions asked. For understory processes, seasonal subcanopy air temperature lapse rates are appropriate, but for questions of open environments or meteorology, air temperature lapse rates based on open measurements are appropriate.

For soil surface temperature lapse rates, aspect and canopy closure were more important than elevation, but for soil temperature lapse rates, the presence or absence of snow largely determined when or if soil temperature lapse rates developed. Low-elevation soils warmed rapidly after snowmelt, while higher elevation soils still under snow were near freezing, resulting in a temporarily steep soil temperature lapse rate. However, once the entire slope was snow free, the temperature differential lessened, and by late winter, soils under the snow over the entire slope approached 0 °C, eliminating elevational differences.

Snowpack

The most important factors in the duration of the seasonal snowpack were, in decreasing priority, aspect, proximity to a ridgeline generally perpendicular to snow-bearing wind, and elevation. Snowstorms generally approached from the southwest, so winds blew snow near ridgelines off these slopes and onto northeast-facing slopes. Southwestern exposures also warmed and melted sooner than northeastern exposures, so southwestern exposures near

ridgelines were often dry, harsh sites. Despite being generally warmer, the lack of snow in these exposed areas during winter resulted in frost heaving and solifluction, making it difficult for plants to establish in the soil.

Summer Soil Moisture

High soil surface temperatures in June were the best estimator of soil drying, but other summer soil temperatures were also negatively correlated with summer soil moisture, indicating the importance of soil warming to evapotranspiration and the resulting soil drought. Other factors were also important, directly or indirectly. For example, soils in canopy gaps in areas with mixed trees and openings warmed the most, and our best estimation model indicated that the driest soils occurred in areas with high, late-day, soil temperatures in June; steep slopes; and convex microtopography. Areas with these features tended to be open, suggesting that soil drought was an important factor in limiting tree establishment and thus the rate of forest succession on these sites.

Species Temperature Relationships

The species most often positively correlated with high air, soil surface, and soil temperatures were more common at lower elevations, including down to sea level. These species have likely become more common in the study area since the climate began warming after the Little Ice Age, and this trend is likely to continue. The species most associated with low air, soil surface, and soil temperatures were a mix of species confined to high elevations, which included (1) species that were likely already becoming less common in the study area in response to physiological stress caused by heat and drought related to the warming climate and (2) other shade-intolerant species with broad temperature tolerance that also grew at low elevations. Many species in this latter category will become less common in the study area in response to the afforestation being driven by climate warming. Species associated with high soil surface temperatures indicated a preference for open environments coupled with a tolerance of hot surfaces and drought, while species associated with cold soils indicated a cold tolerance that provided a competitive advantage and not a physiological need.

Plant Communities and Diversity

The plant communities that we observed were similar to what others have found in the Olympic Mountains, suggesting our findings have wider relevance than just to our study area. However, there were species combinations suggestive of climate-driven migration (e.g., young trees found in alpine tundra and subalpine and remnant tundra species found in lower elevation canopy gaps).

Plant species richness was highest on steep, but stable, dry, rocky, open, warm southwestern exposures. Our results indicate that open stands with mixed, large canopy gaps and shade favor greater species diversity. In contrast, subalpine fir grew densely on cooler aspects where it cast deep shade that maintained cold soil and low species diversity. The low species diversity was likely due to both light competition and temperature root-growth limitations that few species tolerate. Species richness was associated with white pine blister rust severity, reflecting the fact that whitebark pine grows mainly in warm, open southwest-facing stands that harbor diverse species, including several alternate host species. By killing

whitebark pine trees, white pine blister rust also opens canopy gaps that support heliophytic flora, including some alternate host species. Most plots, including 94 percent with whitebark pine, had one or more alternate host species present, the most common of which was giant red Indian paintbrush followed by sickletop lousewort and prickly currant.

Tree Line and Tree Dominance

The tree line was indistinct and lower on south-facing slopes than on north-facing slopes. A mean growing-season soil temperature of 6.7 °C inhibits tree growth and is a strong estimator of tree line elevation (Körner 1998, Körner and Paulsen 2004). Our analysis suggests that our study area is now mostly below the elevation of Körner and Paulsen's (2004) soil temperature-dependent tree line but has some cold-limited microsites. The upper elevations of our study area appeared to be transitional to their thermally defined open alpine flora. Examination of satellite imagery in the surrounding area showed that there were few trees above 1900-m elevation on any aspect and that forest canopies broke up at around 1800-m elevation on northeastern aspects.

In drier areas, tree lines vary with a combination of soil temperature and moisture (de Andrés et al. 2015). Although soil temperature was marginally limiting for forest growth in much of the study area, the largest open areas were due to other limitations or cumulative limitations, including soil temperature, drought, and soil instability. Faster snowmelt and soil warming resulted in warmer and drier soils on southern aspects, contributing to a sparsity of trees where soil temperatures as low as 6.7 °C did not occur. Our summer soil moisture data revealed areas of relative drought with few trees and therefore circumstantially supported this argument.

Whitebark pine was competitively, not physiologically, restricted to these warm, dry sites. Elsewhere, whitebark pine grows largest on cooler, moister sites (Arno and Hoff 1990), but those sites are now not available to it in our study area. Subalpine fir dominated all aspects and elevations of the study area, except for mid-elevation, southwestern aspects where whitebark pine dominated and lower elevation, southwestern aspects where Douglas-fir, whitebark pine, and shore pine codominated. Wildfire could make more productive cooler sites available to whitebark pine, but droughty areas that resist subalpine fir invasion are presently its core habitat and thus important to its long-term survival.

Estimates of regional post-Little Ice Age warming fall between 0.5 and 1 °C (Abatzoglou et al. 2014, Graumlich and Brubaker 1985, Mote 2003), suggesting that vegetation has shifted upward 100 to 200 m based on our air temperature lapse rate. Plants responding to this change migrate at different rates, creating novel combinations. In looking for the tree line, we saw some species combinations indicative of past positions and some suggesting newer and changing positions.

Subalpine fir and whitebark pine canopy covers were increasing in open, tundra-like plant communities, suggesting an upslope migration. We believe that the lower elevations in our study area were the lower boundary of subalpine parkland during the Little Ice Age and that the tree line fell across the slopes within our study area. The current tree establishment over all elevations suggested that the modern tree line based on temperature limitation of tree roots lies higher than our highest plots, which is supported by our temperature measurements. Most mature trees in the study area were younger than 100 years old, and subalpine fir and Douglas-fir ages were negatively correlated with elevation. About 5 percent of lower elevation trees pre-dated 1850, but only ≤ 1 percent of mid- and higher elevation trees did.

There was little evidence of wildfire, and the trees were not reinvading previously occupied forest habitat.

Our ability to understand what habitat may continue to be available to high-elevation species is hampered by our lack of understanding of the physiological tolerances of most of the flora, an inadequate understanding of drought conditions throughout the growing season, the effects of unstable soils, and our current inability to forecast effects of changing climate on soil drought in these habitats.

Subalpine fir was a reproductive generalist, showing more vigor on cooler aspects but with more seedlings than any other species on all aspects. Given its shade tolerance, it may come to dominate all but the driest microsites. That it does not already dominate all areas implies change, of which the most obvious sources are the climatic emergence from the Little Ice Age (post 1850) and the introduction of white pine blister rust. Even now, but increasingly in the future, fire will likely be needed to maintain open habitat for whitebark pine.

White Pine Blister Rust

White pine blister rust was the most important agent of mortality for white and whitebark pines. Mortality of whitebark pine caused by this disease was greater than mortality from all other causes for other species. Around half of the dead trees were whitebark pines, but much fewer than half of all live trees were whitebark pines. The percentage of whitebark pine trees killed increased as tree size increased, suggesting that the longer a tree lived, the more likely it would succumb to the disease. Although many trees live to reproductive age, it seems unlikely that large trees competitive with subalpine fir that could sustain the species between disturbances will be common in the future. Thus, subalpine fir numbers will likely increase at the expense of whitebark pine.

Although the Olympic Mountains population of whitebark pine has likely had one of the longest exposures to white pine blister rust in the Pacific Northwest, disease resistance is low. However, the survival of young trees to reproductive age implies that further selection for resistance is possible. This leaves us with the unanswerable questions of whether the current level of reproduction is adequate, and if not, how much time remains for a solution to be found.

Alternate hosts for white pine blister rust, including paintbrush and lousewort, were at all elevations and near all whitebark pines, so cool, moist air currents operating in any direction can pick up and move basidiospores to the trees. However, cold-air drainage would concentrate basidiospores onto lower slope positions, which together with occasional valley fogs provide suitable conditions for spore germination and infection. Trees growing on the lower slopes near the valley bottom tended to be larger, older, and more severely infected. As lower slopes are increasingly dominated by lower elevation species, such as Douglas-fir, there is less space available in which whitebark pines can establish, suggesting that without wildfire, these areas are or will soon be unavailable to whitebark pine. As the older trees die, whitebark pine will be eliminated from these areas.

Disease indicators increased with whitebark pine canopy cover, so the number and severity of infections were greater in warm areas where most whitebark pines grew. If white pine blister rust virulence is temperature dependent, then a warming climate could exacerbate future infestations. Postinfection mycelial growth is fastest at temperatures of 15.5 to 21 °C

(Harvey 1969), which mostly occurred in July and August at the lowest elevations, suggesting another reason for more severe infections there.

Germination and germ tube elongation is more vigorous between 9 and 15 °C (Hansen and Patton 1975), but high humidity is required. These temperatures are important because it is the germ tube that grows through the stomata to cause infection. Night temperatures in this range were common in summer, but places with the most October night temperatures in this range were the most likely to have severe white pine blister rust infections. Dry, summer conditions likely discouraged infection then, but rain and cloud cover increased in October, raising humidity before becoming too cold in November. Thus, October may be one of the most important months for infection.

In the Olympic Mountains, whitebark pine grows mainly on steep, south- to west-facing slopes; therefore, topography controls the presence or absence of core whitebark pine habitat. But within that constraint, stand structure was more important for controlling the environmental conditions associated with white pine blister rust infections. Thus, infection-prone sites were open woodlands on warm, lower elevation, southwest-facing slopes where nighttime cold-air drainage, especially in October, concentrated basidiospores and caused conditions of high humidity that were conducive to basidiospore germination and infection. Summer afternoon warming of these woodlands was facilitated by direct solar soil heating in large canopy gaps and by wind interference from the scattered trees, resulting in higher bole and branch temperatures that were conducive to mycelial growth. The warm, droughty conditions facilitated whitebark pine dominance, and the mix of sun and shade resulted in higher species diversity, including abundant alternate hosts.

Given the toll taken on whitebark pine by white pine blister rust, its low resistance to the disease even after a history of exposure, and encroachment by subalpine fir, the whitebark pine outlook appears dim. This situation is not unique to the Olympic Mountains population. A model for the Mount Rainier population suggests virtual extinction within 147 years, even when only the effects of white pine blister rust are considered (Ettl and Cottone 2004). More recent modeling for national park populations in Oregon, Washington, and California suggest, on average, a 25-percent loss of trees over the next 100 years (Jules et al. 2020); however, this model assumes a significant impact of mountain pine beetle, which may not apply in the case of the Olympic Mountains population. Nevertheless, a downward trend in whitebark pine populations in the Olympic Mountains and elsewhere seems inevitable without intervention. For the population at our study area and perhaps elsewhere in the Olympic Mountains, a wildfire would disproportionately affect subalpine fir because there is insufficient fuel to carry a fire in the driest whitebark pine woodlands, while most subalpine fir grows in dense stands, which would carry a crown fire. This would open moister, more productive habitat for whitebark pine than is currently available. Clark's nutcrackers favor burned-over areas for cache sites, and whitebark pine can become a long-lived seral species on these sites (Arno and Hoff 1990).

Without such disturbance, subalpine fir trees will continue to dominate the cooler sites while gradually establishing on warmer sites. This will increase fuel continuity, making whitebark pines increasingly vulnerable to fire. In this scenario, a wildfire might kill enough whitebark pines to make this area unattractive to Clark's nutcrackers, sealing the fate of whatever trees might remain. Even with dispersal possible from other Olympic sites, whitebark pine regrowth on the hot, dry, burned-over slopes would be slow.

Whitebark pine's longevity and hardiness allow it to survive long periods of reproductively inhospitable conditions. However, white pine blister rust decreases its longevity and reproduction, negating this advantage. Seedlings might not be recruited in many years, but long-lived trees eventually produce seed in a suitable year. Land managers cannot economically duplicate this service on harsh sites; however, managers could open and plant moister sites. Those trees would supply this service for nearby harsh sites or burns for many years as whitebark pine grows largest and produces more seed on the best sites (Arno and Hoff 1990).

Fire and Tree Establishment

We found almost no evidence of fire on our plots. The absence of charred tree remains on our plots, together with an age structure revealing that trees were mostly absent on the mid- and upper slopes in the past, suggests that our study area lies mostly above the Little Ice Age subalpine zone of discontinuous tree cover and partly above its tree line, lacking the fuels needed to carry a fire. Older Douglas-fir trees had many large, lower limbs, suggesting that they were open grown. Such low limbs can carry ground fire into their crowns, also suggesting that fire has been absent. Gradual tree establishment from the 1800s to the present in a generally upslope direction suggests a response to a changing climate. Also, the presence of species that are more typical of open, subalpine environments surviving in lower elevation canopy gaps suggests more lower elevation habitat was formerly available to them.

Subalpine fir forests now provide continuous fuels on cooler aspects of the study area to around 1800-m elevation, and the warmer aspects, although more open, are gradually infilling. Thus, fire can cross ridges and move from valley to valley in places where this was not possible in the past, making larger, more continuous burns possible, and it is likely that trees will continue to colonize higher slopes.

Future Research

Although much of our work was done at a basic level and is likely widely generalizable, adding additional study sites would provide the statistical basis for generalization. However, working in designated wilderness areas presents significant challenges, and adding study sites requires significant resources. Moving about the landscape was difficult, and multiple days were needed to visit all the plots. In addition, a day was required to hike into the study site, and another day required to hike back out.

As our focus was whitebark pine habitat, we examined only the west-facing side of a mountain ridge where the whitebark pine was found. Although it was dissected with south- to north-facing slopes, the interpretations of temperature and soil moisture data would have benefited by including a wider array of slope aspects. As it stands, our study says nothing about easterly trending aspects. For example, in figure 34, where we arrayed species by temperature and moisture, the cold tier of the diagram was poorly populated because most cold-tolerant species occurrences would have been on northeastern exposures. A more inclusive sampling would have added species to this tier and changed the diagrammatic locations of other species to clarify their relationships to each other.

One challenge of working in a designated wilderness was devising a way to measure temperatures that was not visually intrusive. Our measurements worked for near-ground and subcanopy measurements; however, measuring above-canopy temperatures would have allowed a direct quantification of the canopy effect on lapse rates and other temperature phenomena. This would have required installing towers that were not compatible with

wilderness values. Similarly, establishing free-standing temperature stations away from the tree boles would have permitted a more straightforward way to monitor winter air temperatures and snow depths without the issue of tree snow wells, simplifying the interpretation of these data.

Vegetation zonation in relation to snow depth, although apparent, was not something we could measure. Coupling snow depth measurements with a better understanding of the relationship between snow accumulation and soil moisture would clarify the reasons behind some vegetation patterns. A better understanding of local seasonal wind, topography, and snow interactions could add predictability to these phenomena.

Our manual summer soil moisture measurement record was seasonally too shallow, too short, and too late to fully understand how soil moisture affects vegetation. We found differences among plots, but because of considerable drying at 12-cm depth by the end of July, the differences were small. Measurements initiated during snowmelt and followed through summer would provide a better stratification of the plots based on moisture. This would require the use of data loggers in conjunction with the moisture sensors.

More must be learned about how microclimates arise and how air circulation and air temperature lapse rates are modified by topography and vegetation. This is important because the stability of vegetation, including successional pathways and migration, are determined by the aggregate of localized processes. Shade cooling of soils, heat enhancement in canopy gaps, and cold-air drainage are three of many important local phenomena deserving of more study. However, a true understanding of the microclimatic effect on vegetation also requires a deeper understanding of the physiology, autecology, and life cycles of most, if not all, species.

Extending the study upslope would have clarified where root growth-limiting temperatures responsible for the tree line occurred, better defining core alpine tundra habitat. The potential tree line position may be higher than where trees are currently found. This is important in interpreting alpine community dynamics and in estimating vegetation change.

The effect of soil movement on vegetation affected 15 to 20 percent of the study area, but we were not able to measure the movement nor adequately quantify the thermal and physical characteristics that were involved. Measurements of solifluction could help explain the patterns of vegetation and define what is and is not habitat for many species, including whitebark pine. Some species are probably more sensitive to instability than others, and certain levels of instability may maintain habitat for more tolerant species in the face of forest succession. Another important factor is whether forest succession can disrupt the freeze-thaw cycle and limit solifluction. Temperature limits vegetation in several ways, but in this case, it is its interaction with regolith, moisture, snowpack, and possibly vegetation that determines the kind of vegetation that is possible.

Much has been learned about how white pine blister rust infects and grows, yet it remains difficult to predict how mountain microenvironments affect infection and subsequent growth of the fungal mycelium. Our study suggests that some trees were in more vulnerable landscape positions than others, which makes it difficult to assess the balance of mortality relative to regeneration and subalpine fir encroachment. Thus, it is difficult to know how serious a position is for the population. Although we know some of the temperature thresholds for infection and growth of this pathogen, our inability to adequately identify microsites that enhance or protect from infection and mycelial growth hampers the application of this information.

It would be helpful to understand the relative effectiveness of different alternate host species for white pine blister rust to the infection of whitebark pines. Additional species of Indian paintbrush (*Castilleja* spp.) need evaluation, including harsh Indian paintbrush, which was prominent in our study area. Also, the tradeoff between Indian paintbrush's inability to amplify infections through the production of urediniospores and its presence in sometimes large numbers near whitebark pines should be evaluated. Perhaps amplification is less important where Indian paintbrush is more abundant.

Interpretation of growth and age would be enhanced with larger sample sizes for most tree species, and taking these samples from a larger area and from a greater diversity of site conditions would have added clarity as well as context. For example, the difference in growth rates and curve shape between the older cohort of whitebark pines and the younger cohort begs a better description and clearer explanation. Also, we were unable to fully describe the age potential of krummholz subalpine fir or the reasons for its occasional change to an upright growth form.

Much more can be learned about climatic and fire history in the Olympic Mountains rain shadow. In terms of fire history, extending the study downslope would provide more information. It was obvious in hiking into the site that a dynamic fire history is present below the study area elevation. If this observation holds up elsewhere, then the relation of the Little Ice Age to fire and Olympic Mountains vegetation comes into sharper focus, and a benchmark with which to measure the effects of changing climate on fire and vegetation can be established. This would clarify the recent plant geography and migration of many species in ways needed to understand future ecosystem behavior and species vulnerability.

Repeated measurements of our plots over time offers the opportunity to follow their successional trajectory. This is possible because we recorded high precision GPS data for each plot center. This would be valuable in tracking ongoing white pine blister rust effects on trees and plant communities and would allow assessment of our hypotheses that subalpine fir is likely to dominate all but the driest microsites and that vegetation is migrating upward.

Management Implications

Our study provides a picture of an ecosystem in flux. As elsewhere, Olympic Mountain whitebark pine populations continue to suffer catastrophic loss because of the exotic white pine blister rust. Their habitat is shrinking because of post-Little Ice Age warming, and forest mainly dominated by subalpine fir is moving up into parkland, which is moving up into alpine tundra. Whitebark pine represents a shrinking ecosystem for many plants and animals. Subalpine fir now dominates formerly open, northern aspects, and along with Douglas-fir, it also codominates former parklands in the lower elevations of the study area. Subalpine fir is now slowly invading the warmer, drier, southern exposures of whitebark pine's core habitat. As fuels and canopy cover become more continuous, the remaining population of whitebark pine will become increasingly vulnerable to wildfire.

This trajectory could be changed. Currently, wildfire would mostly burn densely spaced subalpine fir on north-facing slopes and mixed stands at lower elevations, providing caching habitat for Clark's nutcrackers in more productive areas than the dry, open, whitebark pine core habitat. However, wildfire is infrequent here and may not occur before more whitebark pine is lost, meaning that active management provides more certainty for whitebark pine's continued presence.

Research and largely governmental management of whitebark pine conducted elsewhere provides valuable insight into approaches for the conditions just outlined. Various governmental agencies have funded and carried out much of this work. The Whitebark Pine Ecosystem Foundation has also funded stand assessments, monitoring, cone collection, disease resistance testing, growing and planting seedlings, and various other activities involving thinning and prescribed burning (WPEF 2022). In discussing these methods, we must first set aside the fact that virtually all the Olympic Peninsula whitebark pine occurs within designated wilderness areas on national forest or national park lands. We will return to that topic later.

Keane et al. (2012) developed a generalized strategy for whitebark pine restoration to inform restoration across its range. It was later updated to address issues of climate change (Keane et al. 2017). The strategy encourages actions that promote white pine blister rust resistance, conserve seed sources, increase whitebark pine regeneration, create Clark's nutcracker caching habitat, reduce competing vegetation, decrease surface and canopy fuels, and diversify age and stand structure (Keane et al. 2017). Keane (2018) provided four overarching principles for whitebark pine restoration: (1) reduce mortality of whitebark pine trees, particularly those with signs of white pine blister rust resistance; (2) reduce competing, shade-tolerant tree species; (3) create Clark's nutcracker caching habitat that is free from shade-tolerant tree competition with fire to favor planted and natural white pine blister rust-resistant whitebark pine seedlings; and (4) create heterogeneous landscapes for spatial resilience in the face of climate change.

Whitebark pine has climax potential only on harsh sites where establishment is sparse and growth and productivity are poor. The better the site, the more rapidly subalpine fir encroaches. White pine blister rust mortality accelerates the replacement of whitebark pine under these conditions. However, these areas could provide the fastest growing whitebark pine trees and the greatest seed production for wildlife and regeneration. Treatments to facilitate whitebark pine regeneration, increase its vigor and cone crops, and reduce disturbance impacts focus on these areas and involve combinations of mechanical thinning, prescribed burning, and planting white pine blister rust-resistant seedlings (Keane et al. 2017). Prescribed burning or mechanical thinning with slash burning could open new whitebark pine habitat in subalpine fir-dominated areas, such as the northern and western aspects in the study area. Although some trees would establish in these areas from Clark's nutcrackers caches, planting white pine blister rust-resistant nursery stock would provide a more permanent solution. Thus, the development of local, white pine blister rust-resistant whitebark pine nursery stock would be a prerequisite.

Silvicultural treatments require careful planning. In a retrospective study of five sites, Maher et al. (2018) found that although whitebark pines were released when dense stands were thinned, treating more open stands had little or even negative effect. None of the treatments increased whitebark pine regeneration, but competing species increased in some cases. Although some management goals were achieved, many were not, prompting Maher et al. (2018) to call for a closer examination of the ecological basis of silvicultural restoration treatments in whitebark pine. Because of the paucity of whitebark pine regeneration, they recommended combining thinning with planting of white pine blister rust-resistant whitebark pine seedlings (Maher et al. 2018). Keane and Parsons (2010) also found that low levels

of regeneration occurred after both prescribed burning and silvicultural thinning, which they attributed to nutcrackers reclaiming many cached seeds, lack of nearby seed sources, severe sites, lack of plant cover, and the short time since disturbance.

