United States Department of Agriculture
Forest Service

Pacific Northwest
Research Station

Research Paper

PNW-RP-598
February 2014

Responses of Southeast Alaska Understory Species to Variation in Light and Soil Environments

Thomas A. Hanley, Bernard T. Bormann, Jeffrey C. Barnard, and S. Mark Nay

Authors

Thomas A. Hanley is a research wildlife biologist and **Jeffrey C. Barnard** is a fish biologist, Forestry Sciences Laboratory, 11175 Auke Lake Way, Juneau, AK 99801; **Bernard T. Bormann** is a research ecologist and **S. Mark Nay** is an ecologist, Forestry Sciences Laboratory, Corvallis, OR 97331.

Cover photograph of devilsclub, USDA Forest Service.

Abstract

Hanley, Thomas A.; Bormann, Bernard T.; Barnard, Jeffrey C.; Nay, S. Mark. 2014. Responses of southeast Alaska understory species to variation in light and soil environments. Res. Pap. PNW-RP-598. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 17 p.

Aboveground growth rates of seedlings of bunchberry (*Cornus canadensis* L.), oval-leaf blueberry (*Vaccinium ovalifolium* Sm.), salmonberry (*Rubus spectabilis* Pursh), devilsclub (*Oplopanax horridus* (Sm.) Miq.), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were compared in a study of their responses to an artificial light gradient in an Oregon greenhouse and in a study of response to overstory and soil type in a field manipulation experiment in southeast Alaska. Seedlings of all five species were grown independently under nine intensities of light for 156 days, and their oven-dry weight of new leaves and twigs was measured and expressed as a percentage of their maximum growth observed under all light treatments. Results indicated strongly differential responses to light, with bunchberry responding most strongly to very low intensities and western hemlock requiring mid to high intensities of light to reach its maximum growth rate. The same five species were planted in plastic grow pots placed in the ground under overstory canopies of red alder (*Alnus rubra* Bong.) and dense, young-growth western hemlock for one annual growing season (May through August). Soils were artificial and of two contrasting types, one strongly mineral and the other mineral mixed with organic matter. Measures of total aboveground production of new leaves and twigs (oven-dry grams per plant) indicated differential responses among the species and significant differences in canopy and soil treatments for all species except bunchberry. Statistically significant ($P < 0.05$) interactions of canopy by soil (alder canopy and "mixed" soil producing greatest growth) were observed in oval-leaf blueberry and salmonberry, both of which also had a significant main effect of soil (mixed > mineral). The canopy main effect (alder canopy > conifer canopy) was significant for all species except bunchberry. Overall, light availability was a strong ecological factor in both studies, but responses to light differed among species. Knowledge of such differential responses is important for designing silviculture treatments for multiple benefits.

Keywords: Light, understory, growth, PAR, soils, autecology, *Cornus canadensis*, *Vaccinium ovalifolium*, *Rubus spectabilis*, *Oplopanax horridus*, *Tsuga heterophylla*, *Alnus rubra*, southeastern Alaska.

Summary

Aboveground growth rates of seedlings of bunchberry (*Cornus canadensis* L.), oval-leaf blueberry (*Vaccinium ovalifolium* Sm.), salmonberry (*Rubus spectabilis* Pursh), devilsclub (*Oplopanax horridus* (Sm.) Miq.), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) were compared in a study of their responses to an artificial light gradient in an Oregon greenhouse and in a study of response to overstory and soil type in a field manipulation experiment in southeast Alaska.

Principal implications of the study for silviculture are (1) the identification of light as the major environmental factor affecting growth rates of understory species, and (2) the identification of a window of opportunity at low intensities of light where western hemlock seedlings do relatively more poorly than all the other understory species we studied. The results indicate that silviculture prescriptions designed to favor nonconifer understory vegetation should open the forest canopy but also strive to maintain relatively low intensities of light at the seedling layer when western hemlock seedlings are abundant. These findings provide the beginning of a basis for designing prescriptions based on desired understory environments rather than simply trying to repeat empirical responses of given treatments observed elsewhere.

Contents

Introduction

Within the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)-Sitka spruce (*Picea sitchensis* (Bong.) Carrière) forests of southeast Alaska, old-growth forests have been recognized as providing much better wildlife habitat than young-growth forests regenerating from clearcut logging, primarily because of a relatively productive and species-rich understory vegetation in old-growth forests and a very sparse, unproductive understory in dense, closed-canopy young-growth stands (Alaback 1982, 1984a, 1984b; Samson et al. 1989; Schoen et al. 1981, 1988; Wallmo and Schoen 1980). Precommercial thinning of young-growth stands for wood production has been common since the 1970s (Ruth and Harris 1979), but early results for understory production and wildlife habitat were not encouraging as understory responses tended to be short lived and dominated by only a few shrub species (Alaback and Tappeiner in Hanley et al. 1989: 6, Doerr and Sundburg 1986, Hanley 2005, McClellan 2005). Even more problematic, when young-growth stands were thinned to wider spacings, western hemlock seedlings appeared to benefit greatly, resulting in a dense second cohort of western hemlock within the understory (Deal and Farr 1994, Doerr and Sandburg 1986, Zaborske et al. 2002), a phenomenon also observed in young-growth Sitka spruce-western hemlock forests of coastal Oregon (Alaback and Herman 1988). Although some partial cutting of old-growth forests (Deal 2001, Kirchhoff and Thomson 1998, McClellan et al. 2000) and commercial thinning of older young-growth forests (Zaborske et al. 2002) have occurred in the Alaska region, most timber management has been by clearcut logging old-growth forests followed by precommercial thinning of the young growth (McClellan 2005, Ruth and Harris 1979). Therefore, much interest exists in designing new silviculture systems that might be optimal for both timber production and wildlife habitat (Hanley et al. 2013, McClellan 2008). That requires maintaining productive and species-rich understory vegetation in the young-growth stands.

