

Chapter 6: Effects of Climate Change on Forest Vegetation

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Introduction

Projected rapid changes in climate will affect vegetation assemblages in the Intermountain Adaptation Partnership (IAP) region directly and indirectly. Direct effects include altered vegetation growth, mortality, and regeneration, and indirect effects include changes in disturbance regimes (Chapter 8) and interactions with altered ecosystem processes (e.g., hydrology, snow dynamics, nonnative species) (Bonan 2008; Hansen and Phillips 2015; Hansen et al. 2001, 2016; Notaro et al. 2007). Some species may have decreased abundance, whereas others may expand their range (Landhäusser et al. 2010). New vegetation communities may form, and historical vegetation complexes may shift to other areas of the landscape or become rare. The consequences of land management policies and activities, including fire exclusion, fuels treatments, and grazing, interact with potential climate change effects.

Here we assess the effects of climate change on vegetation in the IAP region, based on species autecology, disturbance regimes, current conditions, and modeling results (table 6.1). We summarize how climate change affects vulnerability of important tree species, vegetation types, and resources of concern (box 6.1). We have integrated modeling results with a detailed synthesis of climate change literature for western North America.

This assessment is focused on vegetation types listed in table 6.1, where the vulnerability of each vegetation type is inferred from the aggregate vulnerability of its dominant species (table 6.2). Vulnerability is also considered with respect to heterogeneous landscapes, including both vegetation disturbance and land use history.

All projections of future conditions contain uncertainty (box 6.2). Uncertainty can result from a lack of information or from a disagreement about what is known or predictable. Uncertainty can also result from known and unknown errors. It may have many sources, including quantifiable errors in data, ambiguously defined concepts or terminology, and uncertain projections of human behavior. Uncertainty can be represented by quantitative measures (e.g., a range of values) or by qualitative statements (e.g., judgment of a team of experts).

Climate Change Assessment Techniques

Ecologists have invested considerable effort to project the effects of climate change on ecosystem processes across various scales (Clark et al. 2001; Joyce et al. 2014; Schumacher et al. 2006). Using traditional field methods to explore climate change response is difficult because of the complex interactions between ecological processes, disturbance, and climate at multiple temporal and spatial scales (McKenzie et al. 2014).

Four techniques exist to assess and project the effects of climate change on vegetation and related resource concerns. First, **expert opinion** involves experts in the fields of climate change, ecology, and vegetation dynamics qualitatively assessing what will happen to vegetation under various climate change scenarios. Second, **field assessment** involves monitoring or remote sensing to monitor vegetation change as the climate warms. Field sampling involves establishing plots across the landscape, detecting change between plot measurements, and correlating these changes to climate data. Demographic studies track individuals over time, rather than using plot-scale inventories, to understand the role of climate relative to other factors. The U.S. Department of Agriculture Forest Service (USFS) Forest Inventory and Analysis database, the only demographic dataset in the IAP region, has not been analyzed for the interaction of vegetation and climate. Although field assessment techniques are the most reliable and useful, they are often intractable because of the large areas and long time periods for which sampling is needed to detect changes.

Third, **statistical analysis can be used to create empirical models** that project climate change response. Many studies that project habitat, range, or occupational shifts of tree species from climate warming use species distribution models (SDMs; also called bioclimatic envelope models or niche models) to project future geographic ranges (Hansen and Phillips 2015; Iverson and Prasad 2002; Warwell et al. 2007). However, SDMs are inherently flawed for projecting future species distributions because they rely on recent or historical climate-species relationships, resulting in predictions of potential species habitat, not actual species distribution (Iverson and McKenzie 2013). One of the biggest limitations of this approach is that most species distributions are not in equilibrium with climate, thereby causing SDMs to miss areas favorable for a species but where the species is currently absent. In addition, SDMs do not include critical ecological processes (e.g., reproduction,

Table 6.1—Vegetation types included in the IAP vulnerability assessment.

Vegetation type ^a	Description
Subalpine pine forest	Forest communities dominated or co-dominated by bristlecone, limber, and/or whitebark pine for long periods of time. Other co-dominant trees may include subalpine fir, Engelmann spruce, white fir, and aspen.
Subalpine spruce-fir forest	Upland forest communities in which the most shade-tolerant tree capable of occupying the site is subalpine fir, Engelmann spruce, and/or blue spruce. Major seral species include lodgepole pine, aspen, and Douglas-fir.
Mesic mixed conifer forest	Upland forest communities where the most shade-tolerant tree capable of occupying the site is grand fir, white fir, Shasta red fir, mountain hemlock, or Sierra lodgepole pine. Major seral species include lodgepole pine, Douglas-fir, ponderosa pine, Jeffery pine, and aspen.
Dry mixed conifer forest	Upland, lower montane, forest communities where the most shade-tolerant tree capable of occupying the site is Douglas-fir, white fir, or limber pine; and woodland species such as curl-leaf mountain mahogany, Gambel oak, bigtooth maple, pinyons, and junipers are usually present. Ponderosa pine is a major seral species. Lodgepole pine is absent. Aspen is sometimes an important seral species.
Aspen-mixed conifer forest	Upland forest communities where the most shade-tolerant tree capable of occupying the site is a conifer species but aspen is (or was) an important component due to periodic disturbances. Following a disturbance, conifers can return to dominance in less than 150 years.
Persistent aspen forest	Upland forest communities dominated by aspen in which succession to conifer dominance is not possible or takes longer than 150 years.
Ponderosa pine forest	Upland forest communities where ponderosa pine is the only forest tree species capable of occupying the site, or where natural under-burning periodically eliminates other conifers and maintains ponderosa pine dominance.
Riparian forest	Forest communities occurring adjacent to water bodies or around seeps and springs. They may be dominated by any of the species listed above in addition to cottonwoods, willows, alders, birch, or nonnative trees such as saltcedar and Russian olive.

^aVegetation types are those used by the U.S. Forest Service Intermountain Region.

tree growth, competitive interactions, disturbance) (Iverson and McKenzie 2013; Watling et al. 2012).

Finally, the most effective technique uses **modeling to assess climate-mediated vegetation responses** (Gustafson 2013; Iverson and McKenzie 2013; McKenzie et al. 2014), incorporating projected future climate into ecological models to simulate climate change effects (Baker 1989; He et al. 2008; Keane et al. 2004; Merriam et al. 1992; Perry and Millington 2008). Many existing models simulate ecological change at broad (global, regional) and fine (point, ecosystem, stand) scales (Bugmann 2001; Cramer et al. 2001). However, models focused on large spatial scales (50–500 square miles) are best suited for projecting climate change effects because most ecosystem processes operate and most management decisions are made at large scales (Cushman et al. 2007; Littell et al. 2011; McKenzie et al. 2014).

To realistically model species composition changes, a mechanistic, process-driven simulation approach is needed to emphasize physical drivers of vegetation dynamics that are directly related to climate (Falk et al. 2007; Gustafson 2013; McKenzie et al. 2014). However, mechanistic model design is complex, containing detailed parameterization of species life histories and physiologies, interacting disturbance factors, and high-resolution modeling over large areas

(Lawler et al. 2006). Dynamic global vegetation models operate at scales from regional (hundreds of miles) to global (degrees of latitude and longitude), projecting aggregates of species as life forms or plant functional types, which may not be directly relevant for resource managers (Bachelet et al. 2003; Bonan 2008; Neilson et al. 2005). Most of these models project shifts to more drought-tolerant and disturbance-tolerant species in a warmer climate. In some models, increased water-use efficiency in trees, induced by elevated carbon dioxide (carbon dioxide fertilization), may offset this general shift in vegetation as forests expand into areas where the climate is currently too dry (Bachelet et al. 2003).

Ecosystem models that accurately project climate change effects must simulate disturbances, vegetation, climate, and their interactions across multiple spatial scales (Purves and Pacala 2008), but few models simulate ecosystem processes with the mechanistic detail needed to realistically represent important interactions (Keane et al. 2015b; Riggs et al. 2015) (table 6.2). For example, direct interactions between climate and vegetation may be more realistically represented by simulating the daily dynamics of carbon (photosynthesis, respiration), water (evapotranspiration), and nutrients at the plant level than by simulating vegetation development

Box 6.1—Summary of the Primary Effects of Climate Change on Vegetation Types in the IAP Region

Syntheses of autecological information, empirical data, and modeling were used to identify expected responses of forest vegetation in the IAP region through the end of the 21st century, summarized here for vegetation types (table 6.1)

Subalpine Pine Forest

Highly vulnerable

- Whitebark pine will be especially vulnerable, because warming is expected to exacerbate existing stressors (white pine blister rust, mountain pine beetle, fire exclusion).
- Limber pine, Engelmann spruce, and white fir may grow faster with less snowpack (longer growing season), although limber pine could be stressed by more bark beetles.
- Great Basin and Rocky Mountain bristlecone pines growth may decrease but with high variability among locations.
- Quaking aspen will be minimally affected by a warmer climate, especially compared to aspen at lower elevations.

Subalpine Spruce-Fir Forest

Moderately vulnerable

- Subalpine fir, Engelmann spruce, and blue spruce may grow faster in the upper subalpine zone because of less snowpack (longer growing season).
- Lodgepole pine will be more susceptible to mountain pine beetle.
- Quaking aspen will be minimally affected by a warmer climate, especially compared to aspen at lower elevations.
- Douglas-fir could increase at the lower end of the subalpine zone.
- Increased wildfire could reduce the distribution of all subalpine species except aspen.

Mesic Mixed Conifer Forest

Moderately vulnerable; some winners, some losers

- Douglas-fir, ponderosa pine, and Jeffrey pine (early seral, fire tolerant) may become relatively more common than other (late seral) species that are less fire tolerant, but they will probably grow slower.
- Shasta red fir will grow slower, and distribution may decrease because of increased wildfire.
- Lodgepole pine and quaking aspen, which regenerate rapidly after wildfire, will persist across the landscape, possibly with increased stress from insects and pathogens.

Dry Mixed Conifer Forest

Moderately vulnerable; some winners, some losers

- Curl-leaf mountain-mahogany, Gambel oak, and bigtooth maple can cope with both drier soils (drought tolerant) and increased wildfire (vigorous sprouting), and they may become more abundant in some locations.
- Two-needle pinyon and singleleaf pinyon are sensitive to long periods of drought combined with insects, and they may have reduced growth and some mortality; frequent wildfire may reduce abundance.
- Limber pine may be challenged by a combination of mountain pine beetles, white pine blister rust, and increasing wildfire.
- Douglas-fir and white fir growth will decrease; white fir will be less abundant if wildfire frequency increases.

Aspen-Mixed Conifer Forests

Moderately vulnerable, depending on vegetation

- Mature spruce-fir forest will become less common if wildfire frequency increases.
- At higher elevations, early-seral species such as quaking aspen will become more abundant and possibly more widely distributed.
- At lower elevations, ponderosa pine will persist, and quaking aspen and Gambel oak will become more abundant.

Box 6.1—continued.

- Changes in species distribution and abundance will depend on topography (north vs. south aspect, canyons vs. side slopes, etc.).

Persistent Aspen Forests

Moderately vulnerable, depending on vegetation

- Mature spruce-fir forest will become less common if wildfire frequency increases.
- Aspen will maintain dominance because of its ability to sprout after wildfire.
- At lower elevations, ponderosa pine will persist, and quaking aspen and Gambel oak will become more abundant.
- Douglas-fir will probably persist because it has relatively high drought and fire tolerance, but will grow slower.

Montane Pine Forests

Moderately vulnerable

- Ponderosa pine will maintain and probably increase dominance over associated species that are less tolerant of drought and wildfire, but it may grow slower.
- Limber pine and bristlecone pine will probably persist at higher elevations where fuel loads are low.
- If bark beetles become more prevalent, they could increase stress and mortality in pine species, especially during drought periods.