Supplementing natural regeneration with planting provides an opportunity to increase white pine blister rust resistance in the population with resistant planting stock, thus improving future survival. To maximize planting success, Laufenberg et al. (2020) recommended planting sites with a low water deficit and an actual evapotranspiration that is between 200 and 500 mm, preferably above 300 mm. Although postfire seedling establishment may sometimes be low, releasing established regeneration is more certain. Retzlaff et al. (2018) showed that prescribed fire and selective cutting could release suppressed whitebark pine regeneration, but that success was greater among younger trees.

Careful planning is required to avoid unacceptable mortality following stand-opening treatments. Murray et al. (2021) found 20 to 83 percent mortality of retained whitebark pines 8 years after timber harvest. The biggest factor was storm blowdown, so they recommended selecting retention trees with an adequate number of neighbor trees and orienting retention patches to avoid predominant storm wind directions.

Prescribed burning can maintain low fuel levels and eliminate subalpine fir encroachment. However, whitebark pine is also thin-barked and prone to fire damage. Keane and Parsons (2010) documented more than 40 percent mortality in prescription burns. Keane et al. (2020) made several recommendations to address this issue, including reducing fuels before burning, protecting mature trees, burning under moister conditions, lighting thinner strips, applying fire sparingly, and leaving unburned patches.

Recognizing that wildfire has the potential to harm whitebark pine stands loaded with fuels from invading late-seral trees, Keane (2018) presented a set of actions to implement before, during, and after wildfires. Conditions where whitebark pine stands would benefit from full suppression, partial suppression, or no suppression of a wildfire should be determined before a wildfire occurs to guide decision making when they do occur. Where populations of whitebark pine are small and key white pine blister rust-resistant pines are few, such as in the Olympic Mountains and Cascade Range, it is important to consider whether prescribed wildfire is appropriate (Keane 2018) because of the vulnerability of such small populations. Even with advanced planning, wildfire control is uncertain, making advanced preparations advisable. Keane (2018) suggests the use of fuel treatments, such as mechanical thinning and prescribed burning, prior to wildfires to lessen their impact on whitebark pines. Fuel reduction treatments simultaneously protect whitebark pine trees from damage or mortality and improve their vigor. Vigorous trees are more likely to produce larger, more frequent cone crops over a longer lifespan. After fire, planting white pine blister rust-resistant seedlings and monitoring fire effects are important.

The location of most Olympic Mountain whitebark pine in designated wilderness constrains management as these areas have been set aside for natural processes to prevail; and to date, interpretations of the Wilderness Act of 1964 have not favored active forms of management. Forty-five percent of whitebark pine habitat in the United States occurs in designated or recommended wilderness (Keane 2000). However, the Wilderness Act of 1964 states that wilderness will be “managed so as to preserve its natural conditions,” implying that some forms of management are expected so long as they preserve natural conditions.

There is no question about the unnatural introduction of white pine blister rust. Also, a century of fire suppression has affected landscapes, including that of the Buckhorn

Wilderness in an unnatural way. Finally, the current rapid climate warming is generally agreed to be partly or largely unnatural. These three anthropogenic influences are forcing whitebark pine into a precarious position. The combination of past fire suppression and a warming climate are increasing the density of vegetation in and around the Olympic Mountain whitebark pine population, making it more vulnerable to wildfire. The philosophical question before managers and the public is, How unnatural will this wilderness become before interventions are justified?

One view is that the gradual diminishment of whitebark pine given these conditions is a natural process and does not need to be managed. However, if wilderness is to be managed to preserve natural processes, does that imply that mitigation of human disturbance (climate, fire cycle, exotic disease) is allowed or even mandated? Is management—such as prescribed burning to correct unnatural fuel accumulation due to runaway forest succession that threatens whitebark pines that are already vulnerable because of introduced white pine blister rust—allowable? On the Olympic Peninsula, restoration of this unique population, growing as it does at the maritime western edge of the distribution of whitebark pine, will have to take place in the wilderness. Ultimately, whether to manage in such areas is an issue to be decided by the public through established legal and political processes.

Wildfire is currently the only obvious way of increasing whitebark pine habitat in the Buckhorn Wilderness. Currently, the open, core areas of the whitebark pine population are not likely to burn because of the low quantity of ground fuels, while subalpine fir, which frequently grows in dense stands, is likely to burn. Nevertheless, many older whitebark pines around the periphery of the core area would die in such a scenario. A let-burn fire policy might result in a one-time opening of new Clark's nutcracker seed caching habitat, allowing some establishment of faster growing, better seed-producing whitebark pine trees on these better sites with benefits to both wildlife and future tree regeneration. However, these trees would not necessarily be more resistant to white pine blister rust and thus might still fail to provide these services. Also, with the passage of time, subalpine fir and fuels in general are increasing in the core whitebark pine habitat. Without fuel reduction management, there may come a time when wildfire will burn nearly all whitebark pine trees in the area.

Thus, prescribed fire offers the best alternative to wildfire for maintaining, enlarging, and protecting whitebark pine habitat; however, current Forest Service policy makes this difficult. Forest Service policy allows prescribed fire to reduce the risks and consequences of wildfire to an acceptable level within wilderness but restricts its use for other applications. However, as forest succession and fuel accumulation continue, the risk that wildfire may burn much of the whitebark pine in the Buckhorn Wilderness increases, and the effectiveness of formerly open, rocky ridgetops to interrupt the spread of fire is progressively being compromised.

If the planting of resistant stock could take place after prescribed or natural fire, the prospects of whitebark pine in this area might be considerably improved. The window for such action would be narrow as subalpine fir would soon establish on all but the driest sites. Much of the new habitat created by the fire would gradually become vulnerable to future fires again as forest succession advanced, but it is possible that some, or even considerable amounts of seed production would occur before that happened, and additional prescribed burning could be used for maintenance.

It is doubtful whether mechanical thinning could be approved for use in the wilderness. That said, the Forest Service Manual (FSM 2323.52: Policy, item 4) (USDA FS 2021) states

that vegetation may “be cut or sold when necessary for wilderness purposes... when emergency conditions like fire, insect and disease, or protecting public safety make it necessary.” In the authors’ opinion, it is not an exaggeration to call the precarious situation of this whitebark pine population an emergency given its increasing vulnerability to wildfire. Mechanical thinning could be useful to prepare for prescribed burning, but given the areas involved and the prevalence of subalpine fir regeneration, its effectiveness as a stand-alone treatment would be low.

As with other management activities, it is difficult to justify planting in the wilderness. However, the Forest Service allows reforestation if a loss of the wilderness resource occurs as a result of human influence and there is no reasonable expectation of natural reforestation (FSM 2323.54: Reforestation) (USDA FS 2021). Unless it can be shown that natural resistance to the white pine blister rust is developing sufficiently to preserve the Olympic Mountains population, the planting of resistant seedlings might be justifiable. The best evidence currently available indicates that Olympic Mountain whitebark pine trees remain highly susceptible to this disease. Keane and Parsons (2010) suggest that planting white pine blister rust-resistant seedlings is essential for preventing local extirpation in areas of high whitebark pine mortality.

Whitebark pine is considered an endangered species in Canada, and the USDI Fish and Wildlife Service issued a rule listing whitebark pine as a threatened species in the United States effective on January 17, 2023 (USFWS 2022). A recovery outline required by the rule guides the making of the recovery plan as well as the immediate implementation of urgent recovery actions. The recovery outline specifies 10 interim recovery actions for whitebark pine populations and habitat: (1) inventorying populations; (2) producing fine-scale maps of the populations; (3) establishing long-term monitoring plots; (4) monitoring plantings; (5) monitoring Clark’s nutcracker populations; (6) protecting areas with healthy and disease-resistant trees; (7) restoring damaged, unhealthy, or extirpated whitebark pine stands; (8) reducing surface and ladder fuels; (9) providing public education; and (10) entering into public and private collaborations for funding gene conservation, including seed collection and seedling planting, conducting health surveys, implementing silvicultural treatments, and conducting public outreach.

For populations of whitebark pine on the Olympic Peninsula, inventorying, monitoring, mapping, surveying, and public education and outreach can be easily implemented. However, the Wilderness Act of 1964 may preclude acting on some of the recovery actions. It may be difficult to justify planting disease-resistant trees, reducing surface and ladder fuels, or conducting silvicultural treatments, and if these things cannot be done, it is hard to see a path forward for restoring these damaged, unhealthy whitebark pine stands.

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U.S. Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	.394	Inches
Meters (m)	3.28	Feet
Cubic meters (m ³)	35.3	Cubic feet
Cubic meters per ha (m ³ /ha)	14.29	Cubic feet per acre
Kilometers (km)	.621	Miles
Hectares (ha)	2.47	Acres
Tonnes (t)	1.102	Tons
Tonnes per hectare (t/ha)	893	Pounds per acre
Tonnes per hectare (t/ha)	.446	Tons per acre
Trees per hectare	.405	Trees per acre
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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Appendix 1: Species List

Table A1.1—Plant species referenced in this Olympic Mountain whitebark pine communities study report, their USDA PLANTS Database symbols, plot constancy, and mean cover over all plots studied

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
				PERCENT
ABGR	<i>Abies grandis</i> (Douglas ex D. Don) Lindl.	Grand fir	—	—
ABLA	<i>Abies lasiocarpa</i> (Hook.) Nutt.	Subalpine fir	80.0	21.50
ACMI2	<i>Achillea millefolium</i> L.	Common yarrow	75.0	0.60
ACRU2	<i>Actaea rubra</i> (Aiton) Willd.	Red baneberry	5.0	0.30
ADBI	<i>Adenocaulon bicolor</i> Hook.	American trailplant	2.5	<0.01
AGAU2	<i>Agoseris aurantiaca</i> (Hook.) Greene	Orange agoseris	55.0	0.10
AGGL	<i>Agoseris glauca</i> (Pursh) Raf.	Pale agoseris	27.5	0.04
AGHU	<i>Agrostis humilis</i> Vasey	Alpine bentgrass	2.5	<0.01
ALCE2	<i>Allium cernuum</i> Roth	Nodding onion	17.5	0.40
ALCR4	<i>Allium crenulatum</i> Wiegand	Olympic onion	17.5	0.30
ALRU2	<i>Alnus rubra</i> Bong.	Red alder	—	—
ALVI5	<i>Alnus viridis</i> (Chaix) DC.	Green alder	7.5	1.10
AMAL2	<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem.	Saskatoon serviceberry	27.5	0.08
ANLY	<i>Anemone lyallii</i> Britton	Little Mountain thimbleweed	7.5	<0.01
ANMU	<i>Anemone multifida</i> Poir.	Pacific anemone	20.0	0.03
ANGE2	<i>Angelica genuflexa</i> Nutt.	Kneeling angelica	5.0	0.02
ANAL4	<i>Antennaria alpina</i> (L.) Gaertn.	Alpine pussytoes	2.5	0.03
ANHO	<i>Antennaria howellii</i> Greene	Howell's pussytoes	17.5	0.10
ANLA3	<i>Antennaria lanata</i> (Hook.) Greene	Woolly pussytoes	10.0	0.60
ANMI3	<i>Antennaria microphylla</i> Rydb.	Littleleaf pussytoes	—	—
ANRA	<i>Antennaria racemosa</i> Hook.	Raceme pussytoes	25.0	0.20
ANRO2	<i>Antennaria rosea</i> Greene	Rosy pussytoes	17.5	0.30
AQFO	<i>Aquilegia formosa</i> Fisch. ex DC.	Western columbine	12.5	0.10
ARLE	<i>Arabis lemmonii</i> S. Watson	Lemmon's rockcress	5.0	<0.01
ARUV	<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	Kinnikinnick	15.0	0.70
ARCA7	<i>Arenaria capillaris</i> Poir.	Slender mountain sandwort	30.0	0.50
ARAM2	<i>Arnica amplexicaulis</i> Nutt.	Clasping arnica	2.5	0.03
ARCO9	<i>Arnica cordifolia</i> Hook.	Heartleaf arnica	40.0	0.70
ARLA8	<i>Arnica latifolia</i> Bong.	Broadleaf arnica	2.5	<0.01
ARMO4	<i>Arnica mollis</i> Hook.	Hairy arnica	2.5	0.05
ARPA13	<i>Arnica parryi</i> A. Gray	Parry's arnica	5.0	0.02
ARAR9	<i>Artemisia arctica</i> Less.	Boreal sagebrush	5.0	<0.01
ARCA12	<i>Artemisia campestris</i> L.	Field sagewort	2.5	0.08
ARFU4	<i>Artemisia furcata</i> M. Bieb.	Forked wormwood	5.0	<0.01
ARLU	<i>Artemisia ludoviciana</i> Nutt.	White sagebrush	50.0	0.90
BRCA5	<i>Bromus carinatus</i> Hook. & Arn.	California brome	10.0	0.40
CANO9	<i>Callitropsis nootkatensis</i> (D. Don) Oerst. ex D.P. Little	Alaska cedar	7.5	1.20

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
				PERCENT
CALE4	<i>Caltha leptosepala</i> DC.	White marsh marigold	—	—
CAPI2	<i>Campanula piperi</i> Howell	Olympic bellflower	5.0	<0.01
CARO2	<i>Campanula rotundifolia</i> L.	Bluebell bellflower	37.5	0.40
CASC7	<i>Campanula scouleri</i> Hook. ex A. DC.	Pale bellflower	5.0	<0.01
CAHO5	<i>Carex hoodii</i> Boott	Hood's sedge	5.0	0.03
CANI2	<i>Carex nigricans</i> C.A. Mey.	Black alpine sedge	7.5	0.50
CAPH2	<i>Carex phaeocephala</i> Piper	Dunhead sedge	5.0	0.04
CARO5	<i>Carex rossii</i> Boott	Ross' sedge	32.5	0.08
CASP5	<i>Carex spectabilis</i> Dewey	Showy sedge	5.0	0.02
CATA	<i>Carex tahoensis</i> Smiley	Tahoe sedge	12.5	0.05
CAME7	<i>Cassiope mertensiana</i> (Bong.) G. Don	Western moss heather	—	—
CASTI2	<i>Castilleja Mutis ex L. f.</i>	Indian paintbrush	—	—
CAAP4	<i>Castilleja applegatei</i> Fernald	Wavyleaf Indian paintbrush	—	—
CAAR11	<i>Castilleja arachnoidea</i> Greenm.	Cobwebby Indian paintbrush	—	—
CAHI9	<i>Castilleja hispida</i> Benth.	Harsh Indian paintbrush	10.0	0.05
CAMI12	<i>Castilleja miniata</i> Douglas ex Hook.	Giant red Indian paintbrush	67.5	0.30
CAPA26	<i>Castilleja parviflora</i> Bong.	Mountain Indian paintbrush	2.5	<0.01
CESA	<i>Ceanothus sanguineus</i> Pursh	Redstem ceanothus	2.5	<0.01
CHAN9	<i>Chamerion angustifolium</i> (L.) Holub	Fireweed	25.0	0.08
CHLA13	<i>Chamerion latifolium</i> (L.) Holub	Dwarf fireweed	2.5	<0.01
CHME	<i>Chimaphila menziesii</i> (R. Br. ex D. Don) Spreng.	Little prince's pine	2.5	<0.01
CHUM	<i>Chimaphila umbellata</i> (L.) W.P.C. Barton	Pipsissewa	2.5	<0.01
CIAL	<i>Circaea alpina</i> L.	Small enchanter's nightshade	5.0	<0.01
CIED	<i>Cirsium edule</i> Nutt.	Edible thistle	12.5	0.09
CLSI2	<i>Claytonia sibirica</i> L.	Siberian springbeauty	2.5	0.90
CLUN2	<i>Clintonia uniflora</i> (Menzies ex Schult. & Schult. f.) Kunth	Bride's bonnet	2.5	<0.01
COME17	<i>Corallorhiza mertensiana</i> Bong.	Pacific coralroot	2.5	<0.01
CRAC3	<i>Cryptogramma acrostichoides</i> R. Br.	American rockbrake	5.0	0.04
CYFR2	<i>Cystopteris fragilis</i> (L.) Bernh.	Brittle bladderfern	7.5	0.02
DAIN	<i>Danthonia intermedia</i> Vasey	Timber oatgrass	2.5	<0.01
DAFR6	<i>Dasiphora fruticosa</i> (L.) Rydb.	Shrubby cinquefoil	12.5	0.30
DEGL	<i>Delphinium glareosum</i> Greene	Olympic larkspur	7.5	0.06
DOLA	<i>Douglasia laevigata</i> A. Gray	Cliff dwarf-primrose	25.0	0.10
ELEL5	<i>Elymus elymoides</i> (Raf.) Swezey	Squirreltail	42.5	0.07
ELGL	<i>Elymus glaucus</i> Buckley	Blue wildrye	12.5	0.70
EPCL	<i>Epilobium clavatum</i> Trel.	Talus willowherb	5.0	<0.01
EPLU	<i>Epilobium luteum</i> Pursh	Yellow willowherb	2.5	0.05
EPMI	<i>Epilobium minutum</i> Lindl. ex Lehm.	Chapparal willowherb	7.5	0.02
EPGI	<i>Epipactis gigantea</i> Douglas ex Hook.	Stream orchid	2.5	0.03
EQAR	<i>Equisetum arvense</i> L.	Field horsetail	5.0	0.03

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
				PERCENT
ERCO4	<i>Erigeron compositus</i> Pursh	Cutleaf daisy	10.0	0.01
ERFL2	<i>Erigeron flettii</i> G.N. Jones	Flett's fleabane	2.5	0.01
ERPE3	<i>Erigeron peregrinus</i> (Banks ex Pursh) Greene	Subalpine fleabane	7.5	0.30
ERSU2	<i>Erigeron subtrinervis</i> Rydb. ex Porter & Britton	Threenerve fleabane	7.5	0.10
EROV	<i>Eriogonum ovalifolium</i> Nutt.	Cushion buckwheat	10.0	0.03
ERAR15	<i>Erysimum arenicola</i> S. Watson	Cascade wallflower	40.0	0.05
ERGR9	<i>Erythronium grandiflorum</i> Pursh	Yellow avalanche lily	—	—
ERMO8	<i>Erythronium montanum</i> S. Watson	White avalanche-lily	2.5	<0.01
ENPA22	<i>Eucephalus paucicapitatus</i> (B.L. Rob.) Greene	Olympic Mountain aster	7.5	0.05
FEIDR2	<i>Festuca idahoensis</i> Elmer ssp. <i>roemerii</i> (Pavlick) S. Aiken	Roemer's fescue	70.0	2.20
FEOC	<i>Festuca occidentalis</i> Hook.	Western fescue	7.5	<0.01
FERU2	<i>Festuca rubra</i> L.	Red fescue	17.5	0.08
FESA	<i>Festuca saximontana</i> Rydb.	Rocky Mountain fescue	2.5	0.05
FRVI	<i>Fragaria virginiana</i> Duchesne	Virginia strawberry	5.0	0.03
GAAP2	<i>Galium aparine</i> L.	Stickywilly	5.0	0.03
GABO2	<i>Galium boreale</i> L.	Northern bedstraw	5.0	<0.01
GATR3	<i>Galium triflorum</i> Michx.	Fragrant bedstraw	5.0	<0.01
GOOB2	<i>Goodyera oblongifolia</i> Raf.	Western rattlesnake plantain	2.5	<0.01
HEMA80	<i>Heracleum maximum</i> W. Bartram	Common cowparsnip	5.0	0.10
HIAL2	<i>Hieracium albiflorum</i> Hook.	White hawkweed	52.5	0.07
HIGR	<i>Hieracium gracile</i> Hook.	Slender hawkweed	15.0	<0.01
HODI	<i>Holodiscus discolor</i> (Pursh) Maxim.	Oceanspray	5.0	<0.01
HYFE	<i>Hydrophyllum fendleri</i> (A. Gray) A. Heller	Fendler's waterleaf	5.0	0.40
HYTE	<i>Hydrophyllum tenuipes</i> A. Heller	Pacific waterleaf	2.5	0.01
JUDR	<i>Juncus drummondii</i> E. Mey.	Drumm'nd's rush	2.5	<0.01
JUPA	<i>Juncus parryi</i> Engelm.	Parry's rush	7.5	1.00
JUCO6	<i>Juniperus communis</i> L.	Common juniper	70.0	5.90
LANE3	<i>Lathyrus nevadensis</i> S. Watson	Sierra pea	7.5	0.20
LECO3	<i>Lewisia columbiana</i> (Howell ex A. Gray) B.L. Rob.	Columbian lewisia	7.5	0.01
LICO	<i>Lilium columbianum</i> Leichtlin	Columbia lily	12.5	<0.01
LIBO3	<i>Linnaea borealis</i> L.	Twinflower	2.5	0.05
LLSE	<i>Lloydia serotina</i> (L.) Salisb. ex Rchb.	Common alplily	17.5	0.02
LOMA5	<i>Lomatium martindalei</i> (J.M. Coult. & Rose) J.M. Coult. & Rose	Cascade desertparsley	65.0	0.80
LOCI3	<i>Lonicera ciliosa</i> (Pursh) Poir. ex DC.	Orange honeysuckle	2.5	<0.01
LOUT2	<i>Lonicera utahensis</i> S. Watson	Utah honeysuckle	17.5	0.07
LUPE	<i>Luetkea pectinata</i> (Pursh) Kuntze	Partridgefoot	5.0	0.20
LULA4	<i>Lupinus latifolius</i> Lindl. ex J. Agardh	Broadleaf lupine	75.0	4.00
LULE2	<i>Lupinus lepidus</i> Douglas ex Lindl.	Pacific lupine	20.0	0.02
LUMU2	<i>Luzula multiflora</i> (Ehrh.) Lej.	Common woodrush	15.0	<0.01
LUPA4	<i>Luzula parviflora</i> (Ehrh.) Desv.	Smallflowered woodrush	5.0	<0.01