Given the lack of literature on empirical results of understory response to thinning in southeast Alaska, knowledge of the autecology of major understory species is especially important for designing optimal silviculture systems (Hanley 2005), yet only a couple of such studies have been conducted (Rose 1990, Tappeiner and Alaback 1989), both of which found strong effects of light. Photosynthetically active radiation (PAR) below the old-growth forest canopy is typically less than 6 percent of incident values and is usually less than 2 percent in young-growth conifer forests of the region (Rose 1990, Tappeiner and Alaback 1989). Tappeiner and Alaback (1989) planted seeds of five common understory species (*Vaccinium alaskaense* Howell, *Cornus canadensis* L., *Coptis aspleniifolia* Salisb., and *Rubus pedatus* Sm.) in conifer forest microsites and studied their germination, establishment, and survival over a 4-year period. They found that seedling survival (but not germination)

of all species except *Cornus canadensis* was highly correlated with the availability of light. Rose (1990), studying sexually mature oval-leaf blueberry (*Vaccinium ovalifolium* Sm.) in a series of manipulation and fertilization experiments, found its growth rates to be strongly affected by light availability but independent of nitrogen availability within the normal range of values.

Soils play a major role in determining tree growth rates and productivity and understory plant community composition in southeast Alaska (Harris and Farr 1974, Ruth and Harris 1979, Viereck et al. 1992). Soils throughout the region are remarkably complex, a product of mixed lithology from plate fragments deposited along the Pacific plate margin, glacial till, and frequent disturbance from gravity flow on steep inclines, floods, historical ground-based logging, and especially windthrow. Disturbance creates complexes of undeveloped soils (Inceptisols) that develop into cryorthods (Spodosols) on disturbed, well-drained microsites, and into cryaquods (Histosols) on poorly drained microsites; these complexes are observed at a scale of less than 20 m^2 (Bowers 1987). The wet-cool climate, frequent disturbance, and conifer growth in southeast Alaska lead to rapid and intense podsolization, resulting in poorly productive Histosols in as little as 300 years without subsequent disturbance (Bormann et al. 1995).

Light and soil, therefore, appear to be especially important factors affecting understory production in southeast Alaska young-growth forests, and plant species probably respond differentially to light availability and soils. Although nitrogen availability may not be limiting to some species in Spodosols (Rose 1990), other nutrients and soil structure may play important roles.

We investigated the effects of light and soils on the growth rates of already established seedlings of five major understory species through a combination of light trials conducted in a greenhouse with artificial lighting and field experiments involving the manipulation of light and soil environments in young-growth forests in southeast Alaska. We were especially interested in differences among the species in how they responded to environmental variation. The five species we selected were (1) bunchberry, an evergreen forb especially important as winter food for black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) (Parker et al. 1999); (2) oval-leaf blueberry, (3) salmonberry (*Rubus spectabilis* Pursh), and (4) devilsclub (*Oplopanax horridus* (Sm.) Miq.), all three of which are common understory-dominant shrubs; and (5) western hemlock, because of its potentially strong competitive effect and propensity for forming a second conifer layer within thinned stands. Specifically, we wanted to learn how the species' growth responses would differ with light intensity (greenhouse study) and with the relative importance of light versus soil in determining growth rates under overstory canopies typical of natural variation in forests of the region (field experiments).

Methods

Greenhouse Light Trials

The light trials were conducted as a gradient study in a greenhouse on the campus of Oregon State University (Corvallis, Oregon) for 156 days during March to August with day length varying from 14.5 to 18.5 (mean 16.5) hours (average day length for Juneau, Alaska, during the 15 April to 15 September growing season = 16.4 hours). The light gradient consisted of nine intensities, all controlled artificially with 400-watt high-pressure sodium grow lights and shade cloth above plants in addition to the natural, ambient greenhouse light. Light treatments were measured with LI-190 Quantum sensors at 30 cm above the plants throughout the trials, and their mean mid-day PAR intensities were 1, 3, 10, 19, 36, 78, 141, 340, and 1118 $\mu mol\ m^{-2}\ sec^{-1}$, or 0.1, 0.3, 0.9, 1.7, 3.2, 7.0, 12.6, 30.4, and 100 percent, respectively, of the 1118 value. Light intensity treatments were skewed toward the low end to provide maximum information relative to the low light intensities within understory environments of southeast Alaskan forests.