Riparian Forests

Highly vulnerable

- Vegetation dominance will transition to species that are more tolerant of seasonal drought, including ponderosa pine and other deep-rooted conifers.
- Hardwood species that rely on periodic high water levels for regeneration will become less common.
- Riparian forests associated with small or transient water sources (e.g., springs) will be more susceptible than forests near large water sources (e.g., rivers). Low-elevation riparian forests near small water sources will be more susceptible than high-elevation forests with persistent snowpack.
- Saltcedar will persist in riparian areas because it is more drought tolerant than native vegetation, but tamarisk beetle is a promising biocontrol.

annually using state-and-transition modeling approaches (Keane et al. 2015a).

Forest Vegetation Responses to Climate

The effects of climate change on forest vegetation are likely to be driven primarily by vegetation responses to altered disturbance regimes, and secondarily through direct effects on vegetation through shifts in regeneration, growth, and mortality (Dale et al. 2001; Flannigan et al. 2009; Temperli et al. 2013) (box 6.3). Effects on vegetation caused by a changing climate (Chapter 3) will vary over different spatial and temporal scales. Trees will respond to reduced water availability, higher temperatures, and changes in growing season in different ways, but because trees are stationary organisms, altered vegetation composition and structure will be the result of changes in plant processes and

responses to disturbance. This section discusses responses of trees and other forest vegetation to projected climate.

Individual Plant Effects

There are several important modes of response of plants to changing climates (Joyce and Birdsey 2000). The first is changes in **productivity**, which could increase in some locations because of increasing temperatures, longer growing seasons, and improved water-use efficiency (Aston 2010; Joyce 1995). The window of successful **seedling establishment** will change (Ibáñez et al. 2007), and increasing drought and high temperatures may narrow the time for effective regeneration in low-elevation forests and widen the window in high-elevation forests. Climate may directly cause **tree mortality** through the effects of increased temperature on moisture stress in trees. Extreme climatic events, such as late growing-season frosts and high winds causing breakage and blowdowns, may increase because of projected increases in climatic variability (Notaro 2008), and these events may cause mortality (Joyce et al. 2014; Vanoni

Table 6.2—Dominant tree species in each vegetation type (see table 6.1) in each IAP subregion. Indicator species are shown in bold text.

Vegetation type ^a	Middle Rockies	Greater Yellowstone	Uintas and Wasatch Front	Plateaus	Great Basin	Intermountain Semi Desert
Subalpine pine forest	<u>PNV</u> Whitebark pine	<u>PNV</u> Whitebark pine	<u>PNV</u> Whitebark pine Limber pine	<u>PNV</u> Limber pine GB bristlecone pine^c	<u>PNV</u> Limber pine GB bristlecone pine	
Subalpine spruce-fir forest	<u>PNV</u> Subalpine fir Engelmann spruce <u>Seral</u> Lodgepole pine Douglas-fir Western larch	<u>PNV</u> Subalpine fir Engelmann spruce <u>Seral</u> Lodgepole pine Douglas-fir	<u>PNV</u> Subalpine fir Engelmann spruce <u>Seral</u> Lodgepole pine Douglas-fir	<u>PNV</u> Subalpine fir Engelmann spruce Blue spruce <u>Seral</u> Douglas-fir	<u>PNV</u> Subalpine fir Engelmann spruce Blue spruce <u>Seral</u> Lodgepole pine Douglas-fir	
Mesic mixed conifer forest	<u>PNV</u> Grand fir Douglas-fir <u>Seral</u> Lodgepole pine Douglas-fir Ponderosa pine Western larch	<u>PNV</u> Douglas-fir <u>Seral</u> Lodgepole pine	<u>PNV</u> White fir Douglas-fir <u>Seral</u> Lodgepole pine Douglas-fir	<u>PNV</u> White fir Douglas-fir <u>Seral</u> Douglas-fir Ponderosa pine	<u>PNV</u> White fir Sierra white fir Shasta red fir Mountain hemlock Sierra lodgepole pine <u>Seral</u> Sierra lodgepole pine Western white pine Jeffrey pine Ponderosa pine	
Dry mixed conifer forest	<u>PNV</u> Douglas-fir Grand fir <u>Seral</u> Ponderosa pine Douglas-fir	<u>PNV</u> Douglas-fir Limber pine <u>Seral</u> Limber pine	<u>PNV</u> White fir Douglas-fir <u>Seral</u> Ponderosa pine Gambel oak Curl-leaf mtn.-mahogany Bigtooth maple Rocky Mtn. juniper	<u>PNV</u> White fir Douglas-fir <u>Seral</u> Ponderosa pine Gambel oak Curl-leaf mtn.-mahogany Bigtooth maple Utah juniper Two-needle pinyon	<u>PNV</u> White fir Sierra white fir Douglas-fir <u>Seral</u> Ponderosa pine Jeffrey pine Gambel oak Curl-leaf mtn.-mahogany Bigtooth maple Utah juniper Singleleaf pinyon	

Table 6.2—Continued.

Vegetation type ^a	Middle Rockies	Greater Yellowstone	Uintas and Wasatch Front	Plateaus	Great Basin	Intermountain Semi Desert
Aspen-mixed conifer forest	PNV Subalpine fir Engelmann spruce Grand fir Douglas-fir <u>Seral</u> Aspen Lodgepole pine Douglas-fir Ponderosa pine	PNV Subalpine fir Engelmann spruce Douglas-fir <u>Seral</u> Aspen Lodgepole pine Douglas-fir	PNV Subalpine fir Engelmann spruce White fir Douglas-fir <u>Seral</u> Aspen Lodgepole pine Douglas-fir Ponderosa pine Gambel oak Curl-leaf mtn.-mahogany Bigtooth maple	PNV Subalpine fir Engelmann spruce Blue spruce White fir Douglas-fir <u>Seral</u> Aspen Douglas-fir Ponderosa pine Gambel oak Curl-leaf mtn.-mahogany Bigtooth maple	PNV White fir Sierra white fir Shasta red fir <u>Seral</u> Aspen Sierra lodgepole pine Jeffrey pine Western juniper	
Persistent aspen forest	None	PNV Aspen Subalpine fir Engelmann spruce Douglas-fir <u>Seral</u> Aspen Lodgepole pine	PNV Aspen Subalpine fir Engelmann spruce White fir Douglas-fir <u>Seral</u> Aspen Lodgepole pine	PNV Aspen Subalpine fir Engelmann spruce Blue spruce White fir Douglas-fir <u>Seral</u> Aspen Douglas-fir Ponderosa pine Gambel oak Curl-leaf mtn. mahogany Bigtooth maple	PNV Aspen White fir Sierra white fir Shasta red fir <u>Seral</u> Aspen Sierra lodgepole pine Jeffrey pine Western juniper	PNV Aspen (snow pockets)
Montane pine forest	PNV Douglas-fir Ponderosa pine Grand fir Limber pine <u>Seral</u> Ponderosa pine Douglas-fir Limber pine	PNV Limber pine Douglas-fir <u>Seral</u> Limber pine	PNV Limber pine Ponderosa pine Douglas-fir White fir GB bristlecone pine <u>Seral</u> Limber pine GB bristlecone pine Ponderosa pine	PNV Limber pine GB bristlecone pine Ponderosa pine Douglas-fir White fir <u>Seral</u> Limber pine GB bristlecone pine Ponderosa pine	PNV Limber pine GB bristlecone pine Ponderosa pine Jeffrey pine Douglas-fir White fir Shasta red fir <u>Seral</u> Limber pine GB bristlecone pine Ponderosa pine Jeffrey pine Douglas-fir	

Table 6.2—Continued.

Vegetation type ^a	Middle Rockies	Greater Yellowstone	Uintas and Wasatch Front	Plateaus	Great Basin	Intermountain Semi Desert
Riparian forest	PNV Subalpine fir Engelmann spruce Grand fir Douglas-fir Ponderosa pine Aspen Black cottonwood White alder Sitka alder Thinleaf alder Water birch	PNV Subalpine fir Engelmann spruce Blue spruce Douglas-fir Aspen Lodgepole pine Narrowleaf cottonwood Black cottonwood Balsam cottonwood Water birch Thinleaf alder Boxelder Crack willow	PNV Subalpine fir Engelmann spruce Blue spruce Douglas-fir Ponderosa pine Aspen Lodgepole pine Narrowleaf cottonwood Fremont cottonwood Water birch Thinleaf alder Boxelder Velvet ash Crack willow Salt cedar	PNV Subalpine fir Engelmann spruce Blue spruce White fir Douglas-fir Ponderosa pine Aspen Narrowleaf cottonwood Fremont cottonwood Water birch Thinleaf alder Boxelder Velvet ash Crack willow Salt cedar	PNV Subalpine fir Engelmann spruce Blue spruce White fir Sierra white fir Shasta red fir Sierra lodgepole pine Douglas-fir Jeffrey pine Ponderosa pine Aspen Lodgepole pine Narrowleaf cottonwood Black cottonwood Lanceleaf cottonwood Water birch Thinleaf alder	

^aVegetation types are those used by the U.S. Forest Service Intermountain Region.

^bPNV indicates potential natural vegetation.

^c“GB bristlecone pine” indicates Great Basin bristlecone pine.

et al. 2016). There will also be disruptions in **phenology** in a warmer climate, with some plants suffering damage or mortality when phenological cues and events are mistimed with new climates (e.g., flowering during dry portions of the growing season) (Cayan et al. 2001). In addition, the **genetic limitation** of species or trees to respond to climate change will vary greatly among species and populations (Hamrick 2004). For example, species restricted to a narrow range of habitat conditions may become maladapted to new climates (St. Clair and Howe 2007).

Plants can respond to climate-mediated changes in different ways (Aitken et al. 2008). Direct effects of temperature at the cellular level may increase photosynthesis and respiration (Waring and Running 1998). Photosynthesis rates increase with temperature up to an optimum and decline thereafter, although potential effects on tree growth vary by species and local soil and moisture conditions. In the IAP region, any decrease in tree growth would be expected to occur at low elevations, whereas some trees at high elevations may have increased growth. Respiration increases with temperature, and respiration occurs even when stomata are closed, so high temperatures coupled with low water availability may result in high respiratory losses with few photosynthetic gains (Ryan et al. 1995).

Increased atmospheric carbon dioxide levels may also directly modify physiological growth processes at the cellular

level. Water-use efficiency may increase for some conifer species, potentially compensating for lower water availability (Waring and Running 1998). Leaf biomass is usually the first to increase as plants attempt to optimize photosynthesis by growing more leaf tissue (i.e., leaf area), although increased leaf area can be transitory depending on available water and nitrogen. Higher atmospheric carbon dioxide levels and temperatures can also interact to increase growth, especially if warmer temperatures are closer to temperature optima for photosynthesis.

Another direct effect of warming temperatures is longer growing seasons (Cayan et al. 2001; McKenzie et al. 2009). In addition, future climate may be more variable, affecting dormancy regulation, bud burst, and early growth (Hanninen 1995; Harrington et al. 2010). Plant phenological cues may be disrupted or triggered inappropriately because of high weather variability, a response that may be fatal for seedlings. Warmer temperatures may reduce growing-season frosts in mountain valleys, thereby allowing more frost-susceptible species, such as ponderosa pine (*Pinus ponderosa*) to exist in habitats currently occupied by lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Increased temperatures may result in decreased winter chilling, which could result in delayed bud burst, reduced flowering, and reduced seed germination (Chmura et al. 2011).