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
				PERCENT
LUSP4	<i>Luzula spicata</i> (L.) DC.	Spiked woodrush	20.0	<0.01
MANE2	<i>Mahonia nervosa</i> (Pursh) Nutt.	Cascade barberry	20.0	0.70
MESU	<i>Melica subulata</i> (Griseb.) Scribn.	Alaska oniongrass	7.5	0.02
MIGU	<i>Mimulus guttatus</i> DC.	Seep monkeyflower	2.5	0.03
MIOB2	<i>Minuartia obtusiloba</i> (Rydb.) House	Twinflower sandwort	5.0	0.10
MIRU3	<i>Minuartia rubella</i> (Wahlenb.) Hiern.	Beautiful sandwort	2.5	<0.01
MIBR6	<i>Mitella breweri</i> A. Gray	Brewer's miterwort	2.5	<0.01
MITR4	<i>Mitella trifida</i> Graham	Threeparted miterwort	2.5	<0.01
MOMA3	<i>Moehringia macrophylla</i> (Hook.) Fenzl	Largeleaf sandwort	37.5	0.80
MOHY3	<i>Monotropa hypopitys</i> L.	Pinesap	2.5	<0.01
NONE3	<i>Nothochelone nemorosa</i> (Douglas ex Lindl.) Straw	Woodland beardtongue	12.5	0.07
ORSE	<i>Orthilla secunda</i> (L.) House	Sidebells wintergreen	22.5	0.01
ORIM	<i>Orthocarpus imbricatus</i> Torr. ex S. Watson	Mountain owl's-clover	27.5	0.03
OSBE	<i>Osmorhiza berteroi</i> DC.	Sweetcicely	25.0	0.30
OXCA4	<i>Oxytropis campestris</i> (L.) DC.	Field locoweed	2.5	0.01
PAFL15	<i>Packera flettii</i> (Wiegand) W.A. Weber & Á. Löve	Flett's ragwort	7.5	0.02
PAMY	<i>Paxistima myrsinites</i> (Pursh) Raf.	Oregon boxleaf	60.0	0.30
PEBR	<i>Pedicularis bracteosa</i> Benth.	Bracted lousewort	—	—
PEGR2	<i>Pedicularis groenlandica</i> Retz.	Elephanthead lousewort	—	—
PERA	<i>Pedicularis racemosa</i> Douglas ex Benth.	Sickletop lousewort	42.5	0.80
PEDA2	<i>Penstemon davidsonii</i> Greene	Davidson's penstemon	30.0	0.20
PEPR2	<i>Penstemon procerus</i> Douglas ex Graham	Littleflower penstemon	52.5	0.80
PHHA	<i>Phacelia hastata</i> Douglas ex Lehm.	Silverleaf phacelia	20.0	0.04
PHSE	<i>Phacelia sericea</i> (Graham) A. Gray	Silky phacelia	12.5	0.04
PHAL2	<i>Phleum alpinum</i> L.	Alpine timothy	7.5	0.03
PHDI3	<i>Phlox diffusa</i> Benth.	Spreading phlox	75.0	5.90
PHHE9	<i>Phlox hendersonii</i> (E.E. Nelson) Cronquist	Henderson's phlox	5.0	0.70
PHEM	<i>Phyllodoce empetriiformis</i> (Sm.) D. Don	Pink mountainheath	—	—
PIAB	<i>Picea abies</i> (L.) Karst.	Norway spruce	—	—
PIEN	<i>Picea engelmannii</i> Parry ex Engelm.	Engelmann spruce	—	—
PIAL	<i>Pinus albicaulis</i> Engelm.	Whitebark pine	80.0	7.50
PICOC	<i>Pinus contorta</i> Douglas ex Loudon var. <i>contorta</i>	Shore pine ^b	20.0	1.10
PICOL	<i>Pinus contorta</i> Douglas ex Loudon var. <i>latifolia</i> Engelm. ex S. Watson	Lodgepole pine	—	—
PIMO3	<i>Pinus monticola</i> Douglas ex D. Don	Western white pine	35.0	1.40
PIMU80	<i>Pinus mugo</i> Turra	Mugo pine	—	—
PIPO	<i>Pinus ponderosa</i> Lawson & C. Lawson	Ponderosa pine	—	—
PIPU	<i>Picea pungens</i> Engelm.	Blue spruce	—	—
PIST	<i>Pinus strobus</i> L.	Eastern white pine	—	—
PIEL4	<i>Piperia elongata</i> Rydb.	Denseflower rein orchid	2.5	<0.01
PLLE2	<i>Platanthera leucophaea</i> (Nutt.) Lindl.	Prairie white fringed orchid	2.5	<0.01

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
				PERCENT
PLST4	<i>Platanthera stricta</i> Lindl.	Slender bog orchid	2.5	<0.01
POGLR2	<i>Poa glauca</i> Vahl ssp. <i>rupicola</i> (Nash ex Rydb.) W.A. Weber	Timberline bluegrass	2.5	0.03
POSE	<i>Poa secunda</i> J. Presl	Sandberg bluegrass	2.5	<0.01
POPU3	<i>Polemonium pulcherrimum</i> Hook.	Jacob's-ladder	25.0	0.09
POBI6	<i>Polygonum bistortoides</i> Pursh	American bistort	5.0	0.06
POMU	<i>Polystichum munitum</i> (Kaulf.) C. Presl	Western swordfern	7.5	<0.01
PODI2	<i>Potentilla diversifolia</i> Lehm.	Varileaf cinquefoil	10.0	0.05
POFL3	<i>Potentilla flabellifolia</i> Hook. ex Torr. & A. Gray	High mountain cinquefoil	—	—
POGR9	<i>Potentilla gracilis</i> Douglas ex Hook.	Slender cinquefoil	25.0	0.40
PSMEM	<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>menziesii</i>	Douglas-fir	40.0	4.80
PTAQ	<i>Pteridium aquilinum</i> (L.) Kuhn	Western brackenfern	2.5	1.10
PUOC	<i>Pulsatilla occidentalis</i> (S. Watson) Freyn	White pasqueflower	7.5	0.02
RAES	<i>Ranunculus eschscholtzii</i> Schltldl.	Eschsholtz's buttercup	5.0	0.08
RAUN	<i>Ranunculus uncinatus</i> D. Don ex G. Don	Woodland buttercup	2.5	<0.01
RHAL2	<i>Rhododendron albiflorum</i> Hook.	Cascade azalea	20.0	4.80
RIBES	<i>Ribes</i> L.	Currant	—	—
RIAC	<i>Ribes acerifolium</i> Howell	Mapleleaf currant	2.5	0.03
RILA	<i>Ribes lacustre</i> (Pers.) Poir.	Prickly currant	12.5	0.09
RIVI3	<i>Ribes viscosissimum</i> Pursh	Sticky currant	—	—
ROGY	<i>Rosa gymnocarpa</i> Nutt.	Dwarf rose	20.0	0.30
RONU	<i>Rosa nutkana</i> C. Presl	Nootka rose	5.0	<0.01
RULA2	<i>Rubus lasiococcus</i> A. Gray	Roughfruit berry	20.0	0.10
RUAC3	<i>Rumex acetosella</i> L.	Common sheep sorrel	2.5	<0.01
SABA3	<i>Salix barclayi</i> Andersson	Barclay's willow	2.5	0.01
SANIC5	<i>Sambucus nigra</i> L. ssp. <i>cerulea</i> (Raf.) R. Bolli	Blue elderberry	2.5	0.03
SARA2	<i>Sambucus racemosa</i> L.	Red elderberry	2.5	0.03
SAUSS	<i>Saussurea</i> DC.	Saw-wort	—	—
SABR6	<i>Saxifraga bronchialis</i> L.	Yellowdot saxifrage	15.0	0.20
SACA50	<i>Saxifraga caespitosa</i> L.	Tufted alpine saxifrage	2.5	<0.01
SANE3	<i>Saxifraga nelsoniana</i> D. Don	Heartleaf saxifrage	2.5	<0.01
SEDI	<i>Sedum divergens</i> S. Watson	Pacific stonecrop	27.5	0.09
SELA	<i>Sedum lanceolatum</i> Torr.	Spearleaf stonecrop	32.5	0.06
SEOR	<i>Sedum oreganum</i> Nutt.	Oregon stonecrop	5.0	<0.01
SERU3	<i>Sedum rupicola</i> G.N. Jones	Curvedleaf stonecrop	2.5	<0.01
SESP	<i>Sedum spathulifolium</i> Hook.	Broadleaf stonecrop	2.5	<0.01
SEWA	<i>Selaginella wallacei</i> Hieron.	Wallace's spikemoss	5.0	0.02
SENEC	<i>Senecio</i> L.	Ragwort	—	—
SENE6	<i>Senecio neowebsteri</i> S.F. Blake	Olympic Mountain ragwort	12.5	0.03
SIAC	<i>Silene acaulis</i> (L.) Jacq.	Moss campion	2.5	0.08
SIDO	<i>Silene douglasii</i> Hook.	Douglas' catchfly	40.0	0.50

Symbol	Scientific name and authority	Common name	Constancy ^a	Mean cover
			PERCENT	
SIPA4	<i>Silene parryi</i> (S. Watson) C.L. Hitchc. & Maguire	Parry’s silene	20.0	0.20
SMCA	<i>Smelowskia calycina</i> (Stephan ex Willd.) C.A. Mey.	Alpine smelowskia	12.5	0.02
SOMU	<i>Solidago multiradiata</i> Aiton	Rocky Mountain goldenrod	47.5	0.70
SOSI2	<i>Sorbus sitchensis</i> M. Roem.	Western mountain ash	22.5	0.10
STCR2	<i>Stellaria crispa</i> Cham. & Schltldl.	Curled starwort	2.5	0.01
STAM2	<i>Streptopus amplexifolius</i> (L.) DC.	Claspleaf twistedstalk	2.5	<0.01
STLA16	<i>Streptopus lanceolatus</i> (Aiton) Reveal	Twistedstalk	2.5	<0.01
SYALL	<i>Symphoricarpos albus</i> (L.) S.F. Blake var. <i>laevigatus</i> (Fernald) S.F. Blake	Common snowberry	25.0	0.40
SYPI	<i>Synthyris pinnatifida</i> S. Watson	Featherleaf kittentails	—	—
THOC	<i>Thalictrum occidentale</i> A. Gray	Western meadow-rue	12.5	0.20
TRBO2	<i>Trientalis borealis</i> Raf.	Starflower	2.5	<0.01
TROV2	<i>Trillium ovatum</i> Pursh	Pacific trillium	2.5	<0.01
TRCA21	<i>Trisetum canescens</i> Buckley	Tall trisetum	10.0	0.20
TRCE2	<i>Trisetum cernuum</i> Trin.	Tall trisetum	5.0	0.03
TRSP2	<i>Trisetum spicatum</i> (L.) K. Richt.	Spike trisetum	20.0	0.10
TSHE	<i>Tsuga heterophylla</i> (Raf.) Sarg.	Western hemlock	—	—
TSME	<i>Tsuga mertensiana</i> (Bong.) Carrière	Mountain hemlock	2.5	0.01
VADE	<i>Vaccinium deliciosum</i> Piper	Cascade bilberry	—	—
VAME	<i>Vaccinium membranaceum</i> Douglas ex Torr.	Thinleaf huckleberry	27.5	0.40
VAAT2	<i>Vahlodea atropurpurea</i> (Wahlenb.) Fr. ex Hartm.	Mountain hairgrass	2.5	0.03
VASI	<i>Valeriana sitchensis</i> Bong.	Sitka valerian	45.0	2.60
VEVI	<i>Veratrum viride</i> Aiton	Green false hellebore	2.5	<0.01
VECU	<i>Veronica cusickii</i> A. Gray	Cusick’s speedwell	17.5	0.30
VIAM	<i>Vicia americana</i> Muhl. ex Willd.	American vetch	37.5	0.50
VIAD	<i>Viola adunca</i> Sm.	Hookedspur violet	57.5	0.10
VIFL	<i>Viola flettii</i> Piper	Olympic violet	—	—
VIGL	<i>Viola glabella</i> Nutt.	Pioneer violet	5.0	0.01
WISE3	<i>Viola sempervirens</i> Greene	Evergreen violet	27.5	0.08

Note: Species with no value (—) for constancy or mean cover did not occur on our plots or, in many cases, the study area but are included because they appear in this report for other reasons.

^a Constancy is the percentage of the plots on which a species was found over the entire sample.

^b The USDA PLANTS Database (USDA NRCS, n.d.) uses the common name “beach pine” for this species; however, we find that “shore pine” is used more frequently and have opted to use it instead in this report.

Appendix 2: Data Tables and Model Statistics

Table A2.1—Seedlings sampled to estimate age and their site characteristics in the Olympic Mountain whitebark pine communities study

Plot	Species	Sample year	Basal diameter CENTIMETERS	Tree height METERS	Basal tree rings NUMBER	Tree origin year	Elevation ^a METERS	Slope steepness ^b PERCENT	Aspect DEGREES	Canopy closure ^c PERCENT
Trees used to calculate a relationship between age and height (n = 34):										
8	Subalpine fir	2008	2	0.6	37	1971	1597	60	220	35
11	Subalpine fir	2008	1.4	0.4	22	1986	1543	32	266	80
11	Subalpine fir	2008	2.1	0.9	39	1969	1543	32	266	80
13	Subalpine fir	2008	2.7	0.8	24	1984	1781	62	291	30
28	Subalpine fir	2010	1	0.3	17	1993	1828	50	300	14
29	Subalpine fir	2010	1.8	0.4	17	1993	1857	41	266	20
29	Subalpine fir	2010	4.1	0.9	49	1961	1857	41	266	20
31	Subalpine fir	2010	0.7	0.2	17	1993	1845	72	295	29
31	Subalpine fir	2010	2.3	0.7	22	1988	1845	72	295	29
32	Subalpine fir	2010	0.1	0.1	2	2008	1595	46	0	75
32	Subalpine fir	2010	0.4	0.2	4	2006	1595	46	0	75
32	Subalpine fir	2010	1.4	0.6	47	1963	1595	46	0	75
32	Subalpine fir	2010	3	1.2	62	1948	1595	46	0	75
33	Subalpine fir	2010	0.6	0.5	40	1970	1513	40	326	85
36	Subalpine fir	2010	0.2	0.1	16	1994	1619	69	311	55
36	Subalpine fir	2010	0.6	0.3	37	1973	1619	69	311	55
36	Subalpine fir	2010	1.4	0.7	43	1967	1619	69	311	55
39	Subalpine fir	2010	1	0.2	15	1995	1639	54	239	35
41	Subalpine fir	2010	1.1	0.3	44	1966	1497	25	230	85
41	Subalpine fir	2010	2.5	1	74	1936	1497	25	230	85
5	Whitebark pine	2008	1.7	0.6	34	1974	1630	59	230	35
8	Whitebark pine	2008	2.2	0.9	44	1964	1597	60	220	35
13	Whitebark pine	2008	0.9	0.1	10	1998	1781	62	291	30
13	Whitebark pine	2008	2.0	0.7	15	1993	1781	62	291	30
28	Whitebark pine	2010	0.8	0.4	22	1988	1828	50	300	14
28	Whitebark pine	2010	1.6	0.9	25	1985	1828	50	300	14

Table A2.1—Seedlings sampled to estimate age and their site characteristics in the Olympic Mountain whitebark pine communities study (continued)

Plot	Species	Sample year	Basal diameter CENTIMETERS	Tree height METERS	Basal tree rings NUMBER	Tree origin year	Elevation ^a METERS	Slope steepness ^b PERCENT	Aspect DEGREES	Canopy closure ^c PERCENT
31	Whitebark pine	2010	1.2	0.6	25	1985	1845	72	295	29
35	Whitebark pine	2010	1.3	0.5	24	1986	1742	40	326	28
35	Whitebark pine	2010	3.5	0.7	45	1965	1742	40	326	28
37	Whitebark pine	2010	1.1	0.2	19	1991	1814	67	233	40
38	Whitebark pine	2010	4.4	1.5	53	1957	1711	56	233	25
39	Whitebark pine	2010	1.1	0.4	23	1987	1639	54	239	35
39	Whitebark pine	2010	1.9	0.8	36	1974	1639	54	239	35
39	Whitebark pine	2010	2.2	1.2	50	1960	1639	54	239	35
Trees not used to calculate a relationship between age and height (n = 10):^d										
17	Subalpine fir	2010	1.5	0.6	79	1931	1814	61	213	80
18	Subalpine fir	2010	0.8	0.2	25	1985	1741	10	275	3
30	Subalpine fir	2010	2.7	1.3	31	1979	1893	33	266	30
30	Subalpine fir	2010	3.5	0.9	52	1958	1893	33	266	30
31	Whitebark pine	2010	1.8	—	52	1958	1845	72	295	29
18	Whitebark pine	2010	1.9	0.7	13	1997	1741	10	275	3
18	Whitebark pine	2010	0.8	0.3	14	1996	1741	10	275	3
24	Douglas-fir	2010	0.4	0.5	7	2003	1754	63	255	3
39	Shore pine	2010	1.4	0.5	20	1990	1639	54	239	35
39	Shore pine	2010	2.6	0.9	21	1989	1639	54	239	35

— = no data.

Note: Seedlings were trees <1 m tall.

^a Mean elevation for all sampled trees was 1668 m.^b Mean slope over all sample plots was 56 percent.^c Mean overstory canopy closure over all sample plots was 34 percent.^d Trees not used to calculate a relationship between age and height were too atypical or too few.

Table A2.2—Trees core sampled to estimate age in the Olympic Mountain whitebark pine communities study

	Plot	Tree code	Species	Diameter at breast height ^a	Basal core height	Time to base ^b	Basal tree rings	Total basal age ^c	Height increment ^d	Breast height tree rings	Age increment ^e
				CENTIMETERS	METERS	YEARS	NUMBER	YEARS	METERS	NUMBER	YEARS
Subalpine fir used to estimate age from diameter (n= 39):											
	14	r	Subalpine fir	8.0	0.20	14.60	30.0	44.60	1.1	16.0	28.60
	14	s	Subalpine fir	10.3	0.10	9.75	46.0	55.75	1.2	21.0	34.75
	15	u	Subalpine fir	13.4	0.10	9.75	41.0	50.75	1.2	23.0	27.75
	15	v	Subalpine fir	15.7	0.20	14.60	45.0	59.60	1.1	30.0	29.60
	21	ee	Subalpine fir	12.6	0.10	9.75	49.5	59.25	1.2	29.8	29.45
	21	ff	Subalpine fir	11.9	0.10	9.75	34.6	44.35	1.2	29.0	15.35
	28	tt	Subalpine fir	6.2	0.20	14.60	31.0	45.60	1.1	20.0	25.60
	29	vv	Subalpine fir	7.8	0.20	14.60	52.0	66.60	1.1	22.0	44.60
	39	fff	Subalpine fir	26.4	0.20	14.60	103.0	117.60	1.1	58.6	59.00
	1	b	Subalpine fir	15.8	0.05	6.52	73.0	79.52	1.3	53.0	26.52
	3	c	Subalpine fir	22.2	0.00	0.00	59.0	59.00	1.3	52.0	7.00
	11	l	Subalpine fir	41.3	0.20	14.60	174.0	188.60	1.1	161.0	27.60
	13	o	Subalpine fir	7.3	0.10	9.75	36.0	45.75	1.2	16.0	29.75
	17	y	Subalpine fir	33.9	0.10	9.75	153.0	162.75	1.2	109.0	53.75
	17	z	Subalpine fir	12.8	0.10	9.75	69.0	78.75	1.2	41.0	37.75
	26	nn	Subalpine fir	23.4	0.00	0.00	114.0	114.00	1.3	87.9	26.10
	26	oo	Subalpine fir	4.7	0.05	6.52	29.5	36.02	1.3	16.0	20.02
	31	yy	Subalpine fir	11.3	0.15	12.35	48.2	60.55	1.2	26.0	34.55
	27	pp	Subalpine fir	21.8	0.00	0.00	116.5	116.50	1.3	99.3	17.20
	27	qq	Subalpine fir	17.1	0.00	0.00	102.0	102.00	1.3	81.0	21.00
	32	zz	Subalpine fir	21.5	0.15	10.64	93.0	103.64	1.2	82.0	21.64
	33	aaa	Subalpine fir	25.4	0.20	14.18	99.4	113.58	1.1	78.0	35.58
	8	j	Subalpine fir	9.0	0.05	6.52	47.2	53.72	1.3	24.0	29.72
	41	ggg	Subalpine fir	31.7	0.10	7.09	104.0	111.09	1.2	80.9	30.19
	16	w	Subalpine fir	32.0	0.20	14.60	71.0	85.6	1.1	58.0	27.60
	16	x	Subalpine fir	10.4	0.00	0.00	35.0	35.00	1.3	16.0	19.00

Table A2.2—Trees core sampled to estimate age in the Olympic Mountain whitebark pine communities study (continued)

Plot	Tree code	Species	Diameter at breast height ^a CENTIMETERS	Basal core height METERS	Time to base ^b YEARS	Basal tree rings NUMBER	Total basal age ^c YEARS	Height increment ^d METERS	Breast height tree rings NUMBER	Age increment ^e YEARS
20	dd	Subalpine fir	6.7	0.00	0.00	42.0	42.00	1.3	19.0	23.00
23	hh	Subalpine fir	13.5	0.10	7.09	59.0	66.09	1.2	34.0	32.09
7	h	Subalpine fir	23.0	0.20	14.60	82.2	96.80	1.1	65.4	31.40
Subalpine fir not used to estimate age from diameter (n = 2):^f										
30	xx	Subalpine fir	22.3	0.20		188.0	NA	NA	NA	NA
35	bbb	Subalpine fir	4.4	0.00		210.0	NA	NA	NA	NA
Whitebark pines used to estimate age from diameter for trees <90 years old (n = 23):										
14	11	Whitebark pine	13.6	0.00	0.00	41.0	41.00	1.3	26.8	14.20
14	p	Whitebark pine	10.6	0.20	15.63	31.0	46.63	1.1	21.0	25.63
14	q	Whitebark pine	12.2	0.10	10.61	32.0	42.61	1.2	21.2	21.41
15	t	Whitebark pine	17.8	0.20	15.63	63.2	78.83	1.1	33.6	45.23
28	42-2	Whitebark pine	4.5	0.20	15.63	24.2	39.83	1.1	12.0	27.83
28	rr	Whitebark pine	5.5	0.20	15.63	27.0	42.63	1.1	15.0	27.63
29	16-2	Whitebark pine	14.7	0.23	16.90	48.0	64.90	1.1	37.0	27.90
29	uu	Whitebark pine	13.7	0.15	13.31	43.7	57.01	1.2	27.2	29.81
1	4a	Whitebark pine	33.6	0.02	4.32	81.0	85.32	1.3	75.1	10.22
1	a	Whitebark pine	17.2	0.00	0.00	45.0	45.00	1.3	25.0	20.00
3	d	Whitebark pine	8.5	0.00	0.00	49.0	49.00	1.3	23.5	25.50
13	n	Whitebark pine	15.9	0.10	10.61	70.8	81.41	1.2	36.0	45.41
4	e	Whitebark pine	18.9	0.20	15.63	50.2	65.83	1.1	32.8	33.03
5	f	Whitebark pine	15.4	0.00	0.00	61.8	61.80	1.3	42.0	19.80
9	k	Whitebark pine	11.5	0.20	15.63	33.0	48.63	1.1	24.0	24.63
12	6	Whitebark pine	—	0.10	10.61	33.0	43.61	1.2	18.0	25.61
12	m	Whitebark pine	9.0	0.10	10.61	39.2	49.81	1.2	21.0	28.81
19	aa	Whitebark pine	13.5	0.10	10.61	58.0	68.61	1.2	48.0	20.61
19	bb	Whitebark pine	13.7	0.10	10.61	60.0	70.61	1.2	38.5	32.11
20	cc	Whitebark pine	24.4	0.05	7.20	68.5	75.70	1.3	57.4	18.30
24	ii	Whitebark pine	14.0	0.10	10.61	48.0	58.61	1.2	31.5	27.11

Table A2.2—Trees core sampled to estimate age in the Olympic Mountain whitebark pine communities study (continued)

Plot	Tree code	Species	Diameter at breast height ^a CENTIMETERS	Basal core height METERS	Time to base ^b YEARS	Basal tree rings NUMBER	Total basal age ^c YEARS	Height increment ^d METERS	Breast height tree rings NUMBER	Age increment ^e YEARS
24	jj	Whitebark pine	18.2	0.20	15.63	40.4	56.03	1.1	30.2	25.83
25	kk	Whitebark pine	7.2	0.10	10.61	31.2	41.81	1.2	19.6	22.21
Whitebark pines used to estimate age from diameter for trees ≥90 years old (n = 5):										
26	mm	Whitebark pine	4.6	0.00	0.00	92.0	92.00	1.3	32.0	60.00
39	eee	Whitebark pine	14.4	0.20	15.63	105.0	120.63	1.1	63.0	57.63
37	ccc	Whitebark pine	21.1	0.20	15.63	97.0	112.63	1.1	78.0	34.63
38	dcd	Whitebark pine	24.9	0.00	0.00	136.0	136.00	1.3	117.0	19.00
8	i	Whitebark pine	14.5	0.05	7.20	95.0	102.20	1.3	52.0	50.20
Whitebark pine not used to estimate age from diameter (n = 1):^g										
6	g	Whitebark pine	19.4	0.20	15.63	178.0	193.63	1.1	168.0	25.60

NA = not applicable; — = no data.