Seedlings of all five species were planted individually in plastic grow pots with common potting mixture soil. Five plants of each species within each light treatment were arranged randomly within a five by five grid under each light treatment. The nine light treatments (each within an area of 122 × 122 cm) were arranged randomly within the greenhouse. Each light treatment was isolated from the others by walls of reflective Mylar glued to hardboard panels and suspended 15 cm above the greenhouse bench to provide for air circulation. Plants were watered throughout the study, and their locations within each light treatment were randomly shuffled monthly.

Salmonberry seedlings were obtained from a commercial nursery in Albany, Oregon, whereas all other seedlings were obtained from a commercial nursery in Juneau, Alaska. Twice as many plants as needed were ordered. All were sorted to maximize consistency of plant size within each species (selecting the 45 plants of most similar size) and transplanted into individual grow pots within the same week. They were placed within light treatments all within the same day for each treatment.

After growing under the light treatments for 156 days, all plants within a treatment were individually harvested at ground level; and new leaves and twigs were clipped and oven-dried at 100 °C for 24 hours and weighed to the nearest 0.01 gram. Because we were not able to control the exact size of our plants, we relied on random assignments to treatments and relative (between-treatment) differences in new growth (leaves and twigs) within each species as our best measure of species-specific responses to light treatments.

Field Experiments

The field experiments were conducted near Juneau, Alaska, within a closed-canopy western hemlock–Sitka spruce young-growth forest (about 30 years old) and an adjacent red alder-dominated stand (24 years old). Both were on near-level ground and probably originated from the same stand that was logged by two different methods. The two stands were not intended to be representative of conifer or alder overstories per se; rather, they simply provided two very different light environments within the range of natural variation in forests of the region. The conifer forest was mostly devoid of understory vegetation; the red alder stand had a mid layer of red elderberry (*Sambucus racemosa* L.) about 3 m tall and a scattered fern-dominated understory at ground level. We conducted our experiments with plants in plastic grow pots of two contrasting types of soil (one strongly "mineral" and one "mixed," a mixture of mineral soil and organic matter) placed into the soil at ground level within the two types of overstory. We worked with the same five species as for the light trials (above) and from the same nursery sources.

Because we wanted to analyze the effects of light and soil and their interaction independently of one another, we needed to grow our plants in the two types of soils under the same two types of forest canopies. We accomplished that by growing the plants in grow pots, each of one or the other soil, and each under one or the other forest canopy in a balanced design of half the mineral soil pots and half the mixed soil pots under the alder canopy and the other half of pots under the conifer canopy. The two canopies provided widely different light environments for the plants in their understories, but because the two types were not replicated (i.e., several different stands of each type of canopy), they cannot be considered representative of "red alder" or "conifer" overstories generally.[1] Similarly, because we could not extract uniform, undisturbed soil cores of sufficient size for each pot, we created our soils to simulate an important contrast found in southeast Alaska, strongly mineral soils (with little organic matter) versus mixed mineral-organic soils. However, our soils were artificial constructs and cannot be considered representative of natural soils per se. Thus, our experiment compared growth rates of plants growing in widely different light and soil environments, but not in environments representative of any particular type of natural forest or soil.

[1] Ideally, we would have replicated our experimental design with several alder and several conifer stands and considered individual plants as subsamples within replicates; then we could generalize our results to "alder" and "conifer" canopy types. However, only one stand of each was available to us for this work, so we must restrict our conclusions to only those two stands (i.e., a "case study" as far as canopy type goes). On the other hand, the two stands provided sharp contrasts in their light environments, which allowed us to test the species' responses to light and soil types within light treatments, which was our principal objective.

Grow pots were plastic, 41 cm deep by 15 cm wide at top and 10 cm wide at the bottom. They were filled with soils the preceding fall and overwintered outside before the experiment began in spring. We collected separate soil layers in the profile, sifted stones and woody sticks from them for uniformity, and then recreated them in the pots as follows: "Mineral soil" pots were constructed from a mostly mineral, organic-matter-poor Inceptisol from a red alder stand growing on a relatively young soil in a landslide area—the bottom 35 cm was a B/C horizon, the next 2.5 cm was an alder B horizon, and the uppermost 2.5 cm was alder litter; 1.0 cm of open space was left at the top of the pot. "Mixed soil" pots were constructed from a Spodosol from an old-growth forest—the bottom 12.5 cm was a B/C horizon, the next 5.8 cm was an iron-rich Bh_{ir} horizon, the next 9.6 cm was an organic-rich Bh horizon, and the uppermost 9.6 cm was an Oe horizon; 3.5 cm of open space was left at the top of the pot. These soils had characteristics that differed from most field soils. The collection of layers and reconstruction of profiles disturbed the horizons and likely acted to mineralize nutrients otherwise tied up in organic compounds. The mixed soil could not be considered an intact podzol because its horizons were disturbed when reconstructing the profile. The mineral soil had developed on nutrient-poor parent material and had only a short time to accumulate nutrients under the alder. Thus, it may have been relatively deficient in total and available nutrients. Disturbed podzols and nutrient-poor soils are common in southeast Alaska, however, so our comparison served to represent widely different soil conditions probably within the range of natural variation in the region.