Box 6.2—Uncertainty and Climate Change Effects on Vegetation

Global Climate Models (GCMs) that project rapidly warming climates have a high degree of uncertainty. Although it is clear that increasing atmospheric carbon dioxide will cause a significant increase in temperature (IPCC 2007), uncertainty exists about the magnitude and rate of climate change (Roe and Baker 2007; Stainforth et al. 2005). This uncertainty is generally higher for climate projections made at fine resolutions and for longer time periods (Knutti and Sedlacek 2013). The range of possible projections of future climate from GCMs (anywhere from a 1.6 to 8 °C increase in global average annual temperature) is much greater than the variability of climate over the past 3 centuries (Stainforth et al. 2005), and the variability across GCMs is greater than the variability in each model's climate projections.

Because it is impossible to know whether society will respond to climate change by employing technological innovations to minimize carbon dioxide emissions or to mitigate its effects, most GCMs also simulate a range of scenarios that capture different strategies and socioeconomic policies to deal with climate change, introducing yet another source of uncertainty. Moreover, it is the high variability of climate extremes, not the gradual change of average climate, that will drive most ecosystem responses to disturbance and plant dynamics—and these rare, extreme events are the most difficult to project (Easterling et al. 2000).

Yet another source of uncertainty is introduced when we try to project how the Earth's vegetation and ecosystems will respond to climate change (Araujo et al. 2005). Mechanistic ecological simulation of climate, vegetation, and disturbance dynamics across landscapes is still evolving (Keane and Finney 2003; Sklar and Costanza 1991; Walker 1994). Many current ecosystem simulation models are missing important direct interactions of disturbance, hydrology, and land use with climate that will affect plant distributions (Notaro et al. 2007). Little is known about the interactions among climate, vegetation, and disturbance, and interactions among different disturbance regimes (e.g., fire and beetles) could create novel landscape behaviors. It is also difficult to determine how plant and animal reproduction, growth, and mortality will respond to changing climate (Gworek et al. 2007; Ibanez et al. 2007; Keane et al. 2001; Lambrecht et al. 2007). These modeling uncertainties greatly increase as projections are made further into the future and at finer spatial scales (Xu et al. 2009).

Uncertainties need to be considered when using this assessment for analysis, planning, and project management. Sometimes there is less uncertainty in implementing conventional restoration designs than in designing restoration or treatment plans that attempt to account for climate change effects. For example, including climate change in restoration of western larch ecosystems may be more straightforward than for ponderosa pine ecosystems. Because all climate effects will be manifest in different ways on different landscapes, there is no “one-size-fits-all” prescription that can be adopted everywhere.

Much of the water used by trees in mountain forests comes from snowmelt, so amount and duration of snowpack influence regeneration and growth patterns of tree species and forest communities. Warmer temperatures will cause earlier snowmelt, leading to an earlier start of the growing season, and longer periods of low soil moisture during the rest of the growing season. In contrast, less snowpack will create longer growing seasons in subalpine communities where cold and snowpack duration limit tree regeneration and growth, potentially facilitating increased productivity (Peterson and Peterson 2001) and regeneration (Woodward et al. 1994).

Climate change can indirectly affect vegetation by altering mycorrhizal dynamics (Amaranthus et al. 1999). Many trees, particularly in the seedling and sapling stages, need mycorrhizae to survive, especially in areas with chronic water shortage (Mohatt et al. 2008; Walker et al. 1995). Migration of tree species to more favorable sites in future climates may be governed by the ability of mycorrhizae to also populate these areas (Lankau et al. 2015). Mycorrhizal responses following wildfire are important because fire is expected to increase significantly in a warmer climate (Chapter 8). Establishment of trees in burned areas can be delayed for

decades or even centuries (Little et al. 1994), as both mycorrhizae and trees revegetate the area (Schowalter et al. 1997).

Migrating to a new site has historically been the main response of plants to climate change (Huntley 1991), requiring that species have the ecological ability to quickly occupy available sites and the genetic capacity to survive and reproduce successfully (Davis et al. 2005). Most tree species in the IAP region are long lived and genetically diverse, so they can survive wide fluctuations of weather, but the interaction of increasing drought and modified disturbance regimes will play a role in the future distribution and abundance of forest species (Allen et al. 2010) (Chapter 8).

A warmer climate is expected to facilitate upward shifts in the elevation distribution of plant species. For example, Lenoir et al. (2008) found that some plant species have moved upward in elevation at a rate of 100 feet per decade, but it is unclear whether such shifts will drive long-term changes in forest communities. For example, wildfire plays a dominant role in most ecosystems in western North America, and increasing wildfire frequency and extent may overwhelm potential shifts in forest species distribution. The potential for tree populations to migrate may vary among diverse mountain ranges, depending on local biophysical conditions.

Box 6.3—How Do Climate Change Vulnerability Assessments and Adaptation Inform Ecological Restoration?

In an ideal sense, *ecological restoration* is defined as the practice of reestablishing historical plant and animal communities in a given area and the renewal of ecosystem and cultural functions necessary to maintain these communities now and into the future (Egan and Howell 2001). However, this ideal may be difficult to manage because: (1) little is known about historic conditions, (2) many key species may already be lost, (3) some efforts may be prohibitively expensive, and (4) future climates will create novel ecosystems. As a result, The Society for Ecological Restoration has opted for a definition that states that ecological restoration is “the process of renewing and maintaining ecosystem health.”

The U.S. Forest Service manual direction (FSM 2020) includes objectives and a policy for restoration:

- *Restore and maintain ecosystems* that have been damaged, degraded, or destroyed by reestablishing the composition, structure, pattern, and ecological processes.
- *Manage for resilient ecosystems* that have a greater capacity to withstand stressors, absorb and recover from disturbances, and reorganize and renew themselves, especially under changing and uncertain environmental conditions.
- *Achieve long-term ecological sustainability* and provide a broad range of ecosystem services to society.

The Forest Service emphasizes ecosystem restoration across all National Forest System lands with the goal of attaining resilient ecosystems. All strategic plans, including the Forest Service Strategic Plan and land management plans, must include goals and objectives to sustain the resilience and adaptive capacity of aquatic and terrestrial ecosystems by reestablishing, maintaining, or modifying their composition, structure, function, and connectivity. The goals and objectives must be established within this framework as defined by laws, Indian treaties and Tribal values and desires, and regulations. The goals and objectives must also consider public values and desires, social concerns, economic sustainability, the historical range of variability, ecological integrity, current and likely future ecological capabilities, a range of climate and other environmental change projections, the best available scientific information, and technical and economic feasibility to achieve desired conditions for National Forest System lands.

A primary element of an integrated approach is to identify and eliminate or reduce stressors that degrade or impair ecosystems. Restoration activities should also take into account social and ecological influences at multiple scales and incorporate the concept of a dynamic system and ecological trajectory. Some ecosystems may have been altered to such an extent that reestablishing components of the historical range of variability may not be ecologically or economically possible. Therefore, goals and activities can focus on restoring the underlying processes that create functioning ecosystems.

Functional restoration, an alternative concept used in the Forest Service, is defined as the “restoration of abiotic and biotic processes in degraded ecosystems.” Functional restoration focuses on underlying processes that may be degraded, regardless of the structural condition of the ecosystem. As contrasted with ecological restoration that tends to seek a historical reference condition, functional restoration focuses on dynamic processes that drive structural and compositional patterns. Functional restoration aims to restore functions and improve structures with a long-term goal of restoring interactions between function and structure. However, a functionally restored system may look quite different than the historical reference condition in terms of structure and composition. In this case, disparities cannot be easily resolved, because a threshold of degradation has been crossed, or environmental drivers (e.g., climate) that influenced structural and compositional development have changed.

Reproduction

Cone and seed crops of some tree species could be affected by climate change (Ibáñez et al. 2007; LaDeau and Clark 2001). Low-elevation, xeric forests may have fewer and smaller cone crops because of increased stand density and water stress. Cone crops may also have a lower percentage of viable seed because of increased stress. Infrequent cone crops coupled with low seed production may cause reduced regeneration in recently burned areas, in some cases resulting in dominance of nonforest vegetation. The opposite may be true in higher, colder environments, where increased temperatures will increase growing season length and thereby increase potential for more cone crops with more seeds. Spruce-fir communities may produce so much

seed that they overwhelm regeneration of other conifers, especially after mixed-severity fires. Species such as whitebark pine (*Pinus albicaulis*) and lodgepole pine have unique cone characteristics; whitebark pine cones require birds for seed dispersal, and lodgepole pine cones may be serotinous and opened only by fire.

Growth and Mortality

Climate adversely affects growth and mortality through decreased water availability, resulting in shorter effective growing seasons (Bugmann and Cramer 1998; Chmura et al. 2011; Keane et al. 2001; Williams et al. 2010). Extended droughts require conifers to close stomata longer to conserve water. Ponderosa pine and limber pine (*Pinus flexilis*)

have excellent stomatal control, and stomata can remain closed for long periods of time; Douglas-fir (*Pseudotsuga menziesii*) has poor stomatal control, which can drive leaf water potentials to low values and contribute to physiological damage (Sala et al. 2005). If photosynthetic production cannot exceed respiration demands, then plants become stressed.

If physiological damage is high enough, carbon storage in plant cells may decline as a result of stomatal closure and insufficient carbon assimilation to meet demands for tissue maintenance. In addition, lack of water for uptake, especially while stomata are open, can greatly reduce hydraulic conductance (McDowell et al. 2008; Sevanto et al. 2014). Both of these physiological responses to low water supply, which typically occur during prolonged drought, can substantially reduce vigor, making weakened trees more susceptible to other stresses. In the most extreme cases, the ultimate outcome is tree mortality, often facilitated by bark beetles or other insects.

In mesic ecosystems in the IAP region, a warmer climate may enhance growth and decrease mortality (Wu et al. 2011). Earlier growing seasons with ample moisture, as projected for some forests, may promote increased productivity. This will be especially true at higher elevations where cold temperatures, not moisture, limit tree growth. Increased biomass will also amplify competition between species, thereby favoring shade-tolerant individuals in the absence of disturbance. Increased biomass could also reduce resistance to forest insect and diseases (Chapter 8).

Regeneration

Microsite conditions required for successful establishment of tree species are typically rare, so seed germination and survival, especially for seeds that are wind dispersed, are rarely successful (Anderson and Winterton 1996). Suitable moisture conditions must persist for long periods of time for seed germination and early seedling growth. In dry forests, most of the successful regeneration occurs in years when soils are moist for an adequate time and heating at the soil level does not kill developing leaves and stems. A warmer climate may decrease the frequency of high-regeneration years, and regeneration may become rare on the driest sites. In contrast, regeneration may be enhanced by warming at high elevation because earlier snowmelt will provide more time for seedlings to survive and grow (Butler 1986).

During mild winters, seed chilling requirements may not be met for some species, thereby reducing germination. In addition, germination may be delayed to drier times during the growing season. For example, Nitschke and Innes (2008) found that in a warmer climate, chilling requirements were not met for most low-elevation tree species in British Columbia. High soil temperatures can stress both germinants and established seedlings (Rocheffort et al. 1994). Climate change may also affect the dispersal properties of seeds. For example, rodent and bird species that disperse seeds may shift habitats because of climate-mediated

changes (Tomback 1998). Longer and drier summers and autumns suggest that seed dispersal may occur when the ground and litter are dry and unsuitable for seed germination and establishment (Neilson et al. 2005).

Genetics and Species Adaptation

Climate affects plant phenotypes and is an agent of natural selection. Plant adaptations to local environments have often developed a **clinal** (or continuous) response to abiotic and biotic factors. In addition, **ecotypic** (or discontinuous) response to environmental gradients may play an important role, depending on local soils and topography. Therefore, a combination of clinal and ecotypic environmental gradients determines long-term plant survival and persistence across the landscape.