Note: Trees were sampled at the base and breast height (1.3 m) to estimate age from stem diameter.

^a Diameter at breast height is the diameter measured at 1.3-m height.^b Time to base is the number of years required for the tree to grow from the surface of the ground to the height of the basal core sample. Models used to calculate this value were derived from seedling height growth relationships (see fig. 5 and associated text).^c Total basal age is assumed to be the total age of the tree that accounts for all its growth above the ground surface. For trees that were not core sampled, this was based on a relationship between diameter and basal age (see figs. 6 and 7 and associated text). Basal age was determined from trees that were core sampled at or near the base (see also footnote ^b above).^d Height increment is the difference in height between breast height (1.3 m) and the basal core sample.^e Age increment is the difference in age between the breast height age and the basal age.^f Krummholz subalpine fir were not used in the relationship to estimate age from diameter because the ring count came from an unknown distance from the point of germination.^g The whitebark pine not used to estimate age from diameter was an outlier with an age much older than its diameter suggested.

Table A2.3—Environmental characteristics of each Olympic Mountain whitebark pine communities study plot

Plot ^a	Elevation METERS	Aspect DEGREES	Slope steepness	PERCENT			5-year mean summer soil moisture	Mean frost- free duration ^b DAYS	Mean annual air temperature ^c DEGREES CELSIUS	Mean growing- season soil temperature ^d DEGREES CELSIUS	Projected growing-season soil temperature ^e
				Overstory canopy closure	Understory canopy closure	Understory canopy closure					
3	1529	251	58	50.0	45	4.4	4.4	122	4.0	12.9	10.7
4	1696	251	58	15.0	25	4.4	4.4	95	3.1	12.9	9.1
5	1630	230	59	35.0	25	3.7	3.7	113	3.4	14.5	11.7
6	1816	222	72	35.0	25	2.8	2.8	92	2.5	8.8	5.9
7	1591	262	49	10.0	3	0.0	0.0	48	2.6	9.7	5.7
8	1597	220	60	35.0	45	3.0	3.0	68	3.3	13.6	10.7
9	1698	238	71	5.0	50	4.3	4.3	94	3.1	13.2	9.0
10	1685	270	57	10.0	30	—	—	—	—	—	—
11	1543	266	32	80.0	20	5.4	5.4	100	3.2	8.5	7.6
12	1803	273	50	3.0	20	5.9	5.9	86	2.3	11.3	7.0
13	1781	291	62	30.0	35	4.4	4.4	88	1.8	10.4	7.3
14	1633	264	69	20.0	15	3.6	3.6	—	—	10.7	7.1
15	1616	256	65	20.0	10	3.0	3.0	—	—	11.5	7.9
16	1632	274	66	25.0	95	4.8	4.8	—	—	9.5	6.2
17	1814	213	61	80.0	27	5.8	5.8	90	2.2	7.5	6.6
18	1741	275	10	3.0	80	12.7	12.7	86	2.3	11.0	6.7
19	1705	222	73	10.0	45	4.2	4.2	90	2.7	10.3	6.3
20	1682	192	69	15.0	68	4.5	4.5	95	3.3	13.8	10.0
21	1571	240	59	45.0	40	4.2	4.2	107	3.8	10.4	8.0
22	1543	206	58	35.0	25	4.4	4.4	126	4.1	13.1	10.2
23	1420	228	52	90.0	55	4.6	4.6	132	3.9	8.1	7.6
24	1754	255	63	—	13	5.7	5.7	90	2.2	12.1	7.8
25	1650	264	82	2.0	35	4.3	4.3	—	—	11.1	6.7
26	1561	274	61	45.0	43	4.3	4.3	—	—	10.5	8.0
27	1586	328	64	50.0	98	5.3	5.3	—	—	8.2	5.9
28	1828	300	50	14.0	35	6.1	6.1	87	2.2	11.5	7.7
29	1857	266	41	20.0	75	7.2	7.2	78	1.6	10.7	7.1

Table A2.3—Environmental characteristics of each Olympic Mountain whitebark pine communities study plot (continued)

Plot ^a	Elevation	Aspect	Slope steepness	Overstory canopy closure	Understory canopy closure	5-year mean summer soil moisture	Mean frost-free duration ^b	Mean annual air temperature ^c	Mean growing-season soil temperature ^d	Projected growing-season soil temperature ^e
	METERS	DEGREES		PERCENT	PERCENT		DAYS		DEGREES CELSIUS	
30	1893	266	33	30.0	65	5.4	57	1.1	12.5	9.4
31	1845	295	72	29.0	37	4.3	86	1.6	10.8	7.7
32	1595	360	46	75.0	30	6.5	96	2.1	9.6	8.5
33	1513	326	40	85.0	25	5.9	122	3.3	7.4	6.8
34	1528	321	41	35.0	95	—	—	—	—	—
35	1742	265	55	28.0	6	3.6	76	1.9	10.8	7.6
36	1619	311	69	55.0	75	—	—	—	—	—
37	1814	233	67	40.0	15	3.2	92	2.4	11.5	8.9
38	1711	233	56	25.0	40	3.6	96	3.1	11.6	8.3
39	1639	239	54	35.0	71	4.6	102	3.3	12.1	9.2
40	1693	216	63	0.1	60	3.9	—	—	12.4	8.0
41	1497	230	25	85.0	3	6.7	111	3.0	7.7	7.1
Minimum	1420	192	10	0.0	3	0.0	48	1.1	7.4	5.7
Maximum	1893	360	82	90.0	98	12.7	132	4.1	14.5	11.7
Mean	1668	NA	56	34.0	41	4.7	94	2.7	10.9	7.9

— = no data; NA = not applicable..

Note: Overstory canopy closure was not obtained for plot 24. Summer soil moisture and frost-free duration were not obtained from all plots. Missing values for temperature data indicates either data gaps due to instrument failure or data was not taken.

^a All plots were 0.05 ha in size except plot 4, which was 0.1 ha in size.^b Frost-free duration is the mean number of days between the first and last recorded freezing temperatures over 3 years of data.^c Mean annual air temperature is the mean air temperature over 3 years of record.^d Growing-season soil temperature is the mean temperature at 20-cm depth in the soil between the dates when the temperature first rose above 6.2 °C in spring and when it dropped below that temperature in the fall.^e Projected growing-season soil temperature is an estimate of the mean 20-cm-deep soil temperature in the growing season (see footnote ^d), assuming 100-percent canopy closure.

Table A2.4—Geologic and soil characteristics of Olympic Mountain whitebark pine communities study plots

Plot	Geologic unit	Texture	Coarse fragments
			PERCENT
3	Sedimentary lens in Crescent basalt	Loamy sand	16.88
4	Sedimentary lens in Crescent basalt	Loamy sand	78.75
5	Sedimentary lens in Crescent basalt	Loamy sand	16.25
6	Crescent basalt	Loamy sand	82.38
7	Crescent basalt	Boulders	100.00
8	Crescent basalt	Loamy sand	66.88
9	Crescent basalt	Loamy sand	46.88
10	Crescent basalt	Boulders	87.50
11	Crescent basalt	Loamy sand	1.38
12	Crescent basalt	Loamy sand	71.88
13	Crescent basalt	Loamy sand	85.50
14	Sedimentary lens in Crescent basalt	Sand	15.63
15	Sedimentary lens in Crescent basalt	Sand	24.38
16	Sedimentary lens in Crescent basalt	Loamy sand	18.13
17	Crescent basalt	Loamy sand	13.38
18	Crescent basalt	Sandy loam	2.88
19	Crescent basalt	Loamy sand	67.50
20	Sedimentary lens in Crescent basalt	Loamy sand	54.38
21	Sedimentary lens in Crescent basalt	Loamy sand	10.13
22	Sedimentary lens in Crescent basalt	Sand	45.00
23	Sedimentary lens in Crescent basalt	Loamy sand	23.75
24	Crescent basalt	Sand	78.13
25	Sedimentary lens in Crescent basalt	Loamy sand	29.38
26	Sedimentary lens in Crescent basalt	Sand	10.13
27	Sedimentary lens in Crescent basalt	Sand	3.00
28	Crescent basalt	Loamy sand	67.50
29	Crescent basalt	Loamy sand	60.00
30	Crescent basalt	Sand	83.13
31	Crescent basalt	Loamy sand	79.38
32	Sedimentary lens in Crescent basalt	Loamy sand	0.63
33	Sedimentary lens in Crescent basalt	Loamy sand	1.13
35	Crescent basalt	Loamy sand	69.38
37	Crescent basalt	Loamy sand	51.25
38	Sedimentary lens in Crescent basalt	Loamy sand	55.63
39	Sedimentary lens in Crescent basalt	Loamy sand	4.13
40	Crescent basalt	Loamy sand	65.00
41	Sedimentary lens in Crescent basalt	Loamy sand	1.50

Note: Geologic units follow Tabor and Cady (1978).

Table A2.5—Mean annual, monthly, seasonal, and estimated soil temperatures, with organic layer (O horizon) depth and temperature regime estimates, for plots in the Olympic Mountain whitebark pine communities study

Plot	MAT ^a	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	20 cm ^b	JJA 20 cm	JJA 50 cm	DJF 20 cm	DJF 50 cm	O horizon depth ^c	Regime
DEGREES CELSIUS																				
CM																				
3	6.2	0.6	0.2	0.2	0.6	6.3	11.4	17.4	18.2	14.4	7.8	2.5	0.7	6.7	15.7	14.2	0.5	2.0	2.0	Cryic
4	4.9	-0.5	-0.2	-0.2	-0.3	3.3	10.3	17.2	16.8	12.2	5.8	0.7	-0.6	5.4	14.8	13.3	-0.4	1.1	0.5	Cryic
5	5.9	0.2	0.0	0.0	0.0	3.4	11.7	19.7	19.4	14.7	6.8	1.4	0.2	6.5	16.9	15.4	0.1	1.6	1.0	Frigid
6	3.5	0.2	-0.1	0.0	1.5	3.7	7.6	11.1	11.9	7.9	3.1	0.9	0.1	4.0	10.2	8.7	0.1	1.6	2.3	Cryic
7	1.4	-1.3	-3.4	-0.8	-0.7	-0.4	4.0	11.1	11.2	6.6	2.1	-2.1	-3.8	1.9	8.8	7.3	-2.8	-1.3	0.4	Cryic
8	—	—	—	—	—	—	—	—	—	—	—	—	—	5.2	14.3	12.8	0.6	2.1	1.6	Cryic
9	5.7	0.7	0.7	0.7	0.5	3.2	9.6	17.0	17.5	13.7	7.2	2.0	0.9	6.1	14.7	13.2	0.8	2.3	0.1	Cryic
10	8.3																			
11	3.5	0.6	0.6	0.5	0.4	2.5	6.1	9.8	10.5	8.7	4.9	1.6	0.8	3.9	8.8	7.3	0.7	2.2	2.4	Cryic
12	4.3	-1.2	-1.0	-0.8	-0.2	5.2	9.0	15.3	15.0	10.9	4.7	0.5	-0.8	4.7	13.1	11.6	-1.0	0.5	0.0	Cryic
13	3.1	0.1	0.2	0.2	0.1	0.0	3.1	12.7	12.7	8.9	3.2	0.6	0.2	3.5	9.5	8.0	0.1	1.6	0.8	Cryic
14	—	—	—	—	—	—	—	—	—	—	—	—	—	5.0	12.6	11.1	0.3	1.8	1.1	Cryic
15	—	—	—	—	—	—	—	—	—	—	—	—	—	6.2	13.5	12.0	0.8	2.3	0.1	Cryic
16	—	—	—	—	—	—	—	—	—	—	—	—	—	3.7	10.5	9.0	0.0	1.5	1.3	Cryic
17	2.6	0.1	-0.1	0.0	0.0	0.4	3.2	8.5	9.8	8.2	4.1	0.9	0.1	2.9	7.2	5.7	0.1	1.6	2.3	Cryic
18	3.0	0.0	0.0	0.1	0.1	0.2	2.6	11.9	12.8	9.4	3.4	0.7	0.1	3.4	9.1	7.6	0.0	1.5	5.1	Cryic
19	4.6	0.4	0.3	0.5	0.4	2.3	9.4	15.3	15.8	10.7	4.4	1.0	0.4	5.1	13.5	12.0	0.4	1.9	0.4	Cryic
20	4.9	0.2	1.1	3.6	3.8	2.7	9.6	16.2	12.9	9.5	5.6	1.5	0.4	5.6	12.9	11.4	0.6	2.1	1.1	Cryic
21	—	—	—	—	—	—	—	—	—	—	—	—	—	4.3	10.8	9.3	0.2	1.7	1.6	Cryic
22	6.7	1.1	0.5	0.5	2.2	8.1	11.4	17.9	17.8	14.2	8.1	2.8	1.0	7.1	15.7	14.2	0.9	2.4	1.3	Cryic
23	4.1	1.0	0.2	0.1	0.9	4.1	6.3	10.4	11.1	9.7	5.8	2.2	0.6	4.4	9.3	7.8	0.6	2.1	6.1	Cryic
24	5.2	-0.2	0.0	-0.1	0.6	6.8	9.9	16.2	16.2	12.1	5.5	1.1	-0.1	5.7	14.1	12.6	-0.1	1.4	0.0	Cryic
25	—	—	—	—	—	—	—	—	—	—	—	—	—	5.3	13.3	11.8	0.8	2.3	0.2	Cryic
26	—	—	—	—	—	—	—	—	—	—	—	—	—	5.0	11.7	10.2	0.4	1.9	3.1	Cryic
27	—	—	—	—	—	—	—	—	—	—	—	—	—	2.8	8.2	6.7	-0.1	1.4	3.3	Cryic
28	3.3	-0.3	-0.2	0.0	0.0	0.0	4.6	14.1	14.2	9.8	2.9	0.1	-0.4	3.7	11.0	9.5	-0.3	1.2	1.4	Cryic
29	—	—	—	—	—	—	—	—	—	—	—	—	—	3.6	10.5	9.0	0.2	1.7	2.0	Cryic

Table A2.5—Mean annual, monthly, seasonal, and estimated soil temperatures, with organic layer (O horizon) depth and temperature regime estimates, for plots in the Olympic Mountain whitebark pine communities study (continued)

Plot	MAT ^a	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	20 cm ^b	JJA 20 cm	JJA 50 cm	DJF 20 cm	DJF 50 cm	O horizon depth ^c	Regime	
DEGREES CELSIUS																				CM	
30	—	—	—	—	—	—	—	—	—	—	—	—	—	3.3	10.4	8.9	−0.4	1.1	1.6	Cryic	
31	3.3	−0.5	−0.2	0.1	0.1	0.0	4.9	13.2	13.6	9.6	3.6	0.5	−0.2	3.7	10.6	9.1	−0.3	1.2	0.7	Cryic	
32	1.9	−0.6	−0.6	−0.5	−0.5	−0.5	2.1	9.3	11.1	7.6	2.0	−0.2	−0.6	2.4	7.5	6.0	−0.6	0.9	2.3	Cryic	
33	—	—	—	—	—	—	—	—	—	—	—	—	—	3.3	8.9	8.9	0.0	1.5	3.3	Cryic	
34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9.7	—	
35	4.4	−1.3	−1.1	−1.2	0.7	6.4	9.6	16.3	16.2	10.2	4.1	0.0	−1.2	4.9	14.1	12.6	−1.2	0.3	0.9	Cryic	
36	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.5	—	
37	—	—	—	—	—	—	—	—	—	—	—	—	—	4.3	12.1	10.6	0.0	1.5	1.4	Cryic	
38	—	—	—	—	—	—	—	—	—	—	—	—	—	4.1	12.8	11.3	−0.5	1.0	2.8	Cryic	
39	—	—	—	—	—	—	—	—	—	—	—	—	—	4.6	12.1	10.6	0.8	2.3	1.1	Cryic	
40	6.5	0.8	0.1	0.1	2.5	8.4	10.9	17.4	17.7	14.1	7.9	2.1	0.6	6.9	15.3	13.8	0.5	2.0	0.0	Cryic	
41	3.3	0.5	0.0	0.0	0.2	1.6	4.9	9.0	10.0	8.5	5.2	2.0	0.5	3.5	8.0	6.5	0.3	1.8	3.1	Cryic	

— = no data; DJF = December, January, and February; JJA = June, July, and August; MAT = mean annual temperature.

Note: Soil temperatures were measured and estimated at 20- and 50-cm depths, respectively. For most plots, the 3-year dataset (September 2011 through August 2014) was used. For these plots, we included mean monthly data. Where this was not possible, we used data as necessary from all 5 years (September 2011 through July 2016). Monthly data is not shown for those plots because months other than June, July, August, December, January, and February were often incomplete. Plots shown without temperature data were too incomplete in the key 6 months to calculate meaningful means. Temperatures estimated for soil at 50-cm depths were derived from the seasonal 20-cm-deep soil temperature by adding (to DJF) or subtracting (from JJA) 0.5 °C for each 10 cm of added soil depth (thus 1.5 °C) (USDA NRCS 1999).

^a Mean annual 20-cm-depth soil temperature calculated from the 3-year dataset for plots that had complete data in this set.

^b O horizon depth is an average of several measurements of the O (organic) horizon depth on each plot. However, for the many cases in which it was only intermittently present, we did not use it to determine the soil temperature regime.

Table A2.6—Summary of regression statistics and coefficients for the relationships between temperatures and elevation for open-canopy, closed-canopy, and all plots by quarter-day for the Olympic Mountain whitebark pine communities study

Quarter-day ^a	Canopy dataset	n	Model <i>P</i>	Adjusted <i>r</i> ²	Intercept	Intercept <i>P</i>	Coefficient
Air temperatures:							
All	All	29	<0.01	0.65	11.06905	<0.01	−0.00494
1	All	29	<0.01	0.71	9.67282	<0.01	−0.00492
2	All	29	<0.01	0.54	8.99962	<0.01	−0.00399
3	All	29	<0.01	0.47	14.20762	<0.01	−0.00553
4	All	29	<0.01	0.73	11.39235	<0.01	−0.00533
All	Closed	6	<0.01	0.81	16.05154	<0.01	−0.00853
All	Open	23	<0.01	0.85	14.98112	<0.01	−0.00713
1	Closed	6	0.02	0.72	17.50663	0.01	−0.01027
2	Closed	6	0.03	0.67	17.00525	0.02	−0.00955
3	Closed	6	0.14	0.32	14.96088	0.05	−0.00653
4	Closed	6	<0.01	0.89	14.73564	<0.01	−0.00779
1	Open	23	<0.01	0.80	11.72116	<0.01	−0.00606
2	Open	23	<0.01	0.81	12.55764	<0.01	−0.00597
3	Open	23	<0.01	0.80	21.03387	<0.01	−0.00937
4	Open	23	<0.01	0.83	14.60588	<0.01	−0.00713
20-cm-deep soil temperatures:							
All	All	22	0.47	0.02	7.45106	0.11	−0.00194
1	Closed	5	0.06	0.64	23.53645	0.05	−0.01350
2	Closed	5	0.06	0.64	25.35145	0.05	−0.01482
3	Closed	5	0.04	0.73	23.32317	0.03	−0.01343
4	Closed	5	0.06	0.68	21.05671	0.04	−0.01179
1	Open	17	<0.01	0.67	25.09231	<0.01	−0.01185
2	Open	17	<0.01	0.71	22.60015	<0.01	−0.01069
3	Open	17	<0.01	0.67	23.88490	<0.01	−0.01127
4	Open	17	<0.01	0.64	28.07312	<0.01	−0.01334
Soil surface temperatures:							
All	All	19	0.22	0.03	9.76497	0.03	−0.00303
1	Open	17	<0.01	0.51	10.14689	<0.01	−0.00460
2	Open	17	<0.01	0.56	14.25736	<0.01	−0.00647
3	Open	17	0.03	0.24	33.64431	<0.01	−0.01439
4	Open	17	0.07	0.15	13.09603	<0.01	−0.00493

P = probability value; *r*² = coefficient of determination.

^a Quarter-day: 1 = 0000 to 0600, 2 = 0600 to 1200, 3 = 1200 to 1800, and 4 = 1800 to 2400.

Table A2.7—Monthly air, soil surface, and 20-cm-deep soil lapse rate regression statistics and coefficients for all Olympic Mountain whitebark pine communities study data

Month	n	Model <i>P</i>	Adjusted <i>r</i> ²	Intercept	Intercept <i>P</i>	Coefficient
Air temperature lapse rates:						
January	29	<0.01	0.42	6.38239	<0.01	−0.00449
February	29	<0.01	0.65	5.78535	<0.01	−0.00549
March	29	<0.01	0.67	7.20646	<0.01	−0.00573
April	29	<0.01	0.68	10.38510	<0.01	−0.00629
May	29	<0.01	0.45	13.53072	<0.01	−0.00573
June	29	<0.01	0.74	15.84746	<0.01	−0.00560
July	29	<0.01	0.43	19.01370	<0.01	−0.00383
August	29	<0.01	0.47	18.56067	<0.01	−0.00369
September	29	<0.01	0.34	16.44748	<0.01	−0.00404
October	29	<0.01	0.50	11.07605	<0.01	−0.00431
November	29	<0.01	0.74	8.04647	<0.01	−0.00546
December	29	<0.01	0.65	3.85578	<0.01	−0.00392
Soil surface temperature lapse rates:						
January	19	0.02	0.24	4.27100	0.03	−0.00272
February	19	0.49	−0.03	0.68900	0.68	−0.00067
March	19	0.41	−0.01	0.86858	0.50	−0.00065
April	19	0.60	−0.04	1.75925	0.52	−0.00086
May	19	0.29	0.01	14.51304	0.16	−0.00631
June	19	0.41	−0.02	18.23311	0.10	−0.00529
July	19	0.58	0.02	11.26736	0.31	0.00354
August	19	0.94	−0.06	17.23941	0.08	−0.00041
September	19	0.18	0.05	23.14026	0.01	−0.00676
October	19	0.02	0.22	18.57444	0.01	−0.00844
November	19	<0.01	0.48	7.13752	<0.01	−0.00423
December	19	0.07	0.13	2.81623	0.13	−0.00204
20-cm-deep soil temperature lapse rates:						
January	22	0.03	0.17	4.56536	0.03	−0.00270
February	22	0.78	−0.05	0.64777	0.82	−0.00047
March	22	0.72	−0.04	1.15287	0.69	−0.00061
April	22	0.68	−0.04	1.97835	0.56	−0.00083
May	22	0.38	−0.01	10.89407	0.22	−0.00466
June	22	0.56	−0.03	13.31936	0.20	−0.00354
July	22	0.63	−0.04	8.91840	0.40	0.00300
August	22	0.74	−0.04	11.14689	0.24	0.00182
September	22	0.58	−0.03	14.75513	0.07	−0.00251
October	22	0.07	0.11	15.04602	0.01	−0.00603
November	22	0.07	0.11	6.98623	0.04	−0.00345
December	22	0.48	−0.02	2.20822	0.49	−0.00134

P = probability value; *r*² = coefficient of determination.

Note: For each month, all the plots with data, regardless of canopy condition or time of day were included.