For each plant species (5) and each overstory (2) and each soil type (2), there were 14 replicate plants, each grown in its own grow pot = 280 grow pots total (56 for each species). The 14 replicates were arranged in 14 groups with one plant of all five species in each group (arranged in random order within the group), and the 14 groups were scattered throughout each of the two stands (one set of 14 in the conifer stand, one set of 14 in the alder stand). Plants had been purchased as seedlings, and extra plants of each species were ordered. Upon arrival in early May, all plants were sorted to obtain the 56 most apparently healthy and similar-sized individuals of each species. The 280 plants were then planted into the grow pots, one plant per pot, and all grow pots were planted within the conifer and alder stands during the third week of May, with their soil surface level with the soil surface of the stand. They were protected from herbivory by deer and porcupines with wire mesh cages. They were watered as judged necessary during the first month and then left unattended after that. At the end of growing season in last week of August, all grow pots were collected and returned to the lab, where each plant was clipped at ground level and its current annual growth of leaves and twigs was clipped, oven-dried (100 °C)

for 24 hours, and weighed to the nearest 0.01 gram. The weight of the oven-dried current annual growth provided our estimate of each plant's total aboveground net production (grams per plant).

Ambient light within both stands was measured with a sunfleck PAR ceptometer (Decagon Devices, Inc., Pullman, Washington) at 30 cm above ground at each of the 28 groups of plants and in a nearby open area (full sunlight) at noon on 11 different dates throughout the experiment. The mean light intensity within each of the two stands, expressed as a percentage of full sunlight in the open area, provided a measure of relative differences between the two overstories.

Plant results were analyzed independently for each species in a 2 by 2 (canopy by soil) factorial analysis of variance with the general linear model GLM procedure of SAS (SAS Institute, Inc. 2004) with canopy (alder, conifer) and soil type (mineral, mixed) as treatments and the 14 individual plants of each canopy-soil group as replicates. Multiple comparisons of significant differences were made with the Tukey-Kramer test. We tested the null hypothesis of no effect of canopy, soil type, or their interaction on total aboveground net production per plant; we used an α level of 0.05 throughout.

Results and Discussion

Greenhouse Light Trials

Average daily total PAR of the nine light treatments ranged from near 0 to 48 mol m^{-2} day^{-1} (table 1). Mean total production of aboveground new growth varied greatly among species and light treatments, ranging from 0.06 (salmonberry at lowest light intensity) to 12.89 g $plant^{-1}$ (western hemlock at highest light intensity) with virtually all species having their lowest production at lowest light and highest production at maximum light. Salmonberry, however, was problematic, as it did very poorly in our trials with very low levels of production throughout (ranging from 0.06 to only 0.69 g $plant^{-1}$). Other than salmonberry, growth rates were lowest for bunchberry and oval-leaf blueberry and highest for devilsclub and western hemlock. Absolute aboveground growth rates can be misleading, though, as species differ in their intrinsic growth rates and relative allocations of growth to roots and shoots, especially as seedlings (Alaback and Tappeiner 1991, Tappeiner and Alaback 1989, Tappeiner and Zasada 1993).

When production of new growth is plotted as a percentage of its maximum growth for each species, however, aboveground production can provide an index of relative growth rate within each species, and the growth rates relative to light intensities can be compared directly among species (fig. 1). Excluding salmonberry, all species exhibited a sharply nonlinear increase in production with increasing light at

Table 1—Mean (± standard error) total oven-dry (100 °C) weight (grams per plant) of new leaves and twigs of each plant species within each of nine light treatments at the end of the light trials

Light treatment		Total oven-dry weight (g plant^{-1}) of new leaves and twigs (mean ± standard error)				
Mean mid-day intensity PAR, (µmol m^{-2} sec^{-1})	Mean daily total PAR, (mol m^{-2} day^{-1})	Bunchberry	Oval-leaf blueberry	Devilsclub	Salmonberry	Western hemlock
1	< 0.1	0.34 ± 0.14	0.15 ± 0.10	1.24 ± 0.45	0.06 ± 0.04	0.10 ± 0.10
3	0.1	0.34 ± 0.11	0.23 ± 0.06	1.90 ± 0.62	0.13 ± 0.05	0.30 ± 0.09
10	0.4	0.55 ± 0.24	0.34 ± 0.08	2.00 ± 0.60	0.32 ± 0.05	0.37 ± 0.13
19	0.7	0.74 ± 0.06	0.47 ± 0.06	1.48 ± 0.33	0.29 ± 0.04	0.31 ± 0.09
36	1.3	0.99 ± 0.05	0.72 ± 0.09	3.49 ± 1.01	0.36 ± 0.05	1.65 ± 0.20
78	3.0	1.06 ± 0.22	0.69 ± 0.20	4.48 ± 0.62	0.69 ± 0.07	4.40 ± 0.56
141	5.9	1.15 ± 0.36	0.99 ± 0.31	3.97 ± 1.01	0.64 ± 0.14	9.21 ± 0.25
340	14.1	1.26 ± 0.35	0.98 ± 0.31	4.75 ± 1.09	0.64 ± 0.21	12.32 ± 1.16
1118	48.0	1.18 ± 0.09	1.37 ± 0.31	6.46 ± 0.88	0.24 ± 0.08	12.89 ± 2.18

PAR = photosynthetically active radiation.