Natural selection, migration, genetic drift, and mating system determine species genetic composition. Thus, the ability of plant populations to respond to climate change is influenced by underlying patterns of genetic variation. Molecular markers can reveal significant genetic diversity and divergence among populations. Populations may diverge because of fire, volcanic activity (Hansen 1949), glaciation (Hamrick 2004), seed dispersal agents (Lorenz and Sullivan 2009), and pollinator history. Plants that are pollinated by insects or rely on animals to disperse seed are more vulnerable to climate change than plants with wind-dispersed seed, because of the requirement for interaction with another organism.

Genetic diversity allows species to adapt to changing environments, colonize new areas, occupy new ecological niches, and produce substantial and robust progeny that persist in the long term (Ledig and Kitzmiller 1992). Populations within a species adapt to environmental change over time. Species and populations of plants most vulnerable to climate change are typically (1) rare species or genetic specialists, (2) species with limited phenotypic plasticity, (3) species or populations with low genetic variation, (4) populations with low dispersal or colonization potential, (5) populations at the trailing edge of a species range, (6) populations at the lower-elevation limit of their distribution, and (7) populations threatened by habitat loss, fire, insects, or disease (Spittlehouse and Stewart 2003; St. Clair and Howe 2011). The ability of a species to respond to environmental change is closely tied to its adaptive strategy (e.g., specialist or generalist) (table 6.3), mechanisms that shape its genetic structure, and the rate of environmental change.

Fragmentation is a critical issue for plant populations because isolation and small populations promote inbreeding and loss of genetic diversity (Broadhurst et al. 2008; Potter et al. 2015). Gene flow from adjacent populations can increase the rate of adaptation by introducing genetic variation that is preadapted to warmer or drier climates (Aitken et al. 2008). This knowledge allows resource managers to select an appropriate population or seed source to increase the likelihood of desired revegetation or restoration (box 6.4).

Table 6.3—Summary of attributes characterizing plant species' adaptive strategies.^a

Attributes	Adaptive strategy	
	Specialist	Generalist
Factor controlling phenotypic expression of adaptive traits	Genotype	Environment
Mechanisms for accommodating environmental heterogeneity	Genetic variation	Phenotypic plasticity
Range of environments where physiological processes function optimally	Small	Large
Slope of clines for adaptive traits	Steep	Flat
Partitioning of genetic variation in adaptive traits	Mostly among populations	Mostly within populations

^aModified from Rehfeldt (1994).**Box 6.4—Using Historical Range and Variability to Assess and Adapt to Climate Change**

To effectively implement ecosystem-based management, land managers often find it necessary to obtain a reference, or benchmark, to represent the conditions that describe fully functional ecosystems (Cissel et al. 1994; Laughlin et al. 2004). Contemporary conditions can be evaluated against this reference to determine status, trend, and magnitude of change, and to design treatments that provide society with valuable ecosystem services while returning declining ecosystems to a more sustainable condition (Hessburg et al. 1999; Swetnam et al. 1999). Reference conditions are assumed to represent the dynamic character of ecosystems and landscapes, varying across time and space (Swanson et al. 1994; Watt 1947).

The concept of *historical range and variability* (HRV) was introduced in the 1990s to describe past spatial and temporal variability of ecosystems (Landres et al. 1999), providing a spatial and temporal foundation for planning and management. HRV has sometimes been equated with “target” conditions (Harrod et al. 1999), although targets can be subjective and somewhat arbitrary, representing only one possible situation from a range of potential conditions (Keane et al. 2009). HRV encompasses a full range of conditions that have occurred across multiple spatial and temporal scales.

HRV represents a broad historical envelope of possible ecosystem conditions—burned area, vegetation cover type area, patch size distribution—that can provide a time series of reference conditions. This assumes that:

- Ecosystems are dynamic, not static, and their responses to changing processes are represented by past variability
- Ecosystems are complex and have a range of conditions within which they are self-sustaining, and beyond this range they transition to disequilibrium (Egan and Howell 2001)
- Historical conditions can serve as a proxy for ecosystem health
- Time and space domains that define HRV are sufficient to quantify observed variation
- Ecological characteristics being assessed for an ecosystem or landscapes match the management objective (Keane et al. 2009).

The use of HRV has been challenged because a warmer climate may permanently alter the environment of ecosystems beyond what was observed under historical conditions (Millar et al. 2007a), particularly altered disturbance processes, shifts in plant species distribution, and hydrologic dynamics (Notaro et al. 2007). However, a critical evaluation of possible alternatives suggests that HRV is still a viable approach in the near term because it has relatively low uncertainty.

An alternative to HRV is projecting future landscape characteristics in a changing climate using complex empirical and mechanistic models. However, the range of projections for future climate from commonly used GCMs is quite broad (Chapter 3; Stainforth et al. 2005). Additional uncertainty accrues from unknown technological advances, behavioral adaptations, and human population growth (Schneider et al. 2007). Moreover, variability of climate extremes, not the gradual change of average climate, will drive most ecosystem response to climate-mediated disturbance and plant dynamics (Smith 2011). Despite these uncertainties, it will be useful to quantify *future range and variability* (FRV) for landscapes where it is feasible and appropriate (Araujo et al. 2005; Keane et al. 2009).

Given cumulative uncertainties, time series of HRV may have lower uncertainty than simulated projections of future conditions, especially because large variations in past climates are already captured in the time series. It may be prudent to wait until simulation technology has improved enough to create credible FRV landscape pattern and composition. In the meantime, attaining HRV would be a significant improvement in the functionality of most ecosystems in the IAP region, and would be unlikely to result in negative outcomes from a management perspective. As with any approach to reference conditions, HRV is useful as a guide, not a target, for restoration and other management activities.

Some species may not be able to migrate quickly enough to keep pace with projected rates of climate change (30–300 feet per year) (Davis 1989; Malcolm et al. 2002). Slow rates of migration may be further impeded by landscape fragmentation (Davis and Shaw 2001; Davis et al. 2005). Therefore, adaptation may be a more important response to climate change than migration. Some authors suggest that long-lived species with high levels of genetic variation can respond favorably to climate change (Hamrick 2004; Hamrick et al. 1992). However, others dispute the ability of forest trees to adapt or migrate and suggest trees may be restricted by their long lifespans, generation intervals, and juvenile phases (Etterson and Shaw 2001; Jump and Peñuelas 2005; Parmesan 2006). Because plant populations are genetically adapted to local climates, the climatic tolerance of individual populations will be critical.

Adaptive strategies for conifers in the IAP region are well documented (Rehfeldt 1994). Differences in adaptive strategy can be characterized by varietal modifications (e.g., *Pinus ponderosa* var. *ponderosa* versus var. *scopulorum*), different elevations, and variable geography. For example, *P. ponderosa* var. *ponderosa* is characterized as having an intermediate (neither generalist nor specialist) adaptive strategy, but at high elevation it has a specialist strategy (genetic variation is organized into numerous local populations, finely tuned to site-specific gradients). Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) is characterized as having a specialist adaptive strategy, but at high elevation it has a generalist adaptive strategy (genetic variation is organized into one or a few populations capable of surviving, growing, and reproducing over a broad range of environments) (Rehfeldt 1989). A generalist adaptive strategy is considered more beneficial for responding to climate change (table 6.3).

Patterns of adaptive variation in other native plants (shrubs, forbs, grasses, sedges) are both clinal and ecotypic. These patterns involve multiple life forms (annual, biennials, perennials) and different ploidy levels (multiple copies of DNA, such as 4X, 6X, or 8X), where 2X is the base level, in which one copy of DNA is inherited on both the maternal and paternal sides. Grasses are largely generalists and less vulnerable to climate change, although ecotypic variation can overlie the generalist adaptive strategy. Forbs, which are mostly insect pollinated and coupled with longer growing seasons and changes in phenology, are considered more vulnerable to climate change than trees and grasses.

Stressors: Biotic and Abiotic Disturbances

A warming climate will rarely be the direct agent of change for tree species and communities. Most changes in vegetation will occur in response to disturbance or some combination of other stressors to climate change (Keane et al. 2015a; McKenzie et al. 2009; Peterson et al. 2014a,

b). The biggest changes across the IAP region are likely to be altered water balance and increasing disturbances such as wildfire, insects, and nonnative species (Chapter 8). Disturbances in combination with other stressors (e.g., drought) will create disturbance regimes in which multiple factors interact to modify ecosystem structure and function (Iverson and McKenzie 2013; McKenzie et al. 2009).

Wildfire is pervasive throughout forest ecosystems in western North America and was historically a dominant landscape disturbance agent in the IAP region. Fire exclusion since the 1920s has disrupted annual occurrence, spatial extent, and cumulative area of wildfires, resulting in increased surface fuel loads, tree densities, and ladder fuels, especially in low-elevation, dry conifer forests. Wildfire regimes, defined by fire frequency, annual area burned, severity, and pattern, are greatly influenced by variability in landscape environmental conditions including vegetation distribution, climate, weather, and topography (McKenzie et al. 2011). Regionally, years with high area burned are correlated with drought, so if drought increases as expected, area burned is expected to increase significantly (McKenzie et al. 2004; Peterson et al. 2014a).

Fire history determines composition and structure of most forests in the IAP region. At the lowest and driest elevations, frequent surface fires historically consumed litter and dead wood and killed seedlings and smaller trees. Fuel accumulations over several decades indicate that future fires may be larger and more intense and may cause higher rates of tree mortality than historical fire (box 6.3). Fire exclusion has not affected fire regimes as much where fires were historically infrequent because of relatively cool, wet conditions (e.g., high elevation) (Romme and Despain 1989; Schoennagel et al. 2004). However, earlier onset of snowmelt, predicted to occur with changing regional climate, will reduce fuel moisture, making these systems flammable for longer periods of time and potentially leading to increased area burned (Miller et al. 2009).

Fire exclusion has resulted in increased tree regeneration and denser forest canopies, coupled with accumulation of understory and canopy fuels in dry forests (Ferry et al. 1995; Keane et al. 2002) (fig. 6.1). These conditions create competition for water, light, and nutrients, making trees in fire-excluded forests susceptible to mortality from biotic and abiotic stressors, such as insects (Anderegg et al. 2012; Wikars and Schimmel 2001), drought (Allen et al. 2010), and fire (Hood et al. 2007).

Native insects and diseases naturally occur throughout forest cover types of the IAP region (Chapter 8). The level of insect and disease activity fluctuates with the availability of host material, stand conditions, environmental factors, and abundance of parasites and predators. These agents typically occur at endemic levels within forest ecosystems and affect mature and weakened trees.

Climate and forest composition and structure influence insect activity and outbreaks. Mountain pine beetle (*Dendroctonus ponderosae*) is an integral component of forest ecosystem processes because of its role in stand



Figure 6.1—Area where fire has been excluded for many decades. Dense stands of ponderosa pine and other species create fuel ladders that can facilitate crown fires (photo: U.S. Forest Service).

thinning and redistribution of resources and nutrients. It is responsible for tree mortality across large areas (Logan et al. 2003), causing significant ecological and economic impacts. Many bark beetle life history traits that influence population success are temperature dependent (Bentz and Jönsson 2015); warming temperatures have directly increased bark beetle-caused tree mortality in some areas of western North America (Safranyik et al. 2010; Weed et al. 2015) (fig. 6.2). Temperature increases will affect tree distribution and tree vigor (Chapman et al. 2012; Hart et al. 2013). Therefore, future bark beetle-caused tree

mortality will depend not only on the spatial distribution of live host trees and heterogeneity of future landscapes but also on the ability of beetle populations to adapt to changing conditions.