Table A2.8—Summary of regression statistics and coefficients for the relationship between air temperatures and elevation for closed- and open-canopy plots by month in the Olympic Mountain whitebark pine communities study

Month	Model <i>P</i>	Adjusted r^2	Intercept	Intercept <i>P</i>	Coefficient
Closed canopy (n = 6):					
January	0.02	0.75	18.08648	0.02	−0.01251
February	<0.01	0.80	12.51791	0.02	−0.01024
March	<0.01	0.93	14.19943	<0.01	−0.01066
April	0.01	0.80	18.55266	<0.01	−0.01201
May	0.02	0.75	25.55119	<0.01	−0.01407
June	0.04	0.61	15.36874	<0.01	−0.00557
July	0.13	0.34	18.81354	<0.01	−0.00406
August	0.11	0.38	18.33241	<0.01	−0.00388
September	0.05	0.59	18.74719	<0.01	−0.00587
October	0.05	0.58	14.17186	0.02	−0.00664
November	0.01	0.76	12.32859	0.02	−0.00851
December	0.01	0.77	8.80510	0.03	−0.00740
Open canopy (n = 23):					
January	<0.01	0.61	9.98015	<0.01	−0.00650
February	<0.01	0.83	9.66861	<0.01	−0.00766
March	<0.01	0.83	11.17672	<0.01	−0.00795
April	<0.01	0.86	14.50272	<0.01	−0.00860
May	<0.01	0.67	18.67304	<0.01	−0.00860
June	<0.01	0.88	19.71844	<0.01	−0.00777
July	<0.01	0.75	23.99988	<0.01	−0.00663
August	<0.01	0.78	23.12017	<0.01	−0.00626
September	<0.01	0.49	20.59249	<0.01	−0.00637
October	<0.01	0.68	14.89514	<0.01	−0.00645
November	<0.01	0.83	10.87929	<0.01	−0.00705
December	<0.01	0.83	6.63177	<0.01	−0.00547

P = probability value; r^2 = coefficient of determination.

Table A2.9—Summary of regression statistics and coefficients for the relationship between soil surface temperatures and elevation for open-canopy plots by month in the Olympic Mountain whitebark pine communities study

Month	n	Model <i>P</i>	Adjusted r^2	Intercept	Intercept <i>P</i>	Coefficient
January	17	0.09	0.12	3.99375	0.12	−0.002560
February	17	0.33	<0.01	1.74465	0.43	−0.001280
March	17	0.50	−0.03	0.94708	0.59	−0.000692
April	17	0.79	−0.06	1.28301	0.73	−0.000575
May	17	0.12	0.10	23.84769	0.07	−0.011580
June	17	0.01	0.32	39.55269	<0.01	−0.017420
July	17	0.17	0.06	33.27355	<0.01	−0.009000
August	17	0.02	0.25	38.42389	<0.01	−0.012500
September	17	<0.01	0.46	40.81791	<0.01	−0.016830
October	17	<0.01	0.49	28.54679	<0.01	−0.014100
November	17	<0.01	0.47	8.37452	<0.01	−0.004920
December	17	0.12	0.10	3.33192	0.19	−0.002330

P = probability value; r^2 = coefficient of determination.

Note: There were only two plots with closed canopies for which we had soil surface temperatures, thus no results are presented for them.

Table A2.10—Summary of regression statistics and coefficients for the relationship between 20-cm-deep soil temperatures and elevation for closed- and open-canopy plots by month in the Olympic Mountain whitebark pine communities study

Month	Model <i>P</i>	Adjusted <i>r</i> ²	Intercept	Intercept <i>P</i>	Coefficient
Closed canopy (n = 5):					
January	0.07	0.64	16.83314	0.07	−0.01098
February	0.32	0.09	18.17346	0.34	−0.01229
March	0.30	0.12	6.19418	0.31	−0.00414
April	0.04	0.75	12.35034	0.04	−0.00803
May	0.03	0.78	38.76570	0.03	−0.0244
June	0.14	0.42	32.05133	0.10	−0.01791
July	0.95	−0.33	9.31050	0.42	0.00040
August	0.72	−0.27	8.49354	0.25	0.00151
September	0.04	0.74	30.44181	0.02	−0.01452
October	0.04	0.74	38.06060	0.03	−0.02229
November	0.11	0.52	31.70320	0.10	−0.02027
December	0.27	0.16	23.94519	0.28	−0.01599
Open canopy (n = 17):					
January	0.01	0.30	7.31062	0.01	−0.00423
February	0.07	0.15	4.50769	0.07	−0.00261
March	0.33	<0.01	4.79794	0.31	−0.00266
April	0.17	0.07	8.12455	0.13	−0.00428
May	0.02	0.28	34.52304	0.01	−0.01797
June	<0.01	0.46	49.92195	<0.01	−0.02423
July	<0.01	0.48	53.02618	<0.01	−0.02198
August	<0.01	0.48	50.18952	<0.01	−0.02030
September	<0.01	0.60	45.06716	<0.01	−0.01964
October	<0.01	0.69	33.72022	<0.01	−0.01655
November	<0.01	0.65	13.41358	<0.01	−0.00712
December	0.02	0.29	6.50128	0.01	−0.00372

P = probability value; *r*² = coefficient of determination.

Table A2.11—Summary of regression statistics and coefficients for the relationships between annual air, soil surface, and 20-cm-deep soil temperatures and aspect and elevation by canopy closure group and quarter-day for the Olympic Mountain whitebark pine communities study

Canopy closure	Quarter-day ^a	n	Model P	Adjusted r ²	Intercept	Elevation coefficient	Aspect coefficient	Intercept P	Elevation P	Aspect P
Air temperature:										
All	1	29	<0.01	0.76	8.75554	-0.00477	0.00521	<0.01	<0.01	0.01
All	2	29	<0.01	0.63	7.87145	-0.00380	0.00641	<0.01	<0.01	<0.01
All	3	29	<0.01	0.71	11.75396	-0.00513	0.01394	<0.01	<0.01	<0.01
All	4	29	<0.01	0.84	10.08381	-0.00512	0.00743	<0.01	<0.01	<0.01
All	All	29	<0.01	0.79	9.61709	-0.00471	0.00825	<0.01	<0.01	<0.01
Open	1	23	<0.01	0.81	10.20148	-0.00550	0.00417	<0.01	<0.01	0.14
Open	2	23	<0.01	0.82	11.56706	-0.00561	0.00272	<0.01	<0.01	0.32
Open	3	23	<0.01	0.85	17.09549	-0.00793	0.01080	<0.01	<0.01	0.01
Open	4	23	<0.01	0.88	11.96212	-0.00617	0.00725	<0.01	<0.01	0.01
Open	All	23	<0.01	0.88	12.70863	-0.00630	0.00623	<0.01	<0.01	0.02
Closed	1	6	0.09	0.65	19.46168	-0.01139	-0.00231	0.05	0.06	0.66
Closed	2	6	0.12	0.60	19.10692	-0.01076	-0.00248	0.06	0.07	0.64
Closed	3	6	0.10	0.63	7.79244	-0.00241	0.00847	0.23	0.51	0.13
Closed	4	6	0.02	0.87	13.51629	-0.00708	0.00144	0.01	0.02	0.52
Closed	All	6	0.06	0.76	14.96662	-0.00791	0.00128	0.04	0.05	0.71
Soil surface temperature:										
All	1	19	<0.01	0.71	7.34043	-0.00358	0.00794	<0.01	<0.01	<0.01
All	2	19	<0.01	0.61	6.85783	-0.00319	0.01291	<0.01	<0.01	<0.01
All	3	19	0.07	0.19	3.09676	0.00019	0.03955	0.75	0.97	0.03
All	4	19	0.02	0.30	3.15349	-0.00053	0.01745	0.38	0.79	<0.01
All	All	19	<0.01	0.40	5.11471	-0.00178	0.01946	0.16	0.36	<0.01
Open	1	17	<0.01	0.62	6.91565	-0.00339	0.00859	<0.01	<0.01	0.04
Open	2	17	<0.01	0.64	10.42380	-0.00503	0.01019	<0.01	<0.01	0.05
Open	3	17	0.05	0.26	23.68405	-0.01066	0.02647	0.09	0.13	0.25
Open	4	17	0.06	0.23	7.53674	-0.00284	0.01477	0.18	0.32	0.13
Open	All	17	<0.01	0.48	12.14567	-0.00548	0.01500	0.02	0.04	0.08

Table A2.11—Summary of regression statistics and coefficients for the relationships between annual air, soil surface, and 20-cm-deep soil temperatures and aspect and elevation by canopy closure group and quarter-day for the Olympic Mountain whitebark pine communities study (continued)

Canopy closure	Quarter-day ^a	n	Model P	Adjusted r ²	Intercept	Elevation coefficient	Aspect coefficient	Intercept P	Elevation P	Aspect P
Closed	1	2	—	—	—	—	—	—	—	—
Closed	2	2	—	—	—	—	—	—	—	—
Closed	3	2	—	—	—	—	—	—	—	—
Closed	4	2	—	—	—	—	—	—	—	—
Closed	All	2	—	—	—	—	—	—	—	—
20-cm-deep soil temperature:										
All	1	22	0.04	0.22	2.63864	-0.00064	0.02091	0.55	0.79	0.01
All	2	22	0.02	0.27	3.01444	-0.00103	0.01975	0.43	0.63	<0.01
All	3	22	0.03	0.25	2.50034	-0.00066	0.02074	0.54	0.77	0.01
All	4	22	0.06	0.18	2.44654	-0.00043	0.02239	0.63	0.88	0.02
All	All	22	0.03	0.23	2.64983	-0.00069	0.02095	0.54	0.77	0.01
Open	1	17	<0.01	0.66	23.00242	-0.01102	0.00496	<0.01	<0.01	0.49
Open	2	17	<0.01	0.72	19.76781	-0.00957	0.00673	<0.01	<0.01	0.25
Open	3	17	<0.01	0.67	21.40686	-0.01029	0.00589	<0.01	<0.01	0.39
Open	4	17	<0.01	0.62	26.42280	-0.01269	0.00392	<0.01	<0.01	0.66
Open	All	17	<0.01	0.67	22.64817	-0.01089	0.00538	<0.01	<0.01	0.45
Closed	1	5	0.26	0.47	25.62221	-0.01470	-0.00227	0.20	0.22	0.86
Closed	2	5	0.25	0.49	29.13427	-0.01699	-0.00411	0.18	0.19	0.76
Closed	3	5	0.20	0.60	24.13069	-0.01389	-0.00088	0.16	0.18	0.93
Closed	4	5	0.24	0.51	20.82964	-0.01166	0.00025	0.20	0.23	0.98
Closed	All	5	0.24	0.52	24.92937	-0.01431	-0.00175	0.18	0.20	0.88

— = no data; P = probability value; r² = coefficient of determination.

Note: There were only two closed-canopy plots with soil surface temperature data, so no modeling was done.

^a Quarter-day: 1 = 0000 to 0600, 2 = 0600 to 1200, 3 = 1200 to 1800, and 4 = 1800 to 2400.

Table A2.12—Summary of species correlations with summer soil moisture and number of statistically significant ($P = 0.05$) solar radiation correlations with summer soil moisture for habitats of 20 species in the Olympic Mountain whitebark pine communities study

Species	Summer soil moisture (r) ^a	Total annual solar radiation (r)				Number of significant monthly solar radiation correlations ^b		
		Direct	Diffuse	Duration	Total	Direct	Diffuse	Duration
Cascade desertparsley	-0.53	NS	NS	NS	NS	5	4	5
Oregon boxleaf	-0.45	NS	NS	NS	NS	8	1	8
Common juniper	-0.40	NS	NS	NS	NS	0	0	0
Orange agoseris	-0.33	NS	NS	0.39	NS	3	3	3
Douglas-fir	-0.31	NS	NS	NS	NS	0	0	0
White hawkweed	-0.30	NS	NS	NS	NS	0	0	0
Whitebark pine	-0.30	NS	NS	NS	NS	0	2	0
Western white pine	-0.28	NS	NS	NS	NS	-4	-1	-4
Spreading phlox	-0.24	NS	NS	NS	NS	0	-2	0
Giant red Indian paintbrush	-0.21	NS	NS	NS	NS	0	0	0
Common yarrow	-0.21	NS	NS	NS	NS	0	0	0
Roemer's fescue	-0.12	NS	NS	NS	NS	0	0	0
Littleflower penstemon	-0.08	NS	NS	NS	NS	0	0	0
Broadleaf lupine	0.01	NS	NS	NS	NS	0	0	0
Shore pine	0.01	NS	NS	NS	NS	0	0	0
Hookedspur violet	0.04	NS	NS	NS	NS	0	0	0
Cliff dwarf-primrose	0.06	NS	NS	NS	NS	0	0	0
Thinleaf huckleberry	0.16	-0.38	-0.46	-0.44	-0.39	-7	-6	-7
Cascade azalea	0.23	-0.53	NS	-0.38	-0.55	-12	-6	-12
Subalpine fir	0.25	NS	NS	NS	NS	0	0	0

NS = not significant

Note: Data are sorted by summer soil moisture correlation coefficients with dry correlations at the top.

^a All summer soil moisture correlations are presented; however, those that were significant at $P = 0.05$ are shown in boldface type.

^b Monthly solar radiation correlations refers to the number of months in a year in which significant correlations were found; positive numbers represent the numbers of positive correlations and negative numbers represent the numbers of negative correlations.

Table A2.13—Summary of species correlations with summer soil moisture, relative timing of snowmelt, and number of statistically significant ($P = 0.05$) temperature correlations with summer soil moisture for habitats of 20 species in the Olympic Mountain whitebark pine communities study

Species	Summer soil moisture (r) ^a	Snowmelt rank ^b	Number of significant temperature correlations ^c		
			Air	Soil surface	20-cm-deep soil
Cascade desertparsley	-0.53	1	28	22	22
Oregon boxleaf	-0.45	1	43	6	0
Common juniper	-0.40	3	0	9	18
Orange agoseris	-0.33	2	0	14	25
Douglas-fir	-0.31	1	44	11	32
White hawkweed	-0.30	1	58	19	22
Whitebark pine	-0.30	3	0	8	0
Western white pine	-0.28	3	29	0	0
Spreading phlox	-0.24	2	-8	1	7
Giant red Indian paintbrush	-0.21	2	-11	-1	9
Common yarrow	-0.21	2	-19	-3	4
Roemer's fescue	-0.12	2	-21	-1	0
Littleflower penstemon	-0.08	3	-2	0	0
Broadleaf lupine	0.01	4	0	-5	0
Shore pine	0.01	1	58	4	16
Hookedspur violet	0.04	3	-16	-3	0
Cliff dwarf-primrose	0.06	4	-57	-17	-20
Thinleaf huckleberry	0.16	4	0	0	0
Cascade azalea	0.23	4	-8	-9	-8
Subalpine fir	0.25	4	0	0	-16

Note: Data are sorted by summer soil moisture correlation coefficients with dry correlations at the top.

^a All summer soil moisture correlations are presented; however, those that were significant at $P = 0.05$ are shown in boldface type.

^b Snowmelt rank refers to the date when our sensors resumed daily fluctuations, indicating snowmelt, and is given in four ranks, with "1" as the earliest and "4" as the latest (see fig. 32). Douglas-fir was the earliest and Cascade azalea the latest species to melt out on average.

^c Temperature correlations refers to the number of significant correlations out of a possible 65 annual, monthly, daily, and quarter-day temperature variables; positive numbers represent the number of positive correlations and negative numbers represent the number of negative correlations.

Table A2.14 — Mean canopy cover for select species on Olympic Mountain whitebark pine communities study plots (part 1 — plots 1 through 21)

[illegible]

Table A2.14—Mean canopy cover for select species on Olympic Mountain whitebark pine communities study plots (part 1—plots 1 through 21) (continued)

Species	Plot																				
	1	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
	PERCENT OF PLOT																				
Largeleaf sandwort	0	0.1	0	0.01	0.1	0	0.5	0.1	0	0.2	0	0	0	0	0	0.01	0	0	0.5	0.5	
Littleflower penstemon	0	1	0	2	1	0	2	0.5	0	0	0.01	0.1	0	0	1	0.01	0	2	1	2	
Mapleleaf currant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Oceanspray	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	
Olympic onion	0	0	0	2	1	0	0	2	0	0	0	0	0	1	0	0.5	0	2	2	0	
Orange agoseris	2	0.01	0.1	0.01	0.01	0	0.01	0.1	0	0	0	0.1	0.02	0	2	0.01	0	0.1	0.01	0	
Oregon boxleaf	0.1	0.5	0.01	0.1	1	1	2	0	3	0.1	0	0	0.2	0.01	0	0.2	0	0.2	0.2	0.02	
Parry's rush	5	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	
Prickly currant	0	0	0	0	0	0	0	0	2	0	0	0	0.2	0	0	0	0	0	0	0	
Rocky Mountain goldenrod	5	0	0.1	3	1	0	0	0	0	0	0.1	0.1	0	0	3	0	5	0	1	0.5	
Roemer's fescue	15	2	0.5	0	1	0	0.5	1	0	0	0.1	5	1	0.1	10	0.02	0.1	0.5	0.5	1	
Shore pine	0	7	0	0	0	0	4	0	0	5	0	0	0	0	0	0	0	0	0	2	
Siberian springbeauty	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Sitka valerian	0.5	0.1	0	0	1	0.05	1	0	0.5	0	0.1	0.1	0.01	0.01	0	0.01	0	0	0	0.01	
Spreading phlox	3	10	10	4	10	0.05	15	25	0.5	0	10	10	5	3	2	3	0	15	8	5	
Subalpine fir	20	30	0	30	20	10	15	0	7	75	0	10	10	10	15	80	0.3	0	0	15	
Sweetcicely	1	0	0	0.01	0.1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	
Thinleaf huckleberry	0	0.1	0	0	0	0	4	0	1	0	0	0.5	0	0	0	0	0	0	0	0	
Western brackenfern	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Western columbine	0	0	0	0	0.5	0	0	0	4	0	0	0.1	0	0	0	0	0	0.1	0	0	
Western white pine	0	2	3	0	0	0	7	0	0	0	0	0.5	4	5	3	0	0	0	0	20	
White hawkweed	0	0.5	0	0.1	0.3	0	0.1	0.1	0	0.01	0	0.01	0	0.01	0.1	0.01	0	0	0	0.01	
White sagebrush	0	0	5	0.1	0.5	0.05	0.1	9	0.1	0	0	0	7	2	3	0	0	0.1	1	0.5	
Whitebark pine	30	4	12	30	15	0	10	5	0	5	2	20	10	5	8	0.2	3	10	15	2	
Woolly pussytoes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	

Table A2.14—Mean canopy cover for select species by USDA PLANTS database symbol on Olympic Mountain Whitebark Pine Communities plots (part 2—plots 22 through 41)

Species	Plot																			
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
	PERCENT OF PLOT																			
Alaska cedar	0	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American rockbrake	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American trailplant	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0
American vetch	3	5	0.7	0.5	1	0	0	0	0	0	0	0	0	0.2	0	0	2	0	0	0
Black alpine sedge	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Blue wildrye	0	0.5	0	0	0.01	0	0	0	0	0	0	0	0.7	0	0	0	0	0	1	0
Bluebell bellflower	0	0	0.1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
Broadleaf lupine	8	0	0	0	15	2	3	4	5	10	0.1	0	0	0.2	0.2	0.2	0	0.5	0	0.1
Cascade azalea	0	0	0	0	0	95	0	0	0	0	25	25	1	0.1	45	0	0	0	0	0
Cascade barberry	0.1	7	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Cascade desertparsley	0.1	0.01	0	0.02	5	0	0	0.1	0	0.02	0	0	0	0	0	0.02	0.1	2	0.5	0
Cliff dwarf-primrose	0	0	0	0	0	0	0.5	0.05	0.5	2	0	0	0	0.5	0	0.5	0	0	0	0
Common juniper	0	0.5	3	0	10	0	4	25	3	1	0	0	0	0.5	0	10	15	45	5	0
Common snowberry	4	8	0	0	0.1	0.5	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0
Common yarrow	0.1	0	1	0.5	0.1	0	1	0.1	2	1	0	0	0	0.05	0.01	0.5	1	0.1	1	0
Currant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cusick's speedwell	0	0	0	0	0	0	0.01	0.1	0	0.5	0	0	0	0	0.05	0	0	0	0	0
Douglas-fir	30	85	0.1	0.2	20	0	0	0	0	0	0	0	0	8	0	15	0	3	0	0
Dwarf rose	5	8	0	0.1	0.2	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
Giant red Indian paintbrush	0.01	0	0.01	0.01	0.01	0	3	0.3	0.5	0.5	0	0	0	0.1	0	0	0.5	0.1	0.5	0
Green alder	0	10	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0
Harsh Indian paintbrush	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heartleaf arnica	0	0.01	0	0	0	0	0.1	0.1	5	1	0.1	5	5	0.1	10	0.1	0	0.2	0	0
Hookedspur violet	0	0	0.01	0.1	0.01	0	0.1	0.1	0.1	0.2	0	0	0	0.01	0	0.01	0.01	0	0.1	0
Kinnikinnick	3	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Largeleaf sandwort	0.5	3	0	0	3	0	0	0	0	0	0	0	20	0	0	0	0	0.5	0	2

Table A2.14—Mean canopy cover for select species by USDA PLANTS database symbol on Olympic Mountain Whitebark Pine Communities plots (part 2—plots 22 through 41) (continued)

Species	Plot																			
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
	PERCENT OF PLOT																			
Littleflower penstemon	0	0	0.05	2	0	0	3	2	5	5	0	0	0	0	0	0.1	1	2	0	0
Mapleleaf currant	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Oceanspray	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Olympic onion	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orange agoseris	0.01	0	0.01	0.01	0.01	0	0	0.01	0	0	0	0	0	0	0	0.01	0.01	0.01	0.01	0
Oregon boxleaf	0.1	0.1	0	0	0.01	0	0	0	0	0	0	0	0.01	0.1	0	0.1	3	1	0	0.2
Parry's rush	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prickly currant	0	0.1	0	0	0.1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rocky Mountain goldenrod	0	0	1	0	0.1	0	2	0.1	2	0	0	0	0	0.1	0	0.2	3	0.5	0	0
Roemer's fescue	0	0	0.5	1	0.02	0	6	32	3	2	0	0	0	0.2	0	0.01	3	0.5	1	0
Shore pine	7	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	8
Siberian springbeauty	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	0	0	0	0	0
Sitka valerian	0	0	0	0	0	40	0	0	0	0	3	3	25	0	30	0	0	0	0	0.01
Spreading phlox	0.5	0	2	25	10	0	9	25	30	12	0	0	0	1	0.05	2	5	4	2	0
Subalpine fir	0.1	22	0	0	14	50	4	9	30	25	75	85	35	20	55	4	1	5	0	80
Sweetcicely	0.01	5	0	0	2	0	0	0	0	0	0	0	1	0	0	0.1	0	0.2	0	0
Thinleaf huckleberry	0	0	0	0	0.2	6	0	0	0	0	0.05	0.5	0.01	0	5	0	0	0	0	0.01
Western brackenfern	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45	0
Western columbine	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Western white pine	1	0	0	1	5	0.1	0	0	0	0	0.2	0	0	0	0	0	0	4	0	0
White hawkweed	0.5	0.1	0	0	0.5	0	0	0	0	0	0.01	0.01	0	0	0	0.05	0.1	0.2	0.1	0.02
White sagebrush	0.1	0	0.7	1	0.02	0	0	0	0	0	0	0	0	0.05	0	0	0.5	0	4	0
Whitebark pine	0	0	3	1	1	0.1	10	15	0.1	4	0.5	0	0	0	2	25	25	25	0.1	0
Woolly pussytoes	0	0	0	0	0	0	0	0	0	2	0	0	0	0.2	0	0	0	0.1	0	0

Note: Plot 2 documented a single, large krummholz (i.e., stunted, twisted growth form of trees near the alpine tree line) whitebark pine tree.