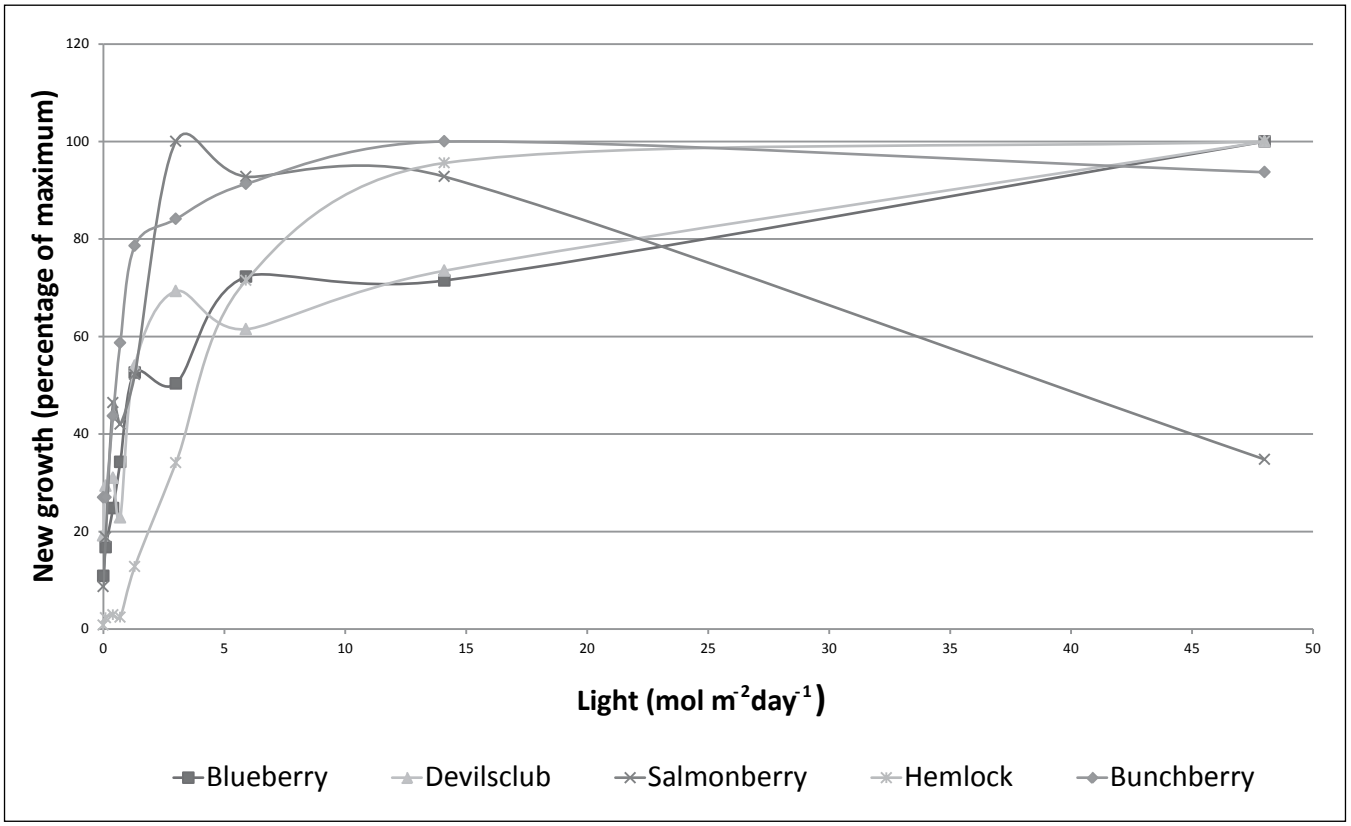

Figure 1—Relative aboveground growth rates (total oven-dry weight of new growth of leaves and twigs expressed as a percentage of their maximum value among all light treatments) of each of five species in each of nine light treatments, where light is mean daily total PAR (mol m^{-2} day^{-1}).