Fungal diseases, dwarf mistletoes (*Arceuthobium* spp.), root diseases, needle casts and blights, and abiotic diseases affect forest ecosystems, although the effects of climate change on forest diseases are difficult to project. The effects of climate change on root disease contribute significantly to mortality and loss of tree vigor, although little is known about climate-disease relationships. Climate-mediated changes to forest tree diseases will be dictated by



Figure 6.2—Stand containing lodgepole pine killed by mountain pine beetle. This insect has killed lodgepole pine across large areas of western North America, including the Intermountain Adaptation Partnership region, during the past 20 years. Chronic damage from the beetle may become more common in a warmer climate (photo: U.S. Forest Service).

disease and host tree responses to new climates and their interactions (Sturrock et al. 2010). Interactions among biotic diseases, abiotic stressors, and host species will drive future pathogen outbreaks.

Soil characteristics, aspect, elevation, and forest stand structure contribute to effective moisture availability for tree establishment and growth, helping to shape spatial patterns of forests. Global climate models (GCMs) indicate that the IAP region will have longer, warmer summers (Chapter 3). Seral species such as ponderosa pine, which can establish on bare soil where high surface temperatures (up to 150 °F) exclude other species, have deep roots that can reach water and avoid competition with shallow-rooted species. In the absence of disturbance, shade-tolerant tree species can establish and grow in the understory, allowing them to take up water from the nutrient-rich soil surface. Leaf surface area increases over time, with leaf areas in excess of 6 square feet per square foot of soil surface area in some forests. Transpiration also increases over time, with the potential to deplete soil water needed to keep trees hydrated throughout the summer.

Climate Change Assessment for Tree Species

Here we assess vulnerability for tree species, vegetation types, and resources of concern in the IAP region, based on (1) ecological characteristics, (2) disturbance interactions,

(3) current and historical conditions, and (4) potential climate change responses (table 6.4). Most of the material in this section was derived from published literature, although observational information is included for context. Scientific literature on climate change effects is limited for some species and forest types, making it necessary in some cases to augment the literature with expert knowledge to develop inferences.

Tree Species

Tree species in the IAP region will respond to climate change through modification, contraction, and expansion. First, a species could increase or decrease in productivity in situ within its current range because of increasing temperatures and adequate precipitation (**modification**, or acclimatization). Second, a species may diminish or be extirpated, if conditions change enough to become inhospitable to that species (Allen et al. 2010) (**contraction**). Finally, a species could migrate to areas that are more conducive to establishment and growth (Johnstone and Chapin 2003) (**expansion**). Any species can have multiple modes of response to climate change, and most species will respond to future climates via all three modes.

Application of these three modes to determine future species dynamics requires integration of variability and scale. For example, assessment of species migration requires a long temporal scope to evaluate species range shifts (Prentice et al. 1991). A tree species could become

Table 6.4—Categories used to assess vulnerability of species and vegetation types.

Evaluation category	Description	Example
Habitat, ecosystem function, or species	Specific biophysical or social entity of interest	Whitebark pine
Broad-scale climate change effect	Overarching change in climate that is expected to affect a resource	Warming temperatures
Current condition, existing stressors	Current status of resource relative to desired conditions, including factors that are reducing the quality or quantity of the resource	Reduced abundance, wildfire, mountain pine beetle, white pine blister rust
Sensitivity to climatic variability and change	Specific sensitivity of a habitat, species, or ecosystem function that responds to climate	Low ability to compete with encroaching conifers
Expected effects of climate change	How specific habitat, species, or ecosystem function is expected to respond to climate change (develop inferences from model projections and known responses to climatic variability)	Regeneration may be reduced by combination of warming and low seed availability
Adaptive capacity	Ability to adjust to climate change, to moderate potential damages, or to cope with the consequences; usually more appropriate for species than for systems and processes	Variable: unable to compete with other tree species, but bird-mediated seed dispersal allows rapid colonization of burned areas
Exposure	The extent to which each species' physical environment will change	High

established in a “new” environment made suitable by climate change, such as subalpine tree expansion, but variability in climate may prevent long-term establishment. In addition, shifts in species distribution and abundance will be governed primarily by disturbance, not competition, so disturbance adaptations will be more important than climatic niches.

Most of the information on vulnerability of tree species to climate change was derived from recent summaries on projected climate change effects (Bollenbacher 2012; Devine et al. 2012; Keane et al. 2015a) and older literature on autecology and silviculture (Burns and Honkala 1990; Minore 1979). The following summaries integrate genetic, morphological, ecological, and disturbance characteristics to project how a tree species will respond to a warmer climate.

In general, the literature is inconsistent on the response of tree species to climate change. Results from SDMs often differ from other sources that include gap modeling, mechanistic ecosystem simulation, and field data summaries. As a result, we do not emphasize SDM results in assessment evaluations. Most climate change studies project few species changes after moderate warming (e.g., B1, B2, A1B, RCP 4.5 scenarios) but major species shifts under the most extreme emissions scenarios (e.g., A1, RCP 8.5). Timeframe also affects inferences about vulnerability. Management timeframes of 10 to 50 years are not long enough to effectively evaluate changes in wildfire, native insects, and tree growth because ecosystem response to disturbance may require two to five times the disturbance return interval. Finally, projections by GCMs vary, so the magnitude and rate of climate change, especially by the end of the 21st century, are uncertain (but are always considerably warmer). We have confidence in these projections at broad spatial scales, but less confidence for specific locations.

Douglas-fir (*Pseudotsuga menziesii*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Douglas-fir (fig. 6.3) is found throughout the IAP region, growing in pure and mixed conifer stands (Hermann and Lavender 1990), often associated with ponderosa pine, Jeffrey pine (*Pinus jeffreyi*), grand fir (*Abies grandis*), subalpine fir, and quaking aspen (*Populus tremuloides*). Regeneration is most successful where Douglas-fir is seral (Ryker and Losensky 1983), and seedling growth is strongly limited by moisture and competing vegetation. Douglas-fir is intermediate in shade tolerance, tolerating drought better than most competitors (except for ponderosa pine and Jeffrey pine) by keeping stomata open to extract soil water at low soil water potentials (Sala et al. 2005; Stout and Sala 2003). The species exhibits high genetic differentiation, which is strongly associated with geographic or topographic features (Rehfeldt 1978). Seed sources on south aspects have adaptive characteristics for a shorter growing season and drier soils and may survive under drought stress better than seedlings from north aspects.

Disturbance Interactions

Mature Douglas-fir is resistant to fire injury because of its thick bark, deep main roots, and high crowns (Ryan and Reinhardt 1988). Ponderosa pine and western larch can survive fire across all life stages, so on sites with frequent fires where Douglas-fir is associated with these other species, its cover is usually kept low by fire (Agee 1991). Douglas-fir is subject to damage from a variety of agents that may increase under future climates (Hermann and Lavender 1990), including Douglas-fir beetle



Figure 6.3—Douglas-fir. Growth of Douglas-fir in the Intermountain Adaptation Partnership region is expected to decrease in a warmer climate (photo: C. Restaino, used with permission).

(*Dendroctonus pseudotsugae*), western spruce budworm (*Choristoneura occidentalis*), and Douglas-fir tussock moth (*Orgyia pseudotsugata*). The latter two insects attack trees of all ages at periodic outbreak intervals, often resulting in severe defoliation during outbreak years. Armillaria (*Armillaria solidipes*) and annosus (*Heterobasidion annosum*) root diseases may intensify in infection and widen in distribution to cause high tree mortality. Annosus root disease is particularly lethal in Douglas-fir (Hagle 2003). Of the many heart rot fungi (more than 300) attacking Douglas-fir, the most damaging and widespread is red ring rot (*Porodaedalea pini*).

Historical and Current Conditions

Historical frequent wildfire kept Douglas-fir from becoming established on some dry sites where it was associated with ponderosa pine. The cumulative effects of fire exclusion and logging have allowed Douglas-fir to become more dominant across some portions of the IAP region, often with high stem densities in fire-excluded stands. This has created areas where both canopy and surface fuels are high (Keane et al. 2002), predisposing Douglas-fir forests to future crown fires. In addition, these dense stand conditions have contributed to decreased vigor, which makes species susceptible to western spruce budworm and Douglas-fir beetle outbreaks.

Climate Change Responses

Some studies suggest that Douglas-fir distribution will increase in a warmer climate (Morales et al. 2015) and that growth will increase (Soulé and Knapp 2013), although a recent study provides convincing evidence that growth will decrease throughout its range (Restaino et al. 2016). It is likely that multiple factors will contribute to reduced distribution and vigor of Douglas-fir forests in some locations. Increased heat loading following severe wildfires is expected to be more common in the future, and may reduce Douglas-fir regeneration at lower-elevation sites and on south aspects (Kemp 2015). Douglas-fir may also face increasing competition from ponderosa pine, which is more drought tolerant (Stout and Sala 2003), and it may not have the genetic potential to rapidly migrate to more conducive sites (Aitken et al. 2008). In addition, Douglas-fir could have less resistance to the native insects previously mentioned if it is chronically stressed by low soil moisture. Increased wildfires, coupled with adverse effects of fire exclusion, could reduce tree survival in the future and make trees more susceptible to Douglas-fir beetle (Hood and Bentz 2007; Hood et al. 2007). Klopfenstein et al. (2009) projected that the range of Armillaria root rot will remain constant in a warmer climate, and if areas where Douglas-fir is maladapted increase, susceptibility to root rot could also increase. With limited genetic diversity at low to middle elevations and a more generalist strategy at higher elevations (St. Clair and Howe 2007), Douglas-fir may retract from the driest portions of its range.

Grand Fir (*Abies grandis*) (Middle Rockies subregion)

Autecology

Grand fir is found on a wide variety of sites, including stream bottoms, valleys, and mountain slopes in the Middle Rockies of the IAP region (Foiles et al. 1990), typically in association with other conifer species. Grand fir grows best on rich soils of valley bottoms but also grows well on shallow exposed soils of mountain ridges, if moisture is adequate (Antos and Shearer 1980). Grand fir is either an early- or late-seral species, depending on site moisture (Ferguson and Johnson 1996). On productive mesic sites, it grows rapidly to compete with other seral species in the overstory, but other conifer species can outcompete it. On drier sites, it is the most shade-tolerant species and can dominate the understory. Grand fir can also share dominance with subalpine fir, especially in narrow valley bottoms, where it can exert dominance in lower elevational zones (Antos and Shearer 1980). Grand fir has high shade tolerance but low drought tolerance. It forms associations with ectomycorrhizae and arbuscular mycorrhizae, which may allow it to outcompete some shade-tolerant conifers. It has low frost tolerance but can tolerate fluctuating water tables.

Disturbance Interactions

Grand fir is susceptible to fire damage in moist creek bottoms but is more resistant on dry hillsides where roots are deeper and bark is thicker (Ryan and Reinhardt 1988). Wildfires that burn grand fir stands are stand replacing or mixed severity, generating sufficient heat to kill even mature trees (Arno 1980; Arno et al. 2000). Grand fir is susceptible to Armillaria and annosus root diseases, which can cause high levels of tree mortality (Hagle et al. 2003). Numerous insects attack grand fir, including western spruce budworm and Douglas-fir tussock moth, which cause widespread defoliation, top kill, and mortality. The western balsam bark beetle (*Dryocoetes confusus*) and fir engraver (*Scolytus ventralis*) are the principal bark beetles that attack grand fir (Foiles et al. 1990).

Historical and Current Conditions

Fire exclusion has increased grand fir on both dry and mesic sites, and higher tree densities have stressed grand fir, making it more susceptible to root rot and insect attacks. Therefore, the condition of most grand fir stands depends on the last severe fire; if fire exclusion has caused grand fir to dominate in both the overstory and understory, then these stands are usually stressed because of high densities and increased root rot and insects. However, in early-seral stands where high grand fir regeneration has not yet occurred, an increase in fir is likely with continued fire exclusion.