Table A2.15—Plant associations or community types and white pine blister rust statistics for Olympic Mountain whitebark pine communities study plots

Plot	Plant association or community type	Whitebark pine trees, 2010 ^a	Mean tree diameter at breast height, 2010 ^b	Mean infected tree diameter at breast height, 2010 ^b	Infected clumps, 2010 ^a	Infected stems, 2010 ^a	Mean infection severity code, 2010 ^b	Mean dead crown, 2013 ^c	Mean dying crown, 2013 ^c	Mean infected stems, 2010–2016 ^d	Mean infection severity code, 2010–2016 ^d
		NUMBER	CENTIMETERS	CENTIMETERS	NUMBER	NUMBER	PERCENT	PERCENT	NUMBER	NUMBER	
1	Subalpine fir/broadleaf lupine	15	15.9	30.7	3	3	3.3	53.0	4.0	5	3.5
3	Subalpine fir/broadleaf lupine	54	4.3	8.4	17	19	3.3	39.6	20.0	12	2.9
4	Spreading phlox	27	5.6	8.1	9	4	3.3	37.5	0.0	3	3.1
5	Subalpine fir/common juniper	85	5.7	6.6	69	19	1.4	35.8	27.0	20	2.2
6	Subalpine fir/broadleaf lupine	6	30.1	38.9	2	2	1.0	52.5	10.0	3	2.7
7	Talus	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	Subalpine fir/thinleaf huckleberry	19	7.1	11.6	3	3	3.0	38.2	0.4	4	3.0
9	Spreading phlox	7	7.1	9.9	5	3	1.7	50.0	0.0	2	2.9
10	Talus	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
11	Subalpine fir/broadleaf lupine	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
12	Spreading phlox	7	5.1	5.4	2	5	1.0	NA	NA	2	0.3
13	Subalpine fir/broadleaf lupine	20	8.7	9.6	5	5	1.0	64.3	66.7	4	2.1
14	Subalpine fir/common juniper	6	13.2	13.2	6	6	2.2	43.4	25.0	9	2.7
15	Subalpine fir/common juniper	9	5.6	5.0	2	2	3.0	NA	NA	1	1.0
16	Subalpine fir/blue wildrye	8	13.2	11.8	2	2	1.5	95.0	50.0	1	2.5
17	Subalpine fir/broadleaf lupine	2	12.4	19.8	2	2	3.0	NA	NA	1	1.0
18	Black alpine sedge	5	2.5	NA	0	0	0.0	NA	NA	0	0.3
19	Spreading phlox	25	6.4	NA	0	0	0.0	NA	NA	0	0.3
20	Spreading phlox	19	9.9	14.4	2	2	2.0	36.0	1.0	2	3.0

Table A2.15—Plant associations or community types and white pine blister rust statistics for Olympic Mountain whitebark pine communities study plots (continued)

Plot	Plant association or community type	Whitebark pine trees, 2010 ^a	Mean tree diameter at breast height, 2010 ^b	Mean infected tree diameter at breast height, 2010 ^b	Infected clumps, 2010 ^a	Infected stems, 2010 ^a	Mean infection severity code, 2010 ^b	Mean dead crown, 2013 ^c	Mean dying crown, 2013 ^c	Mean infected stems, 2010–2016 ^d	Mean infection severity code, 2010–2016 ^d
		NUMBER	CENTIMETERS	CENTIMETERS	NUMBER	NUMBER	PERCENT	PERCENT	NUMBER	NUMBER	
21	Subalpine fir/common juniper	4	6.7	6.2	1	1	3.0	NA	NA	1	1.0
22	Douglas-fir/oceanspray-dwarf rose	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
23	Western hemlock/Cascade barberry	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
24	Spreading phlox	4	9.7	NA	0	0	0.0	NA	NA	0	0.3
25	Spreading phlox	6	6.2	NA	0	0	0.0	2.5	2.5	1	1.0
26	Subalpine fir/broadleaf lupine	4	2.8	NA	0	0	0.0	2.5	12.5	1	2.0
27	Subalpine fir/Cascade azalea	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
28	Subalpine fir/common juniper	37	3.0	NA	0	0	0.0	NA	NA	0	0.0
29	Subalpine fir/common juniper	23	4.1	NA	0	0	0.0	100.0	NA	1	2.0
30	Subalpine fir/krummholz	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
31	Subalpine fir/broadleaf lupine	9	3.0	NA	0	0	0.0	90.0	30.0	1	2.0
32	Subalpine fir/Cascade azalea	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
33	Subalpine fir/Cascade azalea	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
34	Subalpine fir/Sitka valerian	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
35	Subalpine fir/krummholz	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
36	Subalpine fir/Cascade azalea	2	5.3	NA	0	0	0.0	NA	NA	0	0.0
37	Subalpine fir/common juniper	31	9.0	5.6	2	2	2.5	70.0	1.0	3	3.2
38	Spreading phlox	32	7.6	25.2	1	1	1.0	27.5	37.5	3	2.5

Table A2.15—Plant associations or community types and white pine blister rust statistics for Olympic Mountain whitebark pine communities study plots (continued)

Plot	Plant association or community type	Whitebark pine trees, 2010 ^a	Mean tree diameter at breast height, 2010 ^b	Mean infected tree diameter at breast height, 2010 ^b	Infected clumps, 2010 ^a	Infected stems, 2010 ^a	Mean infection severity code, 2010 ^b	Mean dead crown, 2013 ^c	Mean dying crown, 2013 ^c	Mean infected stems, 2010–2016 ^d	Mean infection severity code, 2010–2016 ^d
		NUMBER	CENTIMETERS	CENTIMETERS	NUMBER	NUMBER	PERCENT	PERCENT	PERCENT	NUMBER	NUMBER
39	Subalpine fir/common juniper	45	6.0	6.3	3	4	3.0	17.7	22.0	11	2.7
40	Western brackenfern	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
41	Subalpine fir/thinleaf huckleberry	0	NA	NA	NA	NA	NA	NA	NA	NA	NA

NA = not applicable.

Note: See text for discussion of stems versus clumps and rust severity classification.

^a Whitebark pine tree, infected clump, and infected stem data are total numbers on each plot in 2010.^b Mean tree diameter at breast height, mean infected tree diameter at breast height, and mean infection severity code are plot averages and include only infected whitebark pine trees.^c These data are mean estimates of the amount of individual tree crowns that were either dead or dying for the infected trees on the plot in 2013.^d These data are plot averages over the years 2010, 2013, and 2016.

Table A2.16—Mean seasonal air and 20-cm-deep soil temperatures and standard deviations (SD) associated with the plot occurrences of 73 plant species in the Olympic Mountain whitebark pine communities study

Species	Air JJA			Soil JJA			Air DJF			Soil DJF			Air		Soil		
	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Rank	n ^a	Rank	n ^a	n ^a
Alpine smelowskia	9.92 (0.78)	68		13.03 (1.80)	20		-3.00 (0.74)	67		-0.55 (0.59)	71		71	5	3		
American vetch	10.79 (0.61)	16		13.47 (2.13)	13		-2.04 (0.72)	11		0.10 (0.77)	24		24	10	7		
Shore pine	11.21 (0.35)	2		12.04 (4.23)	48		-1.82 (0.54)	6		0.60 (0.25)	4		4	7	4		
Bluebell bellflower	10.65 (0.64)	24		12.70 (2.94)	29		-2.34 (0.61)	29		0.11 (0.58)	21		21	10	7		
Broadleaf lupine	10.43 (0.80)	41		11.40 (3.44)	57		-2.57 (0.79)	44		-0.13 (0.93)	50		50	22	16		
Cascade azalea	10.17 (0.49)	57		10.36 (3.40)	63		-2.92 (0.66)	62		-0.55 (0.69)	70		70	4	3		
Cascade barberry	11.21 (0.36)	3		12.16 (4.12)	44		-1.57 (0.56)	3		0.58 (0.24)	5		5	6	4		
Cascade desertparsley	10.64 (0.74)	26		12.76 (3.25)	27		-2.23 (0.77)	21		0.29 (0.45)	16		16	18	13		
Cascade wallflower	10.39 (0.53)	45		12.25 (2.40)	42		-2.54 (0.58)	43		-0.38 (1.1)	60		60	13	10		
Cliff dwarf-primrose	9.85 (0.69)	69		12.17 (2.14)	43		-3.16 (0.57)	70		-0.52 (0.51)	69		69	9	6		
Columbia lily	10.95 (0.51)	8		14.38 (2.95)	4		-2.02 (0.50)	9		0.38 (0.34)	12		12	5	4		
Common alplily	9.80 (0.79)	70		13.24 (1.71)	17		-3.08 (0.65)	68		-0.47 (0.40)	65		65	6	4		
Common juniper	10.37 (0.76)	46		12.46 (2.93)	35		-2.53 (0.78)	42		0.03 (0.58)	34		34	23	17		
Common snowberry	10.92 (0.58)	11		11.24 (3.21)	58		-1.81 (0.89)	4		0.57 (0.38)	6		6	6	5		
Common woodrush	10.61 (0.87)	28		13.81 (3.33)	8		-2.33 (0.92)	28		-0.05 (0.67)	42		42	4	4		
Common yarrow	10.42 (0.81)	43		13.08 (2.80)	19		-2.52 (0.79)	40		0.04 (0.62)	30		30	22	16		
Cusick's speedwell	9.68 (0.40)	73		10.03 (0.92)	66		-3.27 (0.44)	73		-0.11 (0.25)	46		46	5	4		
Davidson's penstemon	10.65 (0.64)	25		15.03 (1.18)	1		-2.36 (0.65)	31		-0.22 (0.67)	54		54	7	5		
Douglas' catchfly	10.59 (0.67)	32		13.87 (1.86)	7		-2.43 (0.60)	36		-0.05 (0.72)	41		41	11	9		
Douglas-fir	10.81 (0.69)	13		14.19 (2.33)	5		-2.08 (0.75)	13		0.07 (0.81)	28		28	12	8		
Dwarf rose	11.11 (0.35)	4		12.62 (3.32)	31		-1.47 (0.41)	2		0.68 (0.41)	1		1	5	3		
Evergreen violet	10.73 (0.51)	18		11.13 (4.43)	59		-2.21 (0.30)	20		0.15 (0.41)	19		19	6	5		
Fireweed	10.08 (0.54)	59		12.44 (2.64)	38		-2.86 (0.54)	57		-0.47 (1.36)	67		67	8	6		
Giant red Indian paintbrush	10.45 (0.83)	39		13.47 (2.38)	14		-2.49 (0.82)	37		0.04 (0.64)	31		31	20	15		
Heartleaf arnica	10.07 (0.74)	61		9.91 (2.40)	69		-2.88 (0.80)	59		-0.19 (0.56)	52		52	13	8		
Hookedspur violet	10.27 (0.78)	52		12.80 (2.64)	26		-2.63 (0.78)	49		-0.03 (0.64)	40		40	18	13		

Table A2.16—Mean seasonal air and 20-cm-deep soil temperatures and standard deviations (SD) associated with the plot occurrences of 73 plant species in the Olympic Mountain whitebark pine communities study (continued)

Species	Air JJA			Soil JJA			Air DJF			Soil DJF			Air		Soil		
	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Rank	n ^a	Rank	n ^a	n ^a
Jacob's-ladder	10.00 (0.80)	63		10.00 (3.61)	67		-2.87 (0.78)	58		-1.32 (1.5)	73		73	5	3		3
Kinnikinnick	11.36 (0.24)	1		13.55 (3.70)	12		-1.44 (0.52)	1		0.67 (0.21)	2		2	5	3		3
Largeleaf sandwort	10.94 (0.52)	10		11.94 (3.70)	52		-1.91 (0.56)	7		0.46 (0.35)	9		9	13	10		10
Littleflower penstemon	10.34 (0.79)	48		12.45 (2.96)	36		-2.58 (0.77)	45		0.08 (0.51)	27		27	19	12		12
Littleleaf pussytoes	10.49 (0.70)	36		13.46 (2.27)	15		-2.33 (0.79)	27		0.03 (0.45)	33		33	4	3		3
Mountain owl's-clover	10.67 (0.71)	21		13.19 (2.31)	18		-2.29 (0.69)	26		0.23 (0.51)	17		17	8	7		7
Nodding onion	10.99 (0.50)	6		14.63 (1.53)	2		-2.03 (0.68)	10		0.66 (0.41)	3		3	5	3		3
Olympic onion	10.49 (0.50)	37		12.57 (3.54)	32		-2.24 (0.41)	22		0.34 (0.33)	14		14	6	6		6
Orange agoseris	10.61 (0.72)	31		13.38 (3.04)	16		-2.35 (0.69)	30		0.30 (0.43)	15		15	16	12		12
Oregon boxleaf	10.81 (0.55)	15		11.98 (3.44)	50		-2.12 (0.60)	15		-0.02 (1.04)	38		38	18	13		13
Pacific anemone	10.01 (0.77)	62		12.52 (2.78)	34		-2.96 (0.76)	66		-0.43 (0.58)	64		64	8	6		6
Pacific lupine	10.23 (0.53)	55		12.75 (2.10)	28		-2.78 (0.47)	54		-0.49 (0.53)	68		68	8	6		6
Pacific stonecrop	10.61 (0.62)	30		12.40 (2.96)	39		-2.38 (0.63)	32		-0.39 (1.26)	61		61	8	7		7
Pale agoseris	9.97 (0.61)	65		11.63 (2.13)	54		-2.93 (0.66)	63		-0.40 (0.53)	62		62	10	7		7
Parry's silene	10.39 (0.75)	44		11.80 (3.63)	53		-2.81 (0.67)	55		0.01 (0.24)	35		35	6	4		4
Raceme pussytoes	10.33 (0.65)	49		9.69 (1.90)	70		-2.65 (0.71)	51		-0.07 (0.25)	43		43	9	5		5
Red fescue	10.46 (0.66)	38		12.44 (3.56)	37		-2.58 (0.57)	46		-0.16 (0.57)	51		51	5	4		4
Rocky Mountain goldenrod	10.29 (0.77)	51		12.56 (2.73)	33		-2.67 (0.72)	52		-0.21 (0.57)	53		53	16	10		10
Roemer's fescue	10.30 (0.76)	50		12.38 (2.74)	40		-2.62 (0.74)	48		-0.02 (0.59)	39		39	21	15		15
Ross' sedge	10.91 (0.63)	12		13.75 (3.10)	9		-2.09 (0.80)	14		0.41 (0.37)	11		11	9	7		7
Rosy pussytoes	10.61 (0.58)	29		13.74 (2.83)	10		-2.29 (0.37)	25		0.00 (0.74)	37		37	5	4		4
Roughfruit berry	10.58 (0.44)	33		8.10 (1.01)	73		-2.40 (0.60)	33		0.13 (0.65)	20		20	4	3		3
Saskatoon serviceberry	11.04 (0.43)	5		12.02 (2.97)	49		-1.82 (0.60)	5		0.53 (0.45)	8		8	8	4		4
Sickletop lousewort	10.10 (0.81)	58		10.06 (2.87)	65		-2.90 (0.78)	60		0.03 (0.44)	32		32	12	8		8
Sidebells wintergreen	10.62 (0.55)	27		9.46 (2.73)	71		-2.21 (0.63)	19		0.09 (0.78)	26		26	7	5		5
Silverleaf phacelia	10.65 (0.28)	23		14.11 (1.27)	6		-2.05 (0.28)	12		0.56 (0.32)	7		7	4	4		4

Table A2.16—Mean seasonal air and 20-cm-deep soil temperatures and standard deviations (SD) associated with the plot occurrences of 73 plant species in the Olympic Mountain whitebark pine communities study (continued)

Species	Air JJA			Soil JJA			Air DJF			Soil DJF			Air		Soil		
	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Mean (SD)	Rank	DEGREES CELSIUS	Rank	n ^a	Rank	n ^a	n ^a
Sitka valerian	10.51 (0.64)	34		10.00 (3.11)	68		-2.40 (0.69)	34		-0.40 (1.13)	63		63	11	8		
Slender cinquefoil	10.07 (0.72)	60		13.00 (1.81)	23		-2.92 (0.66)	61		-0.34 (0.53)	57		57	9	6		
Slender hawkweed	9.96 (1.05)	67		11.48 (2.96)	56		-3.11 (0.77)	69		-0.23 (0.26)	55		55	6	3		
Slender mountain Sandwort	10.18 (0.91)	56		12.08 (3.68)	46		-2.84 (0.78)	56		0.00 (0.32)	36		36	10	6		
Spearleaf stonecrop	9.96 (0.77)	66		12.12 (2.03)	45		-2.94 (0.82)	65		-0.24 (0.56)	56		56	10	6		
Spike trisetum	10.51 (0.93)	35		11.13 (2.93)	60		-2.50 (1.01)	39		0.20 (0.39)	18		18	8	5		
Spiked woodrush	9.98 (0.89)	64		10.75 (3.58)	62		-2.94 (0.71)	64		-0.12 (0.22)	48		48	7	3		
Spreading phlox	10.42 (0.79)	42		12.82 (2.90)	24		-2.52 (0.77)	41		-0.13 (0.94)	49		49	23	17		
Squirreltail	10.25 (0.70)	54		12.81 (2.17)	25		-2.76 (0.64)	53		-0.08 (0.64)	44		44	15	12		
Subalpine fir	10.45 (0.79)	40		10.81 (3.34)	61		-2.49 (0.84)	38		-0.12 (0.95)	47		47	23	15		
Sweetcicely	10.94 (0.57)	9		13.03 (3.84)	22		-1.99 (0.78)	8		0.42 (0.39)	10		10	6	4		
Tahoe sedge	9.72 (0.63)	71		12.28 (1.80)	41		-3.21 (0.65)	71		-0.37 (0.66)	59		59	5	4		
Thinleaf huckleberry	10.67 (0.67)	22		10.17 (3.91)	64		-2.42 (0.81)	35		0.11 (0.50)	22		22	6	4		
Utah honeysuckle	10.25 (0.51)	53		9.18 (3.34)	72		-2.65 (0.55)	50		-0.35 (0.70)	58		58	5	4		
Western meadow-rue	10.67 (0.80)	20		14.52 (0.96)	3		-2.26 (0.71)	23		0.09 (0.45)	25		25	4	4		
Western mountain ash	10.81 (0.58)	14		11.94 (4.35)	51		-2.27 (0.66)	24		-0.47 (1.25)	66		66	6	6		
Western white pine	10.98 (0.68)	7		12.63 (3.88)	30		-2.17 (0.88)	17		0.11 (0.63)	23		23	8	5		
White hawkweed	10.77 (0.58)	17		11.57 (3.83)	55		-2.16 (0.71)	16		0.34 (0.42)	13		13	17	12		
White sagebrush	10.72 (0.57)	19		13.72 (2.46)	11		-2.18 (0.58)	18		-0.11 (1.12)	45		45	13	11		
Whitebark pine	10.36 (0.75)	47		12.05 (3.17)	47		-2.58 (0.73)	47		0.07 (0.51)	29		29	23	17		
Yellowdot saxifrage	9.70 (0.64)	72		13.03 (1.80)	21		-3.25 (0.48)	72		-0.55 (0.59)	72		72	6	3		

DJF = December, January, February; JJA = June, July, August.

Note: The mean monthly temperature was first calculated for each plot on which the species was present. Then the average and standard deviation of the mean monthly plot temperatures over all the plots on which the species was present was calculated. Then, each of the three monthly means and standard deviations were averaged. Rank is the order from warmest to coldest (1 is the species associated with the highest mean plot temperature, and 73 is the species associated with the lowest mean plot temperature).

^a Number of plots on which each species was found and used in calculating mean temperatures.