low intensities of light, plateauing toward an asymptote at mid to high intensities of light. Experimental error (variation within treatments) caused some small dips and humps in the response curves, but most important, it is clear that all the understory species responded better to the lower light intensities (< 4 mol m^{-2} day^{-1}) than did western hemlock. Although western hemlock's growth was lower than that of other species in the low end of the response curves, it reached a near-asymptote level of production earlier than did blueberry and devilsclub (fig. 1), and it was by far the most productive species in absolute terms (table 1). This has important implications for silviculture treatments, as it indicates that there exists a window of opportunity favoring desired understory species at the lower end of the potential light gradient in forests (<about 4 mol m^{-2} day^{-1}), while above that window (e.g., 15 mol m^{-2} day^{-1} and greater), western hemlock has the advantage. Among all five species studied here, bunchberry has been the most problematic from the standpoint of silviculture for improving deer habitat in young-growth forests of the region (Hanley 1993; Hanley et al. 1989, 2013), but bunchberry had the highest relative growth rate at the lowest light intensities provided (reaching nearly 80 percent of its maximum growth rate at only 1.3 mol m^{-2} day^{-1}). Bunchberry apparently would be most favored competitively by very low intensities of light in the understory environment. That is fortunate, because this very low growing, small species is subject to shading by virtually all other layers of vegetation.

Field Experiments

Although the maximum mid-day intensity PAR measured in the open (full sun) at the field site was 1662 µmol m^{-2} sec^{-1}, which was very similar to the maximum mid-day value observed in the greenhouse trials (1606 µmol m^{-2} sec^{-1}), the mean mid-day intensity PAR in the open at the field site was only 789 µmol m^{-2} sec^{-1}, or 71 percent of the mean mid-day intensity PAR in the highest light treatment in the greenhouse (1118 µmol m^{-2} sec^{-1}). Frequent cloud cover was the principal reason for the mean light intensity at the field site being only 47 percent of its maximum (cloud-free) 1662 value.

Light measures under the two forest canopies, expressed as a percentage of light in the open, differed by a full order of magnitude, averaging 19.5 percent (±3.3 percent standard error) for the alder canopy and 1.7 percent (±0.2 percent SE) for the conifer canopy. Average mid-day intensity PAR throughout the study under the alder and conifer canopies was 142 and 16 µmol m^{-2} sec^{-1}, respectively.

The canopy by soil factorial experiments indicated statistically significant effects for all species except bunchberry (fig. 2). Interaction effects between canopy and soil types were significant in salmonberry and oval-leaf blueberry, with both responding most strongly to the combination of alder canopy and mixed soil. The