Climate Change Responses

On dry sites, increased drought and longer growing seasons will exacerbate stress caused by competition, resulting in high mortality of grand fir, mainly from insects and disease. Nitschke and Innes (2008) used a gap model to project major declines in grand fir, and Coops and Waring (2011) used a mechanistic model to simulate a nearly 50 percent decrease in the range of grand fir compared to historical distributions. However, increased productivity may lead to increased grand fir populations in locations with higher soil moisture (Aston 2010; Urban et al. 1993). As noted earlier, increased densities may also lead to increased stress. Longer fire seasons and high fuel loadings from fire exclusion will probably lead to large, severe fires that may reduce grand fir in drier locations. In summary, although grand fir is often stressed by high stem densities, the species is likely to tolerate changes in climate and remain on the landscape at levels that are closer to historical conditions rather than its current abundance.

Shasta Red Fir (*Abies magnifica*)

(Great Basin and Semi Desert subregion)

Autecology

Shasta red fir grows best in areas with cold, wet winters and warm, dry summers (Lanner 1983; Oosting and Billings 1943; Rundel et al. 1977). The growing season in these areas is short, with snow often on the ground in July (Barbour 1988; Barbour et al. 1991; Holland 1986; Mitchell and Moir 1976). Red fir can be found growing at lower elevations in canyons and other protected places where significant cold air drainage keeps soil and air temperatures low (Parker 1984). The species also occurs at high elevation on mountain ranges that continue in active formation, where it thrives on young, xeric soils. Red fir has a high frost tolerance and low drought tolerance. It is a late-seral species nearly everywhere it is found. Although red fir grows best in full sunlight, it can survive and grow for long periods in relatively dense shade.

Disturbance Interactions

Shasta red fir sustains moderate damage from low-severity fires but is often killed by mixed-severity fires (Atzet and Wheeler 1982). Openings created in mixed red fir and white fir (*Abies concolor*) stands in the Sierra Nevada tend to regenerate more readily to red fir (Parker 1986). Red fir is susceptible to windthrow after partial cutting, especially when marginal codominant and lower crown classes are left as the residual stand (Gordon 1973). Root diseases such as annosus root rot contribute significantly to lack of wind firmness. Other diseases that reduce tree vigor include dwarf mistletoe and cytospora (*Cytospora* spp.) canker, which, in turn, make trees susceptible to fir engraver attack.

Historical and Current Conditions

Native Americans used Shasta red fir forests for hunting mule deer (*Odocoileus hemionus*) and for other sources of food and materials during summer. Mining, logging, water diversions, railroad development, and sheep grazing altered some lower-elevation fir forests during the late 19th and early 20th centuries (Meyer n.d.). Burning was used to promote growth of grasses and forbs and to remove fuel and young trees from the understory (McKelvey and Johnston 1992), thus reducing fir regeneration. Starting in the 1950s, timber harvest and extensive road infrastructure began in portions of red fir forest, with silvicultural techniques that create even-aged stands being implemented (Potter 1998). By the 1990s, silvicultural practices emphasized shelterwood cutting and uneven-aged silvicultural systems (Laacke and Tappeiner 1996). Despite this history of resource use, red fir is largely undisturbed in many higher-elevation and isolated locations.

Climate Change Responses

Shasta red fir is expected to sustain moderate effects from a warmer climate. If snowpack decreases as expected, a longer growing season may increase growth at higher elevations. Regeneration could also improve under these conditions. Lower-elevation populations may grow more slowly where soil moisture is limited in summer. Red fir is typically found in forests with mixed-severity fire regimes, so if wildfire becomes more frequent than historical records indicate, especially where fuel loadings are elevated, fire severity could cause crown fires with high mortality in younger trees (older trees have thick bark and high crowns). Increased fire could produce a more open forest structure over decades to centuries.

Subalpine Fir (*Abies lasiocarpa*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Although widely distributed, subalpine fir grows within a narrow range of mean temperatures of 25 to 40 °F, with average January temperatures of 5 to 25 °F. Cool summers, cold winters, and deep winter snowpack are more important than precipitation in determining where it grows. Subalpine fir ranges from lower valleys to the upper subalpine zone in the IAP region, typically mixed with other species, most notably Douglas-fir and Engelmann spruce. Subalpine fir is shade tolerant; partial shade usually favors seedling establishment and early survival (Knapp and Smith 1982). It is relatively intolerant of drought, and seedlings can be killed by lengthy droughts. It is a prolific seeder, often having large cone crops every

2 to 3 years (Alexander et al. 1990), and although dense mats of seedlings can occur, they are also susceptible to many herbivores and pathogens.

Disturbance Interactions

Subalpine fir is highly susceptible to fire damage because of thin bark, shallow roots, and low, dense crowns (Ryan and Reinhardt 1988). Even low-intensity fire can cause mortality, and frequent fires can eliminate subalpine fir from both the overstory and understory, thereby maintaining more fire-adapted species such as lodgepole pine (Little et al. 1994; Murray et al. 1995; Wadleigh and Jenkins 1996). In spruce-fir forests, the most important insects are western spruce budworm and western balsam bark beetle (*Drycoetes confusus*). Fir broom rust (*Melampsorella caryophyllacearum*) and wood rotting fungi are responsible for most disease losses, but root and butt rots may be important locally. Decades of intense competition, coupled with a period of moderate to severe drought, can cause mortality in subalpine fir stands.

Historical and Current Conditions

Effects of fire exclusion have not yet become manifest in most subalpine fir ecosystems because of historically infrequent fire and slow successional advancement. However, abundance of subalpine fir has increased in some landscapes (Keane et al. 1994). These dense stands have become stressed from competitive interactions, resulting in susceptibility to disturbances and drought. If these stands continue to escape fire, the seed sources of co-located, fire-adapted species may be eliminated, and high-elevation sites could be converted to grass and shrublands (Keane 2001). In addition, if fire is excluded from these dense forests, fuels will accumulate, inevitably leading to high-severity fires (Keane 2001; Morgan et al. 1994b). Recent USFS Forest Health Monitoring data in the IAP region indicate that dieback of subalpine fir is occurring in some locations, attributed to a complex of drought, insects, and pathogens.

Climate Change Responses

Because subalpine fir is adapted to moist growing conditions, it is likely to respond poorly to increasing temperatures and drought (Alexander et al. 1990; Brunelle et al. 2005; Whitlock and Bartlein 1993). However, it is a good competitor and may be able to expand its range at treeline (Little et al. 1994; Rochefort et al. 1994; Villalba et al. 1994) and increase growth in a longer growing season (Peterson et al. 2002). Seedling establishment may be the bottleneck for subalpine fir establishment in the future because the species needs long periods of high moisture for germination and seedling establishment (Urban et al. 1993), and years that meet these conditions may be less frequent in the future. If stand densities increase, competitive stress will increase, making fir more vulnerable to insects, disease, and abiotic factors. If wildfire increases where subalpine fir is dominant, abundance would

decrease from the direct effects of higher temperature. Subalpine fir is likely to shift across the high mountain landscape, with expansion balancing retraction, although fire, disease, and insects may limit abundance.

White Fir (*Abies concolor* var. *concolor*)

(Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

White fir is distributed throughout most of the American Southwest, from canyon bottoms and ravines up to ridgetops. It is a dominant, late-seral component of some habitat types in Utah and develops best on gentle slopes (Laacke 1990), although the rooting habit is adaptable to depth of the soil profile. It can survive for long periods as a suppressed tree in the understory, then respond with rapid growth if light becomes available. Within mixed conifer forests, white fir tends to achieve dominance on moist sites, especially if long fire return intervals provide the opportunity for it to mature to a point at which it is moderately fire tolerant. White fir is sensitive to frost damage (Laacke 1990), and is susceptible to windthrow following partial cutting.

Disturbance Interactions

In mixed conifer forests with an intact low-severity fire regime, white fir rarely attains dominance because it is more fire sensitive than its associates (Agee 1982; Alexander et al. 1984). Thus, many white fir habitat types are in mid-seral stages, with various species dominating the overstory and white fir dominating the reproductive size classes. White fir mistletoe (*Phoradendron bolleanum* subsp. *pauciflorum*) and white fir dwarf mistletoe (*Arceuthobium abietinum* f. sp. *concoloris*) damage white fir, causing spike tops, loss of vigor, and increased susceptibility to bark beetles (Bega 1978). White fir is susceptible to a number of decay fungi including annosus root disease, Armillaria root disease, laminated root rot (*Phellinus weirii*), yellow cap fungus (*Pholiota limonella*), Indian paint fungus (*Echinodontium tinctorium*), and white pocket rot (*Phellinus mini*). Fir engraver beetle causes major losses throughout the range of white fir (Wilson and Tkacz 1996).

Historical and Current Conditions

White fir, which has historically been dominant on wetter sites and codominant in drier mixed conifer forests, has increased in abundance in areas where fire has been excluded. In some cases, the understory in fire-excluded stands is dense, and surface fuels are high, conditions conducive to a crown fire (Dahms and Geils 1997; McKelvey and Johnston 1992). If dense stands escape fire, the seed sources of other fire-adapted species may be eliminated, and some sites may have increased dominance of grass and shrublands (Keane 2001). White fir mortality following wildfire is often

100 percent, although associated species such as ponderosa pine and Douglas-fir often survive. White fir has never been a primary timber species, although it has been logged in some places. It was often left uncut where more valued species were removed, becoming the residual dominant.

Climate Change Responses

White fir has high shade tolerance but low drought tolerance, so low soil moisture will have the greatest effects in well-drained soils and on south aspects. Sudden temperature increases during May and June can cause damage nearly identical to that of spring frosts, which may be an issue for some fir populations. A modeling study in California suggested that effects of climate change on white fir will be moderate (Battles et al. 2008), and although this may be true in the IAP region, wildfire will play a major role in its future distribution and abundance. White fir is typically found in forests with low-severity and sometimes mixed-severity fire regimes, so if fire becomes more frequent than historically, especially where fuel loadings are elevated, fire severity could cause crown fires with high mortality rates. Over decades to centuries, increased fire could produce a more open forest structure with fewer white fir in both the canopy and understory.

Rocky Mountain Juniper (*Juniperus scopulorum*)

(Uintas and Wasatch Front subregion)

Autecology

Rocky Mountain juniper grows in dry, sub-humid climates. It is a drought-enduring species with a shallow but fairly extensive lateral root system. Rocky Mountain juniper is normally a component of early-seral or near late-seral vegetation. It is relatively shade tolerant during the seedling and sapling stages, but it later becomes more intolerant and is unable to endure excessive shade. In Utah, junipers have been observed occupying sagebrush stands under certain conditions; twoneedle pinyon (*Pinus edulis*) generally follows and tends to replace juniper. Pinyon-juniper communities may encroach into grasslands that have been overgrazed or disturbed. Once established, Rocky Mountain juniper competes well with understory vegetation for water and nutrients.

Recent paleobotanical studies indicate the macroclimate covering much of the Rocky Mountain juniper range has changed from mesic to more xeric conditions. Juniper is generally less drought resistant than other juniper species, and high temperatures are not favorable for regeneration or growth. Rocky Mountain juniper was present in western Nebraska and the Laramie Basin of Wyoming as recently as 1,000 years BP, with some trees over 50 inches in diameter (Tauer et al. 1987; Van Devender 1987).