Table A2.17—Species canopy cover composition for each plant association or community type in the Olympic Mountain whitebark pine communities study (part 1—means for types that had more than one plot)

Species	Plant association or community type					
	Subalpine fir/common juniper (n = 8)	Subalpine fir/broadleaf lupine (n = 8)	Subalpine fir/Cascade azalea (n = 4)	Subalpine fir/thinleaf huckleberry (n = 2)	Subalpine fir/krummholz (n = 2)	Spreading phlox (n = 8)
	PERCENT OF PLANT ASSOCIATION OR COMMUNITY TYPE					
Alaska cedar	0.00	0.00	0.00	0.00	0.00	0.00
Black alpine sedge	0.00	0.25	0.00	0.00	0.50	0.00
Blue wildrye	0.00	0.00	0.00	0.00	0.00	0.00
Broadleaf lupine	1.65	15.25	0.58	0.20	2.60	0.64
Cascade azalea	0.00	0.03	47.50	0.00	0.05	0.00
Cascade barberry	0.03	1.13	0.00	0.00	0.00	0.00
Cascade desertparsley	1.34	1.42	0.00	0.50	0.00	0.90
Cliff dwarf-primrose	0.14	0.25	0.00	0.00	0.50	0.10
Common alplily	0.00	0.00	0.00	0.00	0.05	0.08
Common juniper	14.88	2.14	0.00	3.50	1.75	10.26
Common yarrow	0.36	0.63	0.00	0.25	1.03	0.68
Douglas-fir	3.50	4.38	0.00	1.50	4.00	0.18
Dwarf rose	0.03	0.03	0.00	0.00	0.00	0.04
Giant red Indian paintbrush	0.50	0.19	0.00	0.25	0.30	0.11
Green alder	0.00	0.00	0.00	0.00	0.00	0.00
Harsh Indian paintbrush	0.00	0.01	0.00	0.00	0.00	0.26
Hookedspur violet	0.03	0.42	0.00	0.03	0.06	0.08
Littleflower penstemon	1.39	0.89	0.00	1.00	2.50	0.82
Oceanspray	0.01	0.00	0.00	5.01	0.00	0.00
Orange agoseris	0.01	0.27	0.00	0.01	0.00	0.04
Oregon boxleaf	0.18	0.24	0.00	1.10	0.05	0.43
Pale agoseris	0.15	0.04	0.00	0.00	0.01	0.01
Roemer's fescue	5.08	3.13	0.00	0.25	1.60	0.89
Shore pine	0.28	2.75	0.00	6.00	0.00	0.00
Sitka valerian	0.00	0.21	19.00	0.51	0.00	0.01
Spreading phlox	7.13	7.25	0.01	7.50	15.50	12.5
Subalpine fir	10.88	34.25	66.25	47.50	25.00	0.13
Thinleaf huckleberry	0.00	0.10	2.89	2.01	0.00	0.00
Western brackenfern	0.00	0.00	0.00	0.00	0.00	0.00
Western white pine	4.13	0.94	0.08	3.50	0.00	0.50
White hawkweed	0.05	0.17	0.01	0.06	0.00	0.03
White sagebrush	1.20	0.07	0.00	0.05	0.03	2.16
Whitebark pine	15.25	9.90	0.65	5.00	0.05	9.13

Table A2.17—Species canopy cover composition for each plant association or community type in the Olympic Mountain whitebark pine communities study (part 2—values for types represented by a single plot)

Species	Plant association or community type							
	Douglas-fir/ oceanspray- dwarf rose	Douglas-fir/ cascade barberry	Subalpine fir/green alder	Subalpine fir/blue wildrye	Western brackenfern	Black alpine sedge	Talus plot 7	Talus plot 10
	PERCENT OF PLANT ASSOCIATION OR COMMUNITY TYPE							
Alaska cedar	0	40	0	0	0	0	0	7
Black alpine sedge	0	0	0	0	0	15	0	0
Blue wildrye	0	0.5	0.7	25	1	0	0	0
Broadleaf lupine	8	0	0	1	0	0.01	0.1	3
Cascade azalea	0	0	1	0	0	0	0	2
Cascade barberry	0.1	7	0	0	0	0	0	0
Cascade desertparsley	0.1	0.01	0	0.1	0.5	0.01	0	0.1
Cliff dwarf-primrose	0	0	0	0	0	0	0	0
Common alplily	0	0	0	0	0	0	0	0
Common juniper	0	0.5	0	2	5	0.1	0	0
Common yarrow	0.1	0	0	8	1	0	0	0
Douglas-fir	30	85	0	3	0	0	0	0
Dwarf rose	5	8	0	0	0	0	0	0
Giant red Indian paintbrush	0.01	0	0	2	0.5	0	0	0.1
Green alder	0	10	20	0	0	0	0	15
Harsh Indian paintbrush	0	0	0	0	0	0	0	0
Hookedspur violet	0	0	0	1	0.1	0	0	0
Littleflower penstemon	0	0	0	1	0	0	0	0
Oceanspray	0.2	0	0	0	0	0	0	0
Orange agoseris	0.01	0	0	2	0.01	0	0	0
Oregon boxleaf	0.1	0.1	0.01	0	0	0	1	3
Pale agoseris	0	0	0	0	0	0.01	0	0
Roemer's fescue	0	0	0	10	1	0.1	0	0
Shore pine	7	0	0	0	0	0	0	0
Sitka valerian	0	0	25	0	0	0	0.05	0.5
Spreading phlox	0.5	0	0	2	2	0	0.05	0.5
Subalpine fir	0.1	22	35	15	0	0.3	10	7
Thinleaf huckleberry	0	0	0.01	0	0	0	0	1
Western brackenfern	0	0	0	0	45	0	0	0
Western white pine	1	0	0	3	0	0	0	0
White hawkweed	0.5	0.1	0	0.1	0.1	0	0	0
White sagebrush	0.1	0	0	3	4	0	0.05	0.1
Whitebark pine	0	0	0	8	0.1	3	0	0

Table A2.18 —Site characteristics for each plant association or community type in the Olympic Mountain whitebark pine communities study (part 1 —means for types that had more than one plot)

Variable	Plant association or community type					
	Subalpine fir/ common juniper (n = 8)	Subalpine fir/ broadleaf lupine (n = 8)	Subalpine fir/ Cascade azalea (n = 4)	Subalpine fir/thinleaf huckleberry (n = 2)	Subalpine fir/ krummholz (n = 2)	Spreading phlox (n = 8)
Elevation (m)	1698	1707	1578	1547	1818	1712
Aspect (deviation in degrees from 22° NNE)	129	116	51	157	117	138
Slope steepness (percent)	58	56	55	43	44	65
Overstory canopy closure (percent)	29	50	66	60	29	10
Understory canopy closure (percent)	36	41	57	24	36	37
Sum of species canopy cover (percent)	76	104	147	93	67	52
Frost-free days	97	96	109	90	67	92
Snowpack duration (days)	162	145	181	164	139	130
Summer soil moisture (percent)	4.5	4.5	5.9	4.9	4.5	4.6
Organic horizon depth (cm)	1.2	1.9	2.9	2.4	1.3	0.6
PAR at 1.3-m height (percent)	1236.3	745.6	1001.0	1030.1	779.9	709.3
PAR at ground level (percent)	861.0	345.6	110.2	457.2	568.1	593.1
June through August mean 20-cm-deep soil temperature (°C)	12.4	10.5	8.2	11.2	12.3	13.7
December through February mean 20-cm-deep soil temperature (°C)	0.26	0.23	-0.2	0.5	-0.8	0.1
Mean annual air temperature (°C)	2.8	2.6	2.7	3.1	1.5	2.9
Mean annual soil surface temperature (°C)	4.7	3.9	—	—	—	5.1
Mean annual 20-cm-deep soil temperature (°C)	4.6	3.7	—	—	—	4.9
Maximum air temperature (°C)	27.5	27.6	27.3	28.5	26.1	27.2
Maximum soil surface temperature (°C)	51.56	50.07	26.83	—	47.25	52.42
Maximum 20-cm-deep soil temperature (°C)	21.63	18.72	13.67	18	24	23
Minimum air temperature (°C)	-20.06	-20.07	-18.67	-19	-21.25	-20.13
Minimum soil surface temperature (°C)	-7.94	-7.57	-6.17	—	-10.78	-10.17
Minimum 20-cm-deep soil temperature (°C)	-1.06	-1.33	-1.33	-0.25	-5.25	-2.75

Table A2.18 —Site characteristics for each plant association or community type discussed in the Olympic Mountain whitebark pine communities study (part 2—values for types that had only one plot)

Variable	Plant association or community type									
	Douglas fir/ oceanspray- dwarf rose	Douglas-fir/ cascade barberry	Subalpine fir/ green alder	Subalpine fir/ blue wildrye	Western brackenfern	Black alpine sedge	Talus plot 7	Talus plot 10		
Elevation (m)	1543	1420	1528	1632	1693	1741	1591	1685		
Aspect (deviation in degrees from 22° NNE)	176	154	61	108	166	107	120	112		
Slope steepness (percent)	58	52	41	66	63	10	49	57		
Overstory canopy closure (percent)	35	90	35	25	0.1	3	10	10		
Understory canopy closure (percent)	25	55	95	95	60	80	3	30		
Sum of species canopy cover (percent)	64	211	160	181	68	93	14	55		
Frost-free days	126	132	—	0	0	86	48	—		
Snowpack duration (days)	118	72	—	168	63	229	76	—		
Summer soil moisture (percent)	4.4	4.6	—	4.8	3.9	12.7	0	—		
Organic horizon depth (cm)	1.3	6.1	9.7	1.3	0	5.1	0.4	8.3		
PAR at 1.3-m height (percent)	1201.5	978.1	—	1098.9	1155.8	761.9	971.6	—		
PAR at ground level (percent)	471.6	15.2	—	420.4	991.0	678.6	919.4	—		
June through August mean 20-cm-deep soil temperature (°C)	15.7	9.3	—	10.5	15.3	9.1	8.8	—		
December through February mean 20-cm-deep soil temperature (°C)	0.9	0.6	—	—	0.5	0	-2.8	—		
Mean annual air temperature (°C)	4.1	3.9	—	—	—	2.3	2.6	—		
Mean annual soil surface temperature (°C)	—	4.1	—	—	6.5	0	0	—		
Mean annual 20-cm-deep soil temperature (°C)	6.7	4.1	—	—	6.5	3.0	1.4	—		
Maximum air temperature (°C)	27.5	25.5	—	25.5	—	25.5	27	—		
Maximum soil surface temperature (°C)	52.5	24	—	43	54	42.5	44.5	—		
Maximum 20-cm-deep soil temperature (°C)	25	14	—	16	25.5	18.5	23	—		
Minimum air temperature (°C)	-18.5	-17.5	—	-20.5	—	-20	-20	—		
Minimum soil surface temperature (°C)	-6.5	-8	—	-6	-14	-6.5	-16	—		
Minimum 20-cm-deep soil temperature (°C)	0	-1.5	—	-1.5	-1.5	-2	-14	—		

— = no or insufficient data to calculate a mean; NNE = north-northeast; PAR = photosynthetically active radiation (as a percentage of full sun).

Table A2.19—Global Positioning System coordinates for plots in the Olympic Mountain whitebark pine communities study

Plot	Latitude	Longitude	UTM y	UTM x
1	47.79597466	-123.1421539	5293633.218	489355.3378
2	47.79705870	-123.1385782	5293753.215	489623.3365
3	47.80738983	-123.1443355	5294902.225	489194.3289
4	47.81021292	-123.1421579	5295215.688	489357.9460
5	47.80891088	-123.1432103	5295071.122	489278.8854
6	47.80864044	-123.1373915	5295040.273	489714.4885
7	47.80645152	-123.1405805	5294797.422	489475.2873
8	47.80723205	-123.1416509	5294884.318	489395.2962
9	47.80790075	-123.1392309	5294958.309	489576.6233
10	47.80639610	-123.1383610	5294790.963	489641.4549
11	47.81034876	-123.1481600	5295231.628	488908.6115
12	47.81341739	-123.1381978	5295571.301	489655.0732
13	47.81174327	-123.1389650	5295385.339	489597.2992
14	47.81467999	-123.1423531	5295712.194	489344.2458
15	47.81423625	-123.1426094	5295662.912	489324.9730
16	47.81349696	-123.1424204	5295580.719	489338.9662
17	47.81978224	-123.1345510	5296278.224	489929.3204
18	47.81962600	-123.1373827	5296261.232	489717.3192
19	47.81809689	-123.1370180	5296091.235	489744.3177
20	47.81867951	-123.1388096	5296156.228	489610.3173
21	47.81796596	-123.1411188	5296077.235	489437.3192
22	47.81905134	-123.1438203	5296198.239	489235.3167
23	47.81853426	-123.1471719	5296141.242	488984.3209
24	47.81328936	-123.1394096	5295557.235	489564.3248
25	47.81422235	-123.1416562	5295661.235	489396.3248
26	47.81556027	-123.1438506	5295810.238	489232.3237
27	47.81626435	-123.1419824	5295888.233	489372.3197
28	47.81402974	-123.1371943	5295639.226	489730.3205
29	47.81343647	-123.1367786	5295573.234	489761.3215
30	47.81378532	-123.1353645	5295611.819	489867.2554
31	47.81118291	-123.1378479	5295322.910	489680.8244
32	47.81140142	-123.1454286	5295348.235	489113.3253
33	47.81228957	-123.1475014	5295447.240	488958.3264
34	47.81374450	-123.1452109	5295608.620	489130.1114
35	47.81035419	-123.1410179	5295231.232	489443.3243
37	47.80962966	-123.1387346	5295150.397	489614.1284
38	47.80971431	-123.1418443	5295160.228	489381.3248
39	47.80933327	-123.1435403	5295118.113	489254.2684
40	47.80864822	-123.1408231	5295041.601	489457.5634
41	47.80836617	-123.1478509	5295011.235	488931.3309

Note: Universal Transverse Mercator [UTM] coordinates are for zone 10.

Appendix 3: Plant Association or Community Type Discussion

Subalpine Fir (*Abies lasiocarpa*)/Broadleaf Lupine (*Lupinus latifolius*) Plant Association (ABLA/LULA4)

Henderson et al. (1989) describe this plant association as uncommon, occurring in high-elevation areas of low precipitation with low winter and high summer soil temperatures and low productivity. This plant association has thus far only been recognized in the Olympic Mountains (Henderson et al. 1989). As suggested by our ordinations, it was floristically and environmentally positioned between the subalpine fir/common juniper (*Juniperus communis*) plant association and the subalpine fir/Cascade azalea (*Rhododendron albiflorum*) plant association—a position also recognized by Henderson et al. (1989). Kuramoto and Bliss (1970) described a meadow community that was dominated by Roemer's fescue (*Festuca idahoensis* ssp. *roemerii*) and broadleaf lupine in the northeastern Olympic Mountains that was similar to vegetation in open areas of this type, although they were more heavily dominated by the fescue. They stated that tree invasion of fescue-dominated meadows occurs from forest edges, which was not the case with meadow openings associated with the subalpine fir/broadleaf lupine plant association. Fonda and Bliss (1969) describe an area near Hurricane Ridge that burned more than 70 years prior and recovered to a meadow that included Roemer's fescue and broadleaf lupine, which was slowly being reinvaded by subalpine fir. Although we found no evidence of fire in our study area, subalpine fir was invading a floristically similar community.

Nearly all this plant association appeared to be in a relatively early stage of succession. Successional interpretation is complicated by post-Little Ice Age ongoing climate change. In the lower elevation plots of this type where warm site species, such as Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), shore pine (*Pinus contorta* var. *contorta*), and Cascade barberry (*Mahonia nervosa*) were present, a transition to a different community type that might not be dominated by subalpine fir appeared to be underway. In upper elevation plots, a rapid conversion from nonforest subalpine meadows and alpine tundra to a subalpine fir-dominated community was underway.

Although tree ages in this plant association ranged from 8 to 221 years, few were >100 years old and most were <40 years old. Most plots had open overstory canopies of young trees, suggesting recent colonization, and have yet to experience canopy closure or stem exclusion. Ground-level vegetation was well developed in open areas and canopy gaps but depauperate wherever dense tree shade developed. Roemer's fescue, spreading phlox (*Phlox diffusa*), and common juniper were restricted to sunny openings. Broadleaf lupine grew in sunny areas but also tolerated smaller canopy gaps and light shade. Most of the ground-level species were heliophytes, and most were also present in the nonforest spreading phlox community type.

There were many subalpine fir and whitebark pine (*Pinus albicaulis*) tree seedlings, but there was also considerable mortality of whitebark pine seedlings, which was likely due to white pine blister rust infection. One species that was present on all plots in this type was sickletop lousewort (*Pedicularis racemosa*), which is an effective alternate host species for white pine blister rust (Mulvey and Hansen 2011), but several other known and potential alternate white pine blister rust host species were also present.

The young age of the trees, the floristic similarity to the predominant tundra community in the area, and the relatively low accumulation of dead trees and down wood suggested that the area now occupied by this type was a nonforest meadow or tundra community. However, there appeared to be no reason why relatively high levels of overstory canopy closure will not occur.

Whitebark pine was present and reproducing in most areas of this type, but given the mortality that we found both among large trees and seedlings and the presence of subalpine fir everywhere and generally in greater quantity, we predict that subalpine fir will eventually dominate to the exclusion of whitebark pine. Wherever this has already occurred, the ground-layer vegetation has disappeared and has mostly not been replaced. Temperature modeling suggested that only three of the eight plots might get cold enough to limit root growth as canopy closure increases (Körner and Paulsen 2004). However, one of these plots, an expanding tree island, has already achieved 80 percent canopy closure. This plot and one other were among the higher elevation plots in the study area.

Subalpine Fir/Common Juniper Plant Association (ABLA/JUCO6)

Plots in this plant association were open and on west-southwestern aspects. Henderson et al. (1989) describe this plant association as uncommon, occurring in high-elevation areas of low precipitation and dry topographic positions with high winter and summer soil temperatures and low productivity. It has not been described elsewhere (Henderson et al. 1989). Schreiner (1994) describes a nonforested community from the northeastern Olympic Mountains with about 15 percent common juniper and 4 percent spreading phlox. Our community had 15 percent common juniper and 7 percent spreading phlox, and Henderson et al. (1989) indicate 11 percent common juniper and 2 percent spreading phlox. Subalpine fir/common juniper plant association was environmentally and floristically intermediate between the subalpine fir/broadleaf lupine plant association and the spreading phlox community type in our ordination (see fig. 36).

Ground-level vegetation tended to be low and sparse, and closely resembled spreading phlox tundra. Plots in the subalpine fir/common juniper plant association appeared to be in an early stage of forest encroachment into the spreading phlox community type to which our ordination (fig. 36) indicated a close relation. The area represented by this plant association was most likely spreading phlox community type alpine tundra in the Little Ice Age, as all the trees that we found postdated 1850. Since the Little Ice Age ended around 1850, it has become warm enough to permit tree colonization, which accelerated sharply after 1960. Common juniper also appeared to respond positively to higher temperatures than spreading phlox. This tendency was indicated in several of our correlative analyses, so it too may be an increaser on this type. For example, common juniper consistently had more positive significant correlations to air, soil surface, and soil temperatures than did spreading phlox (fig. 26). Also, although both were positively correlated with soil temperatures in summer, common juniper was positively correlated in 3 to 4 months, and spreading phlox was positively correlated in only 1 to 2 months (see fig. 29). Common juniper also seemed to have the edge in drought tolerance over spreading phlox (see figs. 33 and 34). The differences were small, but our analyses suggested that slight differences in warmth and drought separate these two communities with detectable floristic consequences. Whitebark pine was frequently present in the subalpine fir/common juniper plant association. There was more of it than any other tree species, both in terms of numbers and cover, and it was reproducing. However,

it suffered from considerable mortality from white pine blister rust. All the dead seedlings, most of the larger dead trees, and all the identified downed woody debris were from whitebark pine, indicating the vulnerability of this species. Alternate host species for white pine blister rust were present on all plots, including giant red Indian paintbrush (*Castilleja miniata*) on all but one plot and sickletop lousewort on three of eight plots.

The openness of these plots likely derives from more than one factor. First, it is likely that this area was treeless in the Little Ice Age, as was suggested by the age of the trees that were present. Second, it was a harsh site, with rocky, droughty soils that attained high surficial temperatures in summer. Third, this was one of the plant associations on which solifluction occurred. This last point was especially hard to evaluate as evidence was not present on all plots, and the effects of further warming and tree establishment on this process is unknown.

Subalpine fir was common in this plant association, and in the seedling class, it outnumbered whitebark pine trees two to one. As it was reproducing successfully and was more shade tolerant than whitebark pine, we believe it will eventually dominate this community. An increasing overstory canopy will cool the soils, but from our estimates, we do not expect cooling to be enough to limit root growth in most cases, and in the few cases where it might, temperatures would not be root limiting until high percentages of canopy closure are attained. As soil surface temperatures as high as 58 °C were recorded in this type, developing shade may benefit tree seedling establishment, and in doing so, it may accelerate arboreal dominance. Thus, each new tree may accelerate the successional process by moderating surficial temperatures and permitting further tree establishment. We expect full canopy closure is possible over most of the area occupied by this plant association, assuming it is not prevented by solifluction. If high levels of closure are attained, we expect greatly altered understory composition because most of the former tundra and heliophytic species would be eliminated.

Subalpine Fir/Cascade Azalea Plant Association (ABLA/RHAL2)

Henderson et al. (1989) describe this plant association as minor but locally common in cold, dry sites, with low timber productivity. This plant association has been recognized on several national forests east of the Cascade Range crest (Lillybridge et al. 1995, Williams and Lillybridge 1983, Williams et al. 1995). Although this plant association is dry relative to the rest of the Olympic National Forest, within the context of our study area, it is relatively cool and moist. In our study area, it had the highest mean moisture and longest duration of the seasonal snowpack of any community type, aside from the black alpine sedge community, and the lowest June through August 20-cm-depth soil temperature of any community. A study of a similar Engelmann spruce (*Picea engelmannii*)-subalpine fir/Cascade azalea/western oakfern (*Gymnocarpium dryopteris*)-green false hellebore (*Veratrum viride*) plant association in British Columbia (Coates et al. 1991) failed to find significant moisture stress through the entire growing season. However, the presence of western oakfern and green false hellebore do suggest a moister site than ours.

The subalpine fir/Cascade azalea plant association was the most densely forested community in the area, but it had an age structure suggesting post-Little Ice Age tree invasion, as nearly all the trees were <100 years old, and there was no evidence of fire. Overstory was almost exclusively dominated by subalpine fir, and reproduction was nearly all subalpine fir. Successionally more advanced stands have entered the stem-exclusion stage (Oliver 1980). A few whitebark pine seedlings were present in canopy gaps, but no larger whitebark pines were present.

Virtually all the dead trees ≥ 1.3 m tall and all the coarse woody debris (CWD) came from subalpine fir, suggesting that it has dominated throughout succession. The understory mostly consisted of Cascade azalea, which was present mainly in areas of thin overstory or in canopy gaps. Wherever the overstory was dense, the understory was depauperate. On a per plot basis, the species richness was the lowest of any of the plant communities or associations we identified. Shade, cold soils, and competition from subalpine fir trees may be the causes. Another possible reason could be allelopathic inhibition of plants by Cascade azalea (del Moral and Cates 1971). We estimated that two of the three plots with temperature data would develop soils cold enough to inhibit root growth under a full overstory (Körner and Paulsen 2004). This suggests that the canopy of these stands may currently be close to the maximum density possible, and cold soils may be inhibiting species diversity. Although further closure may be limited, these stands already resembled forests more than parklands.

As the age structure strongly suggested a post-Little Ice Age tree invasion, it is interesting to consider the previous vegetation on these sites. Around the upper edge of these tree stands, there was usually a narrow, thick band of Cascade azalea with no overstory forming a transition between the forest below and late-melting snowbanks above. When these snowbanks melt, mostly barren ground was exposed. This suggests that much of the area of the subalpine fir/Cascade azalea plant association was snowfield at higher elevations with brush fields below. Because of favorable moisture relationships on these mostly northern aspects, once the snow was gone for a long enough season, subalpine fir rapidly invaded. Similar rapid arboreal succession did not occur on open southern and western aspects in the study area, apparently because of moisture limitations.

Subalpine Fir/Thinleaf Huckleberry (*Vaccinium membranaceum*) Plant Association (ABLA/VAME)

Henderson et al. (1989) describe this plant association as minor, occurring in cool, dry sites with low timber productivity. In the context of our study area, this was a plant association of relatively low elevations and warm aspects. This, or closely similar plant associations, are found east of the Cascade Range crest on the Okanogan-Wenatchee and Colville National Forests in Washington (Lillybridge et al. 1995, Williams and Lillybridge 1983, Williams et al. 1995). Although our two plots (plots 8 and 41) were among the lowest elevation plots and on warm aspects, the age structure suggested recent, post-Little Ice Age tree invasion. This area apparently had scattered trees at the end of the Little Ice Age but not forest. Whitebark pine was prominent in this community, but subalpine fir was clearly the dominant species, and we expect it to dominate to the exclusion of whitebark pine in the future, as it already had done on plot 41. In addition to subalpine fir and thinleaf huckleberry, there were also western white pine (*Pinus monticola*), small amounts of Douglas-fir, and shore pine present, reflecting the warm, lower elevations where this type occurred.

Subalpine fir seedlings far outnumbered whitebark pine seedlings, which suffered high levels of mortality. Although open plots, such as plot 8, had well-developed understory vegetation, dense overstories similar to those on plot 41 that are currently in the stem-exclusion stage (Oliver 1980) had almost completely suppressed the understory. It is not known how long the stem-exclusion stage will last, but although the June through August soil temperature (8 °C) was not so low as to prohibit root growth, low soil temperature may still be a factor, along with low light, in creating the depauperate understory. Our model estimated that the growing-season soil temperature on plot 41 could drop to root-growth-limiting levels with further closure.

However, the temperature sensor was already under full canopy closure, and the only further closure possible on the plot was a canopy gap near the edge of the plot. Thus, further canopy closure may not change the temperature at the sensor or in the rest of the stand. This interpretation seems likely considering the low elevation and west-southwestern aspect for this plot.