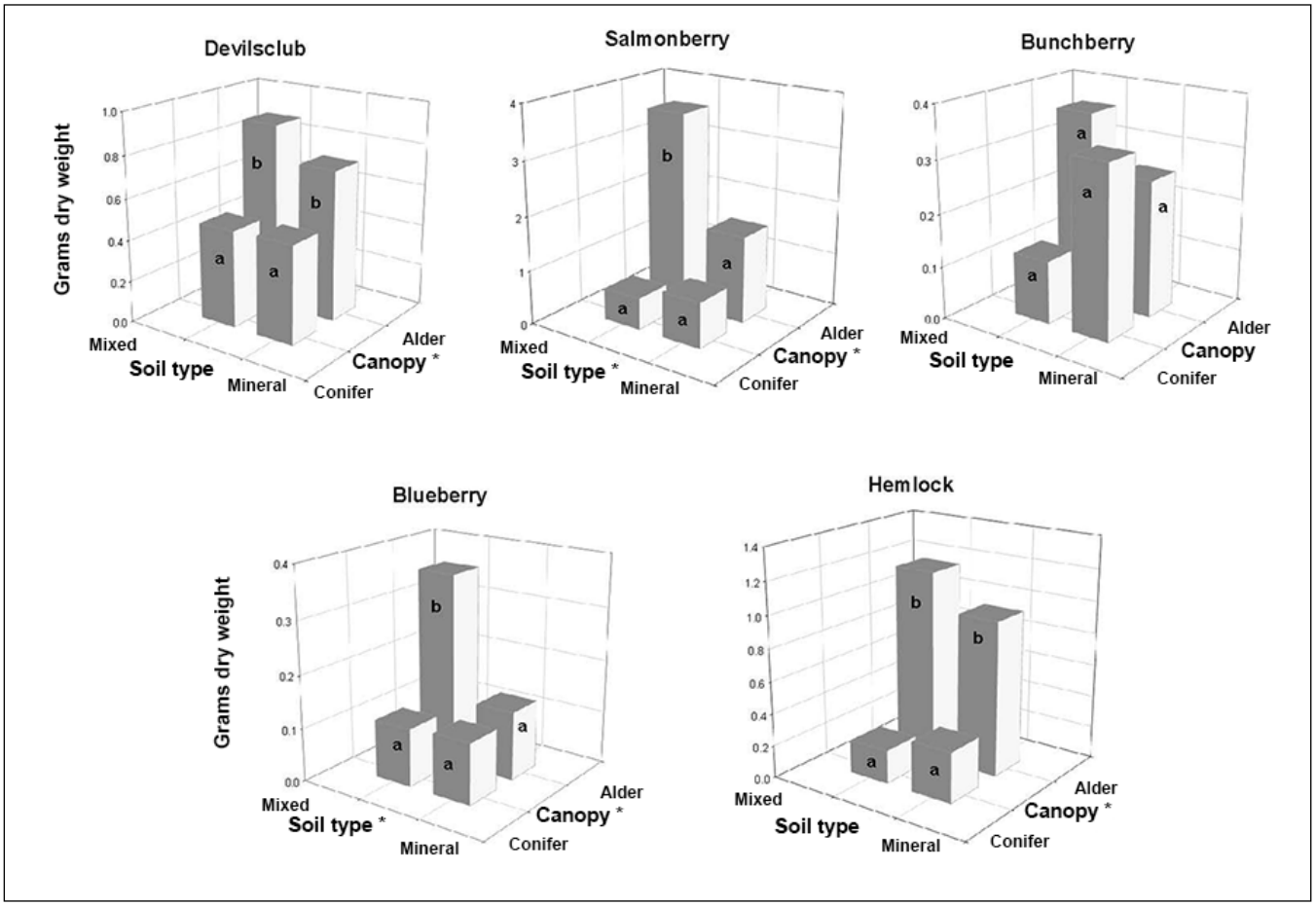

Figure 2—Mean oven-dry weight (grams per plant) of total aboveground new growth of leaves and twigs of plants in five experiments of response to variation in overstory canopy (alder, conifer) and soil type (mineral, mixed). Statistically significant main effects (axes) in the factorial analysis of variation are identified with an asterisk; values identified with different letters are significantly different, all at an α level of 0.05.

main effect of canopy was significant for all species except bunchberry, with alder being greater than conifer in all. Soil type was a significant main effect only in salmonberry and blueberry (with mixed soil > mineral soil in both), but that effect was strongly influenced by the significant interaction with canopy in both those species (fig. 2).

The results of the field experiments parallel those of the light trials in that the canopies' difference in light was overwhelmingly important for western hemlock, moderately important for devilsclub and oval-leaf blueberry, and relatively unimportant for bunchberry. The strong canopy by soil interaction effect for both salmonberry and oval-leaf blueberry is interesting in that it was the same for both species (greatest response for alder canopy with mixed soil) even though the two species tend to respond differently in natural plant communities of the region: oval-leaf blueberry occurs almost exclusively on organic-rich soils and is relatively

rare on mineral soils, whereas salmonberry is common on both but is frequently an understory dominant on mineral soils (Hanley and Hoel 1996, Hanley et al. 2006). Devilsclub, a common dominant on both soil types of the region, responded most strongly to the greater light of the alder canopy and not importantly to the differences in soils.

Although light under the alder canopy was much more favorable for plant production than it was under the conifer canopy, all of our species not only survived but also maintained at least modest levels of productivity under the conifer canopy. Most plants growing in the conifer treatment were not as vigorous as those in the alder treatment, but they did much better than we would have expected on the basis of such a sparse understory as occurred naturally in the conifer stand. Our plants were already established when moved into the forest, and they were protected from large vertebrate herbivores. Perhaps they would not have established as well or survived herbivory at their low levels of productivity over a full life cycle in a more natural setting.

Overall, these results indicate that at the light intensities commonly experienced in understories of young-growth forests of the region, light availability to the understory is clearly a significant factor controlling understory productivity, whereas soil structure and composition, per se, appear less important. Our results, therefore, are consistent with the autecological findings of both Tappenier and Alaback (1989) and Rose (1990), who worked exclusively with Spodosols. We should expect that, at least on Spodosols, most species will germinate, but establishment (especially early survival—Tappenier and Alaback 1989) and subsequent growth will be controlled primarily by the availability of light, with differential sensitivities among species. Perhaps soils play more important roles in germination and establishment than in production of already established plants and thereby exert their principal effects involving species composition of understory plant communities at those stages rather than the latter. Alternatively, soil conditions more extreme than we tested (e.g., waterlogged or nutrient rich) might be more significant than what we observed in our results.

Management Implications

The principal implications of these findings for silviculture are (1) the identification of light as the major environmental factor affecting growth rates of understory species, and (2) the identification of a range of low light intensities where western hemlock seedlings do relatively more poorly than all the other understory species we studied. These findings are consistent with the earlier reported observations of strong western hemlock seedling response to wide, but not narrow, precommercial thinning treatments. They indicate that silviculture prescriptions designed to favor

nonconifer understory vegetation should open the forest canopy but also strive to maintain relatively low intensities of light at the seedling layer when western hemlock seedlings are abundant. Avoiding wide spacings in thinning is one obvious consideration. However, others might include, for example, allowing wider spacings in stands with relatively dense shrubby understories already established (the shrubs shading the seedling layer), gradually opening closed-canopied stands with a series of treatments beginning with narrow thinning and progressing to wide thinning with pruning (gradually increasing the shrub layer throughout), and maintaining a relatively closed overstory in commercial thinning (e.g., opening the lower canopy with thinning from below while maintaining the uppermost canopy, or perhaps vice versa depending on circumstances [e.g., an already moderate mid layer of canopy]). The important point is that these findings provide a basis for designing prescriptions on the basis of desired understory environments rather than simply trying to repeat empirical responses of given treatments observed elsewhere.