Disturbance Interactions

Rocky Mountain juniper is susceptible to loss from erosion simply because it is often established on exposed sites where soils are readily eroded. It is susceptible to death or injury from fire, primarily because the bark is thin, and the lower branches contain volatile oils and normally extend to the ground (Hepting 1971; Noble 1990; Sieg 1997). Rocky Mountain juniper has a compact crown when young, and because it grows slowly, is susceptible to fire for the first 20 years or more (Crane 1982; Fischer and Clayton 1983; Hansen and Hoffman 1988; Mitchell 1984; Mueggler 1976; Stanton 1974). As trees mature, they develop thicker bark and a more open crown, allowing them to potentially survive surface fires. Large-diameter junipers have been documented to survive four to six fires.

Postfire reestablishment is solely by seed (Floyd et al. 2000), and animal transport of seeds is an important factor (Paysen et al. 2000). Regeneration is often high after old trees burn (Stanton 1974; Wright 1972). Frequent fires in pinyon-juniper habitat can maintain a grassland setting, and the absence of fire will allow conversion to woodlands (Gruell 1986). After fire in pinyon-juniper, junipers usually establish first, followed by pinyon pine, which may eventually replace juniper on higher-elevation sites (Holland 1990). The nonnative annual cheatgrass (*Bromus tectorum*) has become increasingly common in the understory over the past few decades, providing abundant fine surface fuels and increasing the potential for more frequent wildfires (Shinneman and Baker 2009).

Historical and Current Conditions

Rocky Mountain juniper was a source of fuel (charcoal) for the mining industry between the 1860s and 1920s (Young and Budy 1979), and it has been used extensively for firewood, fence posts, and other needs, with local deforestation occurring in some locations. In some lower-elevation sites, juniper has been cut or removed from the landscape through chaining and herbicides to encourage the growth of grasses and forage for livestock grazing. Persistent woodlands of Rocky Mountain juniper, pinyon pine, or a mixture of both are found where local soils and climate are favorable, and wildfire has been infrequent (Romme et al. 2009). Pinyon-juniper savannas are found where local soils and climate are suitable for both trees and grasses, and low-severity fires have been relatively frequent. Wooded shrublands are found where local soils and climate support a shrub community, but trees have increased during moist climatic conditions and periods without wildfire. Large increases in juniper density have occurred in portions of all types of pinyon-juniper vegetation, which may have been driven by factors such as natural range expansion, livestock grazing since the 1880s (which reduced fuels and probably decreased fire frequency), fire exclusion, climatic variability, and carbon dioxide fertilization (Romme et al. 2009).

Climate Change Responses

Rocky Mountain juniper is drought tolerant, and reduced soil moisture is not expected to have a significant effect on its abundance and distribution, although its growth and expansion into adjacent shrub-steppe systems could be slowed. The future of Rocky Mountain juniper will largely depend on spatial and temporal patterns of wildfire, which is expected to increase in frequency (Floyd et al. 2004). Junipers can generally survive low-severity fire if they are at least 20 years old, so if fires occur more frequently than that, tree mortality will be high. After an initial fire, accumulation of surface fuels and tree regeneration could be slow because of moisture limitations, resulting in a sparse canopy and disconnected fuels (Rocca et al. 2014). The long-term condition of juniper is complicated by nonnative annual grasses, especially cheatgrass, which increases surface fuels and fire frequency.

Utah Juniper (*Juniperus osteosperma*)

(Plateaus, Great Basin and Semi Desert subregions)

Autecology

Utah juniper is a late-seral species in several pinyon-juniper, sagebrush (*Artemisia* spp.)-grassland, and shrub-steppe habitats. Utah juniper tolerates dry soils (Hickman 1993; Lanner 1983; Meeuwig and Bassett 1983), commonly growing on alluvial fans and dry, rocky hillsides (Barney and Frischknecht 1974; Hitchcock and Cronquist 1973; Pieper 1977; Shantz and Piemeisel 1940) with shallow, alkaline soils (Bunderson et al. 1985). Utah juniper is shade intolerant (Meeuwig and Bassett 1983); it is a late-seral species in areas where stands are open and regeneration can occur without competition for light. Utah juniper has a taproot that extends deep into the soil, responding to low nutrient levels in the soil by developing extensive fine roots. Juniper competes more efficiently for soil moisture than do herbaceous understory plants, and is more likely to maintain a stable population as understory plants decrease (Austin 1987; Everett et al. 1983; Springfield 1976).

Disturbance Interactions

Utah juniper is generally not fire tolerant, although trees more than 4 feet tall are capable of surviving low-intensity fires (Bradley et al. 1992; Springfield 1976). Cheatgrass has become increasingly common in the understory over the past few decades, continually providing abundant fine surface fuels on and increasing the potential for more frequent wildfires (Shinneman and Baker 2009).

Historical and Current Conditions

Utah juniper was a source of fuel (charcoal) for the mining industry between the 1860s and 1920s (Young and Budy 1979), and has been used extensively for firewood,

fence posts, and other needs, with local deforestation in some locations. In some lower-elevation locations, juniper has been removed from the landscape through chaining and herbicides to encourage growth of grasses and forage for livestock grazing. Persistent woodlands of juniper or pinyon pines, or a mixture of both, are found where local soils and climate are favorable, and wildfire has been infrequent (Romme et al. 2009). Pinyon-juniper savannas are found where local soils and climate are suitable for both trees and grasses, and low-intensity fires are relatively frequent. Wooded shrublands are found where local soils and climate support a shrub community, but trees have increased during moist climatic conditions and periods without wildfire. Large increases in juniper density have occurred in portions of all types of pinyon-juniper vegetation, which may have been driven by factors such as natural range expansion, livestock grazing (since the 1880s, which reduced fuels and probably decreased fire frequency), fire exclusion, climatic variability, and carbon dioxide fertilization (Romme et al. 2009).

Climate Change Responses

Utah juniper is drought tolerant, and reduced soil moisture is not expected to have a significant effect on its abundance and distribution, although growth may decline even as it spreads into adjacent shrub-steppe systems. The future of Utah juniper will largely depend on spatial and temporal patterns of wildfire, which is expected to increase in frequency (Floyd et al. 2004). Junipers can generally survive fire only if they are tall enough for the crown to escape flames. Following an initial fire, accumulation of surface fuels and tree regeneration will probably be slow because of moisture limitations, resulting in a sparse canopy and disconnected fuels (Rocca et al. 2014). The long-term condition of juniper is complicated by nonnative annual grasses, especially cheatgrass, which increases surface fuels and fire frequency.

Western Larch (*Larix laricina*)

(Middle Rockies subregion)

Autecology

Western larch grows in relatively cool, moist forests in the Middle Rockies portion of the IAP region (Habeck 1990; Schmidt and Shearer 1990), typically associated with several other conifer species. It is often found in locations that have relatively high snowfall, and is rarely found in xeric sites (Gower et al. 1995). Cone and seed production is abundant when trees are older than 30 years, with good seed crops occurring every 10 to 14 years (Owens 2008). Seed germinates best on seedbeds exposed by burning or mechanical scarification (Antos and Shearer 1980; Beaufait et al. 1977; Schmidt 1969; Shearer 1976), and young seedlings grow fast on suitable sites, although drought reduces seedling survival (Schmidt and Shearer 1995). Shade intolerant, larch grows fast with tall, open crowns, allowing it to outcompete other

species on mesic sites (Milner 1992). It is moderately drought tolerant and can survive seasonal drought, but performs poorly when droughts last more than 2 years.

Disturbance Interactions

Western larch depends on open-canopy, high-light environments and mineral soil seedbeds created by fire for successful regeneration (Schmidt et al. 1976). It can survive intense fire because of thick bark (Ryan and Reinhardt 1988), high crowns, deep roots, and epicormic branch production (Fiedler and Lloyd 1995; Harrington 2012; Schmidt and Shearer 1995; Schmidt et al. 1976), often surviving crown fires that kill other species (Marcoux et al. 2015). Seeds are wind dispersed across large burns, and if mature lodgepole pine occurs with larch, regeneration may be dominated by both species (Hopkins et al. 2013).

Western dwarf mistletoe (*Arceuthobium campylopodum*) is a damaging, parasitic plant of larch (Schmidt and Shearer 1990). It infects seedlings and persists throughout the life of the tree, causing reduced growth, water loss, and deformities. Cool, wet springs favor foliar diseases such as larch needle cast (*Meria laricis*), which, in turn, can reduce cone production. Larch needle blight (*Hypodermella laricis*), brown trunk rot (*Fomitopsis officinalis*), and red ring rot (*Phellinus pini*) are also important pathogens. Western spruce budworm and the nonnative larch casebearer (*Coleophora laricella*) are the two most serious insect pests (DeNitto 2013; Schmidt and Fellin 1973). Although neither insect causes substantial mortality, episodic outbreaks can cause severe defoliation and reduce growth and cone production (Schmidt et al. 1976).

Historical and Current Conditions

Western larch was formerly an important timber species, but extensive logging during the 20th century removed many of the large larches, reducing its dominance on the landscape (Arno 2010). Reduced seed sources for regeneration and fire exclusion have reduced burned mineral soil seedbeds where larch can regenerate. Continued fire exclusion has increased stand densities and increased surface fuel loads, which will make future fires more intense than they have been historically. Considerable effort is underway to increase the distribution and abundance of western larch in locations where it was previously more common.

Climate Change Responses

Western larch may be susceptible to a warmer climate because of its narrow geographic and elevation distribution and its uncertain association with wildfire. If fire increases, larch may have a colonization advantage, as long as fire mortality is moderate and mature trees remain to serve as seed sources. Without seed sources, regeneration may require assistance from management through planting. If fire exclusion continues, stand densities will increase and larch may be outcompeted by shade-tolerant competitors, making it more susceptible to insects and disease. When dense stands burn, crown fires may kill older, seed-producing trees (Hopkins

et al. 2013). Keane et al. (1996) simulated major declines for western larch under fire exclusion and moderate climate change, but found it increased as more fire was allowed to burn over many decades. Larch can take advantage of changes in productivity in colder sites, as long as these areas burn with low intensity and larch survives the fires to provide seed for regeneration.

Great Basin Bristlecone Pine (*Pinus longaeva*) and Rocky Mountain Bristlecone Pine (*P. aristata*)

(Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Great Basin bristlecone pine occurs in montane, subalpine, and treeline communities from 7,200 to 12,000 feet elevation (Hickman 1993; Lanner 1999), typically in multi-aged stands (Bradley et al. 1992). It grows in pure stands at treeline and in the upper subalpine zone, and is codominant with limber pine at lower elevations (Critchfield and Allenbaugh 1969; Vasek and Thorne 1977). Great Basin bristlecone pine is drought tolerant (Bare 1982; Tang et al. 1999), occurring in climates that are cold in winter and dry in summer. It establishes quickly in open mesic sites (Hawksworth and Bailey 1980), but competes poorly for water and nutrients, and is usually excluded from productive sites (Beasley and Klemmedson 1973; Hiebert 1977).

Rocky Mountain bristlecone pine occurs from 8,200 to 11,000 feet elevation (FNAA 2009) and is common on steep, dry, south- or west-facing slopes. It grows in cold, continental climates, with precipitation patterns influenced by summer monsoons bringing afternoon rain. Rocky Mountain bristlecone pine is commonly found on unproductive sites with nutrient-poor, acidic soils. This species often occurs in pure stands or mixed with limber pine.

Disturbance Interactions

As a thin-barked species (Zavarin and Snajberk 1973), Great Basin bristlecone pine is adapted to survive only low-intensity surface wildfires, although fire is infrequent at high-elevation sites (Bradley et al. 1992). White pine blister rust (*Cronartium ribicola*) is present in some stands, but it rarely has a significant effect on populations. Most high-elevation pines eventually die from root rot decay or soil erosion, which exposes and kills roots (Lanner 1999). Small wildfires may kill a few trees.