Douglas-Fir/Cascade Barberry Community Type (PSME/MANE2)

This unique plot (plot 23) was on a steep, west-southwestern aspect at the lowest elevation in our sample. Although we only had one plot in this community type, this kind of vegetation appeared to be common on similar slopes at this elevation. We are not aware that anything like it has been described in the literature, and we suggest that this is so because it is a community in climatic transition. Some of its uniqueness was due to its location near a hillside spring, alongside which much Alaska cedar (*Callitropsis nootkatensis*) was growing. However, even absent this portion of the plot, this community was unique in our sample. The drier parts of the plot keyed to the Douglas-fir/kinnikinnick (*Arctostaphylos uva-ursi*) plant association in Henderson et al. (1989) based on a patch of kinnikinnick in a canopy gap that appeared to be dying but then did not fit the description provided for that plant association (Henderson et al. 1989). For example, it had 22 percent canopy cover of subalpine fir, and even in the less-wet area of the northwestern part of the plot, the vegetation was too lush for this type. If western hemlock (*Tsuga heterophylla*) was present, it would fit the western hemlock/Cascade barberry plant association somewhat better (Henderson et al. 1989). Western hemlock was rare in the study area, but we saw it occasionally, including at a site above plot 21, which was upslope from this plot. It was common along the Dungeness River below the study area.

We believe that this plot was transitioning from a Little Ice Age parkland that included both subalpine fir and Douglas-fir to a more typical montane forest that may include western hemlock at such time as it is able to disperse to this area. Existence of few snags and a low amount of CWD supported a recent occupancy by forest. It is perhaps not a coincidence that the oldest tree on the plot was a subalpine fir that dated to the latter years of the Little Ice Age. The age structure of the plot suggested infilling of a Little Ice Age parkland and thus conversion to the forest currently present. Most of the infilling has occurred in the past 50 to 100 years and with it has come the forest understory species that are gradually replacing typical species of open spaces that most likely dominated in the Little Ice Age. Thus, this plot did not cluster with others in the ordination (see fig. 36). Species that suggested a more open past included common juniper, Cascade desertparsley (*Lomatium martindalei*), kinnikinnick, Columbian lewisia (*Lewisia columbiana*), and white hawkweed (*Hieracium albiflorum*), which survived in a canopy gap. The canopy gap likely represented an area of shallow soil; however, the surrounding trees shaded it except for a few hours during summer afternoons. Thus, none of these species exhibited vigor, and all appeared to be dying out. This area probably had a subalpine parkland structure at the end of the Little Ice Age, similar to what plot 3 exhibited. The presence of large, lower limbs on the dominant Douglas-fir trees suggested that they grew up in open conditions. We postulate that this site is now sufficiently warmer than in the Little Ice Age to have allowed the invasion of the current cohort of lowland species and for canopy closure to occur. According to Luckman et al. (2005), other than a century-long warming around 1400, the 1900 through 1980 average temperature has been 0.5 to 1°C higher than the prevailing temperatures since around 1200. It should be noted that most of the tree ages postdate the Little Ice Age, and there was no evidence of fire on this plot. It may have been too open to carry a damaging fire for much of its development during and since the Little Ice Age, but that has now changed such that a future fire would be damaging.

Subalpine Fir/Green Alder Community Type (ABLA/ALV15)

This was a unique plot (plot 34) on several levels. A spring on the plot created a canopy gap that was dominated by green alder; the plot had a deep, humic organic (O) horizon; it had the largest subalpine fir trees in the study area, and most of them were dead; and we found no tree regeneration older than germinants, even though there was considerable light at ground level. Just as plot 23 uniquely represented low-elevation, warm-aspect vegetation, this plot represented low-elevation, cool-aspect vegetation within the context of our study area. The cooler aspect, wet soils, and older trees probably accounted for the deep, humic O horizon. Even excluding the spring, this plot did not closely resemble any published plant association of which we are aware. The closest match that we could find is the subalpine fir/Sitka valerian (*Valeriana sitchensis*) plant association described for the Mount Baker-Snoqualmie National Forest, although our site was wetter than is indicated for that plant association. At least portions of the plot had some affinity with the subalpine fir/Cascade azalea plant association.

Despite its uniqueness, it was similar to the others in that most of the trees postdated the Little Ice Age; but a greater proportion of trees were dated to before the end of the Little Ice Age than any other plot, especially considering estimates of the dead tree ages. An estimate of the largest dead subalpine fir suggested that it originated around 1776. Thus, in the late Little Ice Age, this area may have been a subalpine fir parkland. The high level of subalpine fir mortality and the complete lack of apparently successful tree regeneration is puzzling, and we saw no obvious reason for either. As most of the CWD and standing dead trees were in decay class 2, we surmise that the mortality was both recent and occurred over a short period. In any case, it did not affect an area appreciably larger than the plot itself.

Subalpine Fir/Blue Wildrye (*Elymus glaucus*) Community Type (ABLA/ELGL)

This community type was a parkland near the upper forest boundary that had more meadow than tree cover. This plot (plot 16) did not key to any plant association in Henderson et al. (1989). In the ordination (fig. 36), this plot stood out as unique but was closest to the subalpine fir/broadleaf lupine and subalpine fir/common juniper plant associations. It resembled a mesic grass community described by Kuramoto and Bliss (1970) for Hurricane Ridge in the Olympic Mountains, but their site had no blue wildrye and had 19 percent cover of Roemer's fescue. In addition to 25 percent overstory canopy closure contributed by four species of conifers, our site had 25 percent blue wildrye and only 10 percent cover of Roemer's fescue.

Although one tree on the plot established before the end of the Little Ice Age, most were established afterward, and at least half were established in the past 50 years. The earliest invaders were subalpine fir, which entered around 1820, but most trees, including all the whitebark pine, entered after 1900. At the time of the study, there was only 25 percent canopy closure, so this community was still fundamentally a meadow that appeared to be gradually succeeding to a woodland. Although the age distribution of trees suggested that they were increasing in dominance, we project, assuming current conditions, that the soils will become too cold for root growth as the canopy develops, which would limit canopy closure (Körner and Paulsen 2004). The whitebark pine on this plot has been heavily affected by white pine blister rust; however, this occurred so recently that none of the stems have had time to fall to the ground. In fact, there were no pieces of dead or down wood detected, indicating the recentness of both the disease on this plot and the tree invasion.

Subalpine Fir/Krummholz Community Types (ABLA/krummholz)

The placement of two plots in this group was based on krummholz structure more than floristics, as each of these plots included more than one community type (plot 30 at 1893-m elevation and plot 35 at 1742-m elevation). Both plots clustered only loosely with the subalpine fir/broadleaf lupine plant association in the ordination. Each included areas of the spreading phlox community type along with the krummholz trees, and in one case, the krummholz form was changing to an upright form (fig. A3.1). This transition seems to have begun, or at least accelerated, in the past 40 or 50 years based on the number of trees that have grown taller than 1.3 m. We were not able to obtain a complete age on any of the trees, as it was difficult to trace their tangled, prostrate, and layered stems through the duff overlying the ground surface. We obtained one age of 210 years from a prostrate subalpine fir stem, but this was still at an undetermined distance from its point of germination. Nevertheless, this age indicates an origin sometime in the Little Ice Age.

Small amounts of broadleaf lupine were closely associated with the subalpine fir, mostly along an edge that provided some shade, wind protection, and possible snow capture. Because of this, the closest plant association to these plots in the ordination (see fig. 36) was with the subalpine fir/broadleaf lupine plant association. Although these plots were heavily dominated by subalpine fir, the presence of whitebark pine CWD suggested that this species played at least a minor role in the past that was most likely curtailed by white pine blister rust. In both plots, the spreading phlox community type dominated the tundra. The slow-growing Douglas-fir growing on the lower elevation plot was clearly struggling with stem and limb breakage, but its presence in a tundra community, along with a high soil temperature of 14.1 °C, suggested community change may be beginning. The presence of Douglas-fir in plot 35 suggested that at least portions of this type were thermally available habitat for this species. Douglas-fir grew more abundantly at lower elevations in communities that appeared to have affinities to the spreading phlox community type, so this plot may simply represent the leading edge of a post-Little Ice Age upslope migration of Douglas-fir. A similar upslope migration of mugo pine (*Pinus mugo*) is occurring in alpine vegetation in Austria (Dirnbock et al. 2003). Our soil temperature modeling suggested that soil temperatures



Figure A3.1—Plot 30 (left) of the Olympic Mountain whitebark pine communities study with upright growth and minimal leader damage of a former krummholz form stand. Plot 35 (right) had extensive leader damage that was maintaining krummholz form and stature. The person in both photos is David H. Peter. USDA Forest Service photos by James Dollins.

would not limit root growth even if the overstory canopy was able to close (Körner and Paulsen 2004). This may have been different in the Little Ice Age, and perhaps warmer soils have permitted more vigorous top growth as well as the invasion of Douglas-fir on one plot. There is currently no indication that wind or snow abrasion is limiting top growth in the higher plot (plot 30) where upright tree form is currently developing, but evidence of such growth-limiting abrasion is present in the lower plot (plot 35) (fig. A3.1).

Douglas-Fir/Oceanspray (*Holodiscus discolor*)-Dwarf Rose (*Rosa gymnocarpa*) Plant Association (PSME/HODI-ROGY)

Henderson et al. (1989) describe this plant association as one that occurs in dry areas with warm soils and low timber productivity. The plot (plot 22) representing the Douglas-fir/oceanspray-dwarf rose plant association was on a warm, dry slope and had the second highest June through August 20-cm-deep soil temperature in our sample at 15.7 °C. Half of the trees were at least 100 years old, which was a unique age structure for our sample. However, we were only able to date one tree to the Little Ice Age. All other trees in this open woodland entered the stand after 1885 and mostly in the 1900s. The age structure, low-limbed wolfy tree structure, lack of mortality, lack of any down wood, and lack of evidence of fire suggested that this was an infilling Little Ice Age dry meadow. Even at the time of our sampling, it had only 35 percent overstory canopy closure. It was unique in having no subalpine fir or whitebark pine and was probably too warm and dry for either. Nearly all the sparse understory vegetation was associated with tree shade, while openings were relatively barren, confirming the droughty nature of the site, and suggested that further canopy closure may be slow and incomplete.

Spreading Phlox Community Type (PHDI3)

This was a relatively warm, dry, high-elevation cushion plant community; however, there were signs of tree invasion on some of the plots. Belsky and del Moral (1982) described a similar community in the Deer Park area of the Olympic Mountains, which they considered to be an alpine community. Kuramoto and Bliss (1970) described a cushion plant community from the northeastern Olympic Mountains that was also similar. It was like the subalpine fir/common juniper plant association but with less subalpine fir and common juniper. Environmentally, it was somewhat cooler than that plant association. Only one tree, a Douglas-fir that germinated around 1846, dated to the Little Ice Age, and most of the trees ≥ 1.3 m tall entered the stand in the past 50 years.

There was relatively little dead wood on the ground. Most identifiable dead wood that was present was from whitebark pine, and white pine blister rust was present on live whitebark pine trees, which suggested that whitebark pine invasion has been slowed by the disease. There was no lack of whitebark pine seedlings on these plots, suggesting that this type was a favored seed-caching area for the Clark's nutcracker. However, their ability to grow to larger sizes seemed to be limited by the white pine blister rust and harsh growing conditions. As solifluction was commonly observed in this type, frost heaving and unstable soils may also limit colonization by trees. The near lack of subalpine fir and the presence of Douglas-fir, along with whitebark pine and shore pine, speaks to summer warmth of these sites. Thus, this was currently poor habitat for subalpine fir, and in a climate-warming scenario, this is not likely to change. However, we estimate that three of eight plots would develop cold enough soils to inhibit root growth at high percentages of canopy closure in the current

climate (Körner and Paulsen 2004). As subalpine fir appeared to tolerate cold soils better than the other tree species, this may indicate an increasing role for subalpine fir if shade from other species increases. All the major species in the spreading phlox community type were present and were often well represented in the subalpine fir/broadleaf lupine plant association; however, the reverse was not true and subalpine fir, as already mentioned, was not successful here.

Western Brackenfern (*Pteridium aquilinum*) Community Type (PTAQ)

This warm, dry mid-elevation plot (plot 40) was on a steep, open-scrub slope with loose, sandy, and stony soil. We are not aware of any other reports of this plant community. Trees were nearly absent in this community, as a result of the instability of the substrate and its lack of water-holding capacity. The complete lack of down wood and the presence of a single dead tree that was only 5.9 cm in diameter at breast height suggests a low probability of success for the only seedling found on the plot. This was a unique open-slope community that we found nowhere else in the study area. It was dominated by western brackenfern, which did not occur on any other plot. There were other areas with similar loose, gravelly soils that were dominated by Olympic onion (*Allium crenulatum*), but we did not sample them, and they did not have western brackenfern. Treeless areas with loose gravelly soils were not uncommon in the study area, but dominance of them by western brackenfern was uncommon. We found no evidence to suggest that the lack of trees, wood, and litter might be due to fire. Harsh, dry soil conditions are likely responsible for low productivity that resulted in few trees, small amounts of dead wood, and scant litter. This community was embedded in a much larger area of nonforest vegetation consisting of various meadow types, including the spreading phlox type. Thus, this appeared to be an opening of long standing.

Black Alpine Sedge (*Carex nigricans*) Community Type (CANI2)

Although we are calling this community a black alpine sedge community type, we recognize that it was clearly transitional between slightly lower areas that were almost exclusively dominated by black alpine sedge and slightly higher areas with no black alpine sedge. In our sample, this community is represented only by plot 18. Black alpine sedge is generally recognized as an indicator of late-melting snowbank communities (Douglas 1972), so calling it by this name emphasizes this characteristic of the environment. Kuramoto and Bliss (1970) described a similar late-snowmelt black alpine sedge community near Hurricane Ridge in the Olympic Mountains, although their community included species that did not occur in our plot, such as white avalanche-lily (*Erythronium montanum*) (21 percent cover) and partridgefoot (*Luetkea pectinata*) (15 percent cover). Kuramoto and Bliss (1970) appear to have sampled lower, wetter parts of the snowmelt community than we did. The melting of the snowpack in another black alpine sedge community near Hurricane Ridge occurred after July 28 (Canaday and Fonda 1974), while the snow melted at our site a month earlier on June 24 (averaged over 2 years). Douglas (1972) described black sedge communities growing in filled in ponds and other poorly drained areas where snow was late melting, adding the observation that the soils usually remained moist for most of the growing season. Key to understanding the vegetation in our plot was the bench, which was positioned to accumulate snow as it blew over a west-facing lip. This extra snow prevented this area from melting out until late June or July, and the meltwater ran off slowly, at lower levels, or not at all. The

resulting black alpine sedge community has built a highly organic surficial soil layer over time, which was water retentive.

The high moisture content of the soil and the late melting of the snowbank made this one of the coldest soils of the open plots, and based on our modeling, we predict that over-story development will be limited by soil temperatures that are too low for root growth (Körner and Paulsen 2004). It appeared that within the past 30 years, the portion of the meadow in which our plot was located was being invaded by trees. However, it is not yet possible to say if these slow-growing seedlings will be successful. Snow mold mortality was observed nearby. Larger trees were present just off the plot, but those were mostly elevated 20 to 50 cm relative to our plot. Below the plot where the snow melts later, trees were even less successful.

Talus Plots

These were nonforested plots that were not described in Henderson et al. (1989), and we have not seen similar communities described elsewhere. These two plots (plots 7 and 10) were in similar habitats but had dissimilar vegetation. Both were on a steep talus slope, consisting of boulders and cobbles with little vegetation. Much of these plots was uninhabitable because of lack of soil, and we assume that there was functionally no soil water over most of both plots. There may have been water at depth, but there was no medium for roots to use to penetrate deeply enough to access it. The environment was also harsh in other ways; both plots were in frost pockets and may have also been subject to snow avalanche and falling rock. The south edge of both plots overlapped the talus edge where enough soil has accumulated to permit growth of vegetation. We assume the difference in floristics reflected different levels of soil development at the margin of the talus. Thus, these were primary successions at different levels of development. In plot 10, the dominant species at the edge of the plot was green alder, which has a well-known association with avalanche chutes (Fonda and Bliss 1969, Hemstrom and Franklin 1982, Taylor 1932). It has also been noted as an important species in primary successions following glacial retreat and avalanches as well as in some secondary successions (Mauri and Caudullo 2016).

The marginal vegetation in both plots indicated post-Little Ice Age tree invasion. The only tree dating to the Little Ice Age was the oldest tree on plot 10—a subalpine fir tree. Otherwise, the shape of the age curve suggested that tree growth postdated the Little Ice Age and has mostly occurred in the past 50 years. However, there is no potential for trees to close canopy on these plots without further soil development. There were no dead trees, down wood, or evidence of fire on either plot.

Appendix 4: Photographs of Olympic Mountains whitebark pine communities study plots

There are two photographs of each plot except for plots 1 and 2, which we only used in limited analyses. For the remaining plots, the photographs were taken from the outer edge of the plot looking directly at the plot center. One was taken from the east cardinal (facing west) and one from the south cardinal (facing north). The single photograph of plot 1 was taken from an open meadow just outside of the plot facing southeast toward the plot center. Plot 2 was not a plot in the sense of the others. Its purpose was to document a large, old krummholz tree. Here we present a single photograph of the base of that tree, with the limb that we core sampled from the bottom on the left of the photograph.



Plot 1 from the northwest just outside of the plot facing southeast toward the plot center (2007). The plot center is under the pink flag (indicated by the arrow). A crewmember is on the left. USDA Forest Service photo by David H. Peter.



Plot 2 under the canopy of an old whitebark pine tree from the east side (2007). The limb that was core sampled for age is the large limb on the left (indicated by the arrow). The core sample was taken from the bottom side of the limb as close to the base of the tree as the bore handle would permit. USDA Forest Service photo by David H. Peter.



Plot 3 from the east edge of the plot facing west toward the plot center (2016). Timothy B. Harrington is right of center. USDA Forest Service photo by David H. Peter.



Plot 3 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 4 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left, and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 4 from the south edge of the plot facing north toward the plot center (2016). Timothy B. Harrington is on the right, and James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 5 from the east edge of the plot facing west toward the plot center (2016). Timothy B. Harrington is above center. USDA Forest Service photo by David H. Peter.



Plot 5 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 6 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center, and Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 6 from the south edge of the plot facing north toward the plot center (2016). James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center, and Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 7 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center, and Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 7 from the south edge of the plot facing north toward the plot center (2016). James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center, and Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 8 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 8 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 9 from the east edge of the plot facing west toward the plot center (2008). A crewmember is at center. USDA Forest Service photo by David H. Peter.



Plot 9 from the south edge of the plot facing north toward the plot center (2008). A crewmember is above center. USDA Forest Service photo by David H. Peter.



Plot 10 from the east edge of the plot facing west toward the plot center (2008). A crewmember is above center. USDA Forest Service photo by David H. Peter.



Plot 10 from the south edge of the plot facing north toward the plot center (2008). USDA Forest Service photo by David H. Peter.



Plot 11 from the east edge of the plot facing west toward the plot center (2016). James Dollins is near center. USDA Forest Service photo by David H. Peter.



Plot 11 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 12 from the east edge of the plot facing west toward the plot center (2008). Two crewmembers are visible. A pole (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 12 from the south edge of the plot facing north toward the plot center (2008). A crewmember is near the plot center. A pole (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 13 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 13 from the south edge of the plot facing north toward the plot center (2008). A crewmember is left of center. USDA Forest Service photo by David H. Peter.



Plot 14 from the east edge of the plot facing west toward the plot center (2016). Timothy B. Harrington is on the far right. USDA Forest Service photo by David H. Peter.



Plot 14 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 15 from the east edge of the plot facing west toward the plot center (2008). A crewmember is next to a pole (indicated by the arrow), which is set in the ground at the plot center. USDA Forest Service photo by David H. Peter.



Plot 15 from the south edge of the plot facing north toward the plot center (2016). Timothy B. Harrington is on the left, and James Dollins is on the right. A pole (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 16 from the east edge of the plot facing west toward the plot center (2008). A crewmember is right of center. USDA Forest Service photo by David H. Peter.



Plot 16 from the south edge of the plot facing north toward the plot center (2008). USDA Forest Service photo by David H. Peter.



Plot 17 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 17 from the south edge of the plot facing north toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 18 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left (near the plot center), and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 18 from the south edge of the plot facing north toward the plot center (2016). James Dollins is right of center next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 19 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left (near the plot center), and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 19 from the south edge of the plot facing north toward the plot center (2016). James Dollins is near center next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 20 from the east edge of the plot facing west toward the plot center (2010). Timothy B. Harrington is right of center. A stick with pink flagging (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 20 from the south edge of the plot facing north toward the plot center (2016). James Dollins is next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 21 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 21 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 22 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 22 from the south edge of the plot facing north toward the plot center (2016). James Dollins is next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 23 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 23 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 24 from the east edge of the plot facing west toward the plot center (2010). A stick with pink flagging (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 24 from the south edge of the plot facing north toward the plot center (2016). James Dollins is on the right, and Timothy B. Harrington is on the left. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 25 from the east edge of the plot facing west toward the plot center (2010). Timothy B. Harrington is left of center. A stick with pink flagging (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 25 from the south edge of the plot facing north toward the plot center (2010). A stick with pink flagging (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 26 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 26 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 27 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 27 from the south edge of the plot facing north toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 28 from the east edge of the plot facing west toward the plot center (2010). Timothy B. Harrington is near center. USDA Forest Service photo by David H. Peter.



Plot 28 from the south edge of the plot facing north toward the plot center (2016). James Dollins is right of center next to a tripod (indicated by the arrow), which is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 29 from the east edge of the plot facing west toward the plot center (2010). A stick with pink flagging (indicated by the arrow) marks the plot center. USDA Forest Service photo by David H. Peter.



Plot 29 from the south edge of the plot facing north toward the plot center (2010). Timothy B. Harrington is near the plot center. USDA Forest Service photo by David H. Peter.



Plot 30 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left, and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 30 from the south edge of the plot facing north toward the plot center (2010). Timothy B. Harrington is on the left. USDA Forest Service photo by David H. Peter.



Plot 31 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left, and Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 31 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 32 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 32 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 33 from the east edge of the plot facing west toward the plot center (2010). A crewmember is right of center. USDA Forest Service photo by David H. Peter.



Plot 33 from the south edge of the plot facing north toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 34 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 34 from the south edge of the plot facing north toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 35 from the east edge of the plot facing west toward the plot center (2016). James Dollins is at the center of the photo. USDA Forest Service photo by David H. Peter.



Plot 35 from the south edge of the plot facing north toward the plot center (2016). James Dollins is on the left next to a tripod (indicated by the arrow), which is positioned at the plot center. Timothy B. Harrington is on the right. USDA Forest Service photo by David H. Peter.



Plot 36 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 36 from the south edge of the plot facing north toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 37 from the east edge of the plot facing west toward the plot center (2010). USDA Forest Service photo by David H. Peter.



Plot 37 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 38 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 38 from the south edge of the plot facing north toward the plot center (2016). James Dollins is on the left, and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 39 from the east edge of the plot facing west toward the plot center (2010). Timothy B. Harrington is on the right, and another crewmember is on the left. USDA Forest Service photo by David H. Peter.



Plot 39 from the south edge of the plot facing north toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 40 from the east edge of the plot facing west toward the plot center (2016). James Dollins is on the left, and Timothy B. Harrington is on the right. A tripod (indicated by the arrow) is positioned at the plot center. USDA Forest Service photo by David H. Peter.



Plot 40 from the south edge of the plot facing north toward plot center (2016). James Dollins is on the left near the plot center, and Timothy B. Harrington is on the right. The tripod (indicated by an arrow) is over the plot center. USDA Forest Service photo by David H. Peter.



Plot 41 from the east edge of the plot facing west toward the plot center (2016). USDA Forest Service photo by David H. Peter.



Plot 41 from the south edge of the plot facing north toward the plot center (2016). James Dollins is left of center. USDA Forest Service photo by David H. Peter.

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