Conclusions

Our results are limited in several important respects. First, we did not study the germination and establishment processes and how they might be affected by light and, especially, soils. Germination and establishment play large roles in determining which species even have the opportunity to respond to light and soils in their subsequent growth. Second, our measures of light in the light trials are important in only a relative scale; they do not correspond directly to the natural light environment in young-growth forests, at least not in quality (wavelengths and their variation). Our measures of light in the field experiment were from only two stands and cannot be considered representative of all conifer and red alder young-growth forests. Similarly, our soils in both studies were artificial—a simple potting mixture in the light trials and simulated soils in the field experiment that were unavoidably disturbed when profiles were reconstructed. Thus, the implications of our studies are difficult to relate directly to the field, especially quantitatively. Nevertheless, despite those limitations, our results point to several important qualitative conclusions:

1. Several key understory species of southeast Alaska forests differ in their growth responses to variation in the quantity of light in their environment, with some species such as bunchberry being able to benefit greatly from even extremely low levels of light, and other species such as western hemlock requiring greater levels of light to respond fully. All four of our nonconifer understory species were relatively more efficient at low light intensities than was western hemlock, indicating the potential existence of a window of opportunity at low intensities of light for silviculture treatments designed to benefit understory species but not western hemlock seedlings.

However, above those low levels of light, western hemlock should be a very strong competitor.

2. At light intensities common in young-growth forests of southeast Alaska, light availability is a major, if not most important, factor in controlling understory productivity. Once established, most species respond strongly to light availability.
3. Environmental factors affecting other stages of plant life cycles (dispersal, germination, establishment) and perhaps the role of herbivory need further study to determine the relative importance of light and soils in those processes as well.

Although western hemlock has long been considered a very shade-tolerant species by foresters and silviculturists ("Only Pacific yew and Pacific silver fir are considered to have equal or greater tolerance of shade than western hemlock."—Packee 1990: 618), our results demonstrate that in comparison with major understory species of southeast Alaska, western hemlock is quite sensitive to light availability and is comparatively shade intolerant in terms of its growth. Southeast Alaska is a region of dense forests with dark understories. It is not surprising that availability of light might be such a critical environmental factor and that common understory species are so well adapted to exploiting low intensities of light. A better understanding of differential species responses to light throughout their life cycles may yield disproportionate advances in the design of silviculture systems for multiple benefits.

Acknowledgments

We thank Robert Deal, Michael Newton, Michael McClellan, and Patrick Cunningham for their helpful reviews of an earlier draft of this paper. We thank Mark "The Human Backhoe" Miller for his indefatigable effort in helping with the installation of the Alaska field experiments.

English Equivalents

When you know:	Multiply by:	To find:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Grams (g)	0.0352	Ounces
Kilograms (kg)	2.205	Pounds
Degrees Celsius (°C)	1.8 °C + 32	Degrees Fahrenheit

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Appendix: About the Experimental Design of the Field-Manipulation Experiments

As explained in footnote 1, our experimental design lacked replication of the alder and conifer light treatments, because we had only one stand of each available to us for this work. Therefore, although we replicated soil treatments within those two stands, and the two canopies provided very different light intensities for testing our hypotheses about light and its interaction with soils, our analysis cannot say anything about differences between alder and conifer canopies per se. Also, we must acknowledge that, from a strictly technical point of view, our light-intensity treatment can be viewed as a case of pseudoreplication instead of true replication, because with only one stand of each overstory, there was not spatial intermixing of the two light treatments. It could be argued that some other, unspecified environmental factor may have varied spatially with the two stands too, and effects of that unknown factor would not be distinguishable from the effects of light.

However, from a practical and much more real point of view, we point out that the difference in light intensities between the two stands was a full order of magnitude, and the two stands were adjacent to one another and both on near-level ground (i.e., no difference in elevation, slope, exposure, etc.). Any other factor that we can think of (e.g., light wavelengths, relative humidity, air temperature) would have been independent of spatial replication and therefore not affected by "true replication" (note that all our soils were in pots, and truly replicated understories would have been similar among replicates). Therefore, unless one argues the potential existence of some unknown factor that depended on spatial location rather than canopy type, we argue that the case for bias from pseudoreplication is exceptionally weak here—far too weak to outweigh the insights from the factorial analysis of the data.

Problems from correlation among potential factors independent of true replication (e.g., light, relative humidity, and air temperature all varying together with stand type) are inherent in field experiments. They can't be controlled by replication; they require a laboratory setting (e.g., growth chambers), but that makes the experiment even more removed from the natural environment. Our experiments, using replicated artificial soils in pots under unreplicated natural forest canopies were a compromise between the natural environment and a more rigorously controlled experiment. Our conclusions and implications must be evaluated accordingly.

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Pacific Northwest Research Station
333 SW First Avenue
P.O. Box 3890
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