Wildfires are common in Rocky Mountain bristlecone pine sites, but are usually small in extent and cause minimal damage because patchy stand structure and low fuel loadings limit fire spread (Crane 1982). Although fire is not a major disturbance factor, Rocky Mountain bristlecone pine is favored in early postfire succession because it is a shade-intolerant seral species (Baker 1992; Schoettle 2003). Blister rust has been

recorded in this species only recently (Blodgett and Sullivan 2004) and is rarely observed in the IAP region.

Historical and Current Conditions

Great Basin bristlecone pine and Rocky Mountain bristlecone pine are located at high elevation in relatively inaccessible locations. Because these species have no commercial value, they generally remain undisturbed by human activity and exist in intact subalpine forests and woodlands.

Climate Change Responses

Great Basin bristlecone pine and Rocky Mountain bristlecone pine are tolerant of cold temperatures and deep snowpack in winter, low soil moisture in summer, and high winds. Therefore, they are expected to be moderately vulnerable to climate change, with considerable variation among sites. A recent study showed that Great Basin bristlecone has a threshold at 60 to 250 vertical feet below treeline, above which trees have a positive growth response to temperature (Salzer et al. 2014). Growth chronologies from 250 feet or more below treeline had a change in climate response and did not correlate strongly with temperature-sensitive chronologies developed from trees growing at upper treeline. At the highest sites, trees on south-facing slopes grew faster than trees on north-facing slopes. High growth rates on the south aspect have declined since the mid-1990s, suggesting that temperature may no longer be as limiting to growth. Therefore, increasing warmth may lead to a divergence between growth and temperature at previously temperature-limited sites. Neither species of bristlecone pine is expected to change in distribution and abundance significantly during the 21st century. Increased wildfire could affect Rocky Mountain bristlecone pine in mixed-species stands with high surface fuels, but not in higher-elevation locations where trees are scattered and fuels are low.

Jeffrey Pine (*Pinus jeffreyi*)

(Great Basin and Semi Desert subregion)

Autecology

Jeffrey pine is shade intolerant and drought adapted, occupying low- to mid-elevation, dry forests (Minore 1979). It is both an early- and late-seral species, often associated with other conifer species on moist sites. Moisture typically limits growth, especially in summer, and distribution of Jeffrey pine on drier sites is limited by available soil moisture, which, in turn, is affected by soil texture and depth. Jeffrey pine tolerates dry soil conditions by efficiently closing stomata to avoid water loss and xylem cavitation (Sala et al. 2005), tolerating intense drought, and drawing groundwater at low soil water potentials. Jeffrey pine is associated with several species of ectomycorrhizae, giving it the capacity to survive in dry environments. Soil texture, plant competition, and seedbed conditions reduce seed germination and limit seedling survival and growth, although it can often germinate under moisture stress (Oliver and Ryker 1990).

Disturbance Interactions

Disturbance plays a major role in Jeffrey pine forests. The most damaging of the tree-killing insects are several species of *Dendroctonus* (Oliver and Ryker 1990), followed by ips beetles, all of which are native and present naturally in many stands. Dwarf mistletoe is widespread in Jeffrey pine stands but rarely fatal. Bark beetles can cause extensive mortality given availability of preferred host stand conditions. Jeffrey pine has a high capacity to survive fire (Minore 1979; Ryan and Reinhardt 1988), and wildfire favors the growth of large (thicker bark) Jeffrey pine by killing its primary competitors and small-diameter Jeffrey pines (Arno 1988; Steele et al. 1986).

Historical and Current Conditions

Fire exclusion, mining, timber harvest, and livestock grazing have contributed to reductions in distribution and abundance of Jeffrey pine. Changes in fire regime have altered the composition and structure of many dry forests, with area burned by surface fires decreasing and crown fires increasing in many areas (Hann et al. 1997). Landscapes where fire has been excluded for many decades typically have high stand densities and surface fuel loadings, setting the stage for future crown fires.

Climate Change Responses

Jeffrey pine is expected to be relatively tolerant of increasing temperatures and longer droughts. This species has high phenotypic plasticity and is therefore adapted to drought, although regeneration may decrease if precipitation decreases or becomes more variable. Some studies project an increase in distribution for ponderosa pine in western North America (Hansen et al. 2001; Morales et al. 2015; Nitschke and Innes 2008) that may be true for Jeffrey pine as well. Advancing competition resulting from fire exclusion, increased wildfire extent and intensity, and potential increases in mountain pine beetle, western pine beetle (*Dendroctonus brevicomis*), several *Ips* species, and western pine shoot borer (*Eucosma sonomana*) will dictate the future of Jeffrey pine. If fires are too frequent, established regeneration will not grow above the lethal scorch height. Increasing wildfire extent and severity (crown fires) could also eliminate the mature Jeffrey pine trees that provide seed sources for populating future burns.

Limber Pine (*Pinus flexilis*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Limber pine is a shade-intolerant, early-seral species (Steele 1990) that is slow growing but long lived. It occupies xeric sites across a wide range of elevations (Jackson et al. 2010). Because it is easily killed by fire, the species

is found in fire-protected sites (e.g., rocky outcrops) with infrequent fires of low severity (Steele 1990). It can be associated with a wide range of other conifer species and quaking aspen (Langor 2007; Steele 1990). It is associated with both ectomycorrhizae and arbuscular mycorrhizae that facilitate its ability to exist in extremely dry environments. Limber pine seedlings are poor competitors with grass, but grow reasonably well on rocky substrates and with shrubs. Limber pine has difficulty competing with encroaching species on productive mesic sites and is often succeeded by Douglas-fir and subalpine fir. Its seeds are dispersed by rodents and by Clark's nutcracker (*Nucifraga columbiana*), which relies on pine seeds as a food source and caches them throughout the subalpine zone (Lanner 1980; Lanner and Vander Wall 1980).

Disturbance Interactions

Thin bark and low crowns make limber pine susceptible to damage from wildfire. It is also susceptible to white pine blister rust, and some stands in newly infected areas are currently undergoing high mortality (Smith et al. 2013). Limber pine also facilitates the expansion of currant (*Ribes* spp.) into traditional grasslands (Baumeister and Callaway 2006), thus increasing rust infections and subsequent mortality. Mountain pine beetle (Jackson et al. 2010) and severe dwarf mistletoe infections can cause mortality. Porcupine (*Erethizon dorsatum*) damage is prevalent in some areas.

Historical and Current Conditions

Fire exclusion has allowed limber pine to expand its range from fire-protected sites into areas where frequent fires historically restricted it (Arno and Gruell 1983; Brown and Schoettle 2008). Expansion into some grass and shrub rangelands has facilitated expansion of other species as well (e.g., Douglas-fir) (Baumeister and Callaway 2006; Jackson et al. 2010). Some of the newly established limber pine forests have suffered recent mortality from white pine blister rust, mountain pine beetle, and red belt (*Fomitopsis pinicola*) (Jackson et al. 2010; Langor 2007; Taylor and Sturdevant 1998). Increasing wildfire extent has also affected some stands.

Climate Change Responses

Limber pine has a generalist adaptive strategy with broad phenotypic plasticity (Devine et al. 2012; Feldman et al. 1999), so it is expected to be moderately vulnerable to climate change. The ability of limber pine to occupy shallow, infertile soils and tolerate periods of drought will confer resistance to warmer temperatures and drought. Reduced snowpack could increase growth of limber pine at higher elevations by lengthening the growing season (Aston 2010). However, warmer temperatures could also reduce soil moisture for seed germination and seedling growth, and lack of ectomycorrhizal associations could inhibit establishment in some locations (Coop and Schoettle 2009). Increasing wildfire extent and intensity may impact some limber pine

stands in the future, causing higher mortality and reducing encroachment into grasslands.

Lodgepole Pine (*Pinus contorta* var. *latifolia*, P.c. var. *murrayana*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Great Basin and Semi Desert subregions)

Autecology

Lodgepole pine has broad ecological amplitude and environmental tolerance, including both the *murrayana* variety in the western portion of the IAP region and the *latifolia* variety elsewhere in the region (Lotan and Critchfield 1990). It grows well on gentle slopes and in basins but is also found on steep slopes and shallow soils. It is shade intolerant but highly tolerant of frost and drought. Lodgepole pine grows in pure stands and in association with many other conifer species, including subalpine fir, Engelmann spruce, Douglas-fir, and western larch (Steele et al. 1983). It can be either early or late seral, depending on location. Its ability to remain on xeric landscapes is enhanced by its association with many types of mycorrhizae. Lodgepole pine is generally a prolific seed producer, and the prevalence of cone serotiny in most individuals of the *latifolia* variety promotes rapid regeneration following wildfire (Hardy et al. 2000).

Disturbance Interactions

Fire plays a critical role in lodgepole pine forest succession (Brown 1973; Lotan et al. 1984). Mature lodgepole pine appears to be able to survive low-intensity fire, despite having thin bark (Ryan and Reinhardt 1988). In many cases, natural regeneration is prolific via abundant seed from serotinous cones (Lotan and Perry 1983; Nyland 1998), although drought is a common cause of mortality in first-year seedlings. Mountain pine beetle has played a significant role in the dynamics of lodgepole pine ecosystems. Beetles and wildfire create an important stress complex for lodgepole pine in some locations (Brown 1973; Geiszler et al. 1980), but can also act independently (Axelson et al. 2009; Moran and Corcoran 2012).

Historical and Current Conditions

Advancing succession associated with fire exclusion is contributing to replacement of lodgepole pine by subalpine fir in some areas of the IAP region. Concurrent increases in recently burned areas are creating new lodgepole stands, some of which may become very dense. Increased drought in these dense stands may exacerbate stress from other factors, including competition and insects. Warming temperatures have contributed to unprecedented mountain pine beetle outbreaks in lodgepole pine in western North America, including in the IAP region, causing 100 percent mortality in many mature lodgepole pine stands (Carroll et al. 2003; Jenkins et al. 2008; Page and Jenkins 2007).

Climate Change Responses

Longer drought periods and warmer temperatures in drier lodgepole pine forests may cause decreased growth and regeneration, perhaps resulting in a transition to more xeric tree species. Chhin et al. (2008) and Nigh (2014) projected that growth will decrease in moderate future warming, but the species probably has sufficient genetic capacity to compensate for this loss. Given that lodgepole pine is a generalist and capable of regenerating and growing in a wide range of environments, it is likely that any reduction in lodgepole pine dominance in dry sites would occur only under extreme warming scenarios over many decades to centuries.

In high-elevation subalpine systems where seasonal drought is not a problem, a warmer climate may increase productivity (Aston 2010; Johnstone and Chapin 2003). Wang et al. (2006) found major increases in lodgepole pine productivity under future climates with moderate warming, but decreased productivity and perhaps local extinctions were associated with extreme warming. Romme and Turner (1991) projected increases in the lodgepole pine zone in the Greater Yellowstone Area under moderate warming. Lodgepole pine could migrate into upper subalpine areas where it is currently excluded by cold, windy conditions (Hamann and Wang 2006; Romme and Turner 1991). The *latifolia* variety is well adapted to increased fire occurrence, depending on level of serotiny (Turner et al. 1999), although if fire is too frequent, it could be eliminated from sites where fire returns before established seedlings and saplings become reproductively mature (Larson et al. 2013). Projected increases in climatic conditions that facilitate mountain pine beetle outbreaks (higher reproductive rates) (Bentz et al. 2010) could reduce the abundance of lodgepole pine in some landscapes (Creeden et al. 2014; Gillette et al. 2014) (Chapter 8), especially where fire has been excluded (Temperli et al. 2013).

Ponderosa Pine (Pinus ponderosa var. ponderosa, P.p. var. scopulorum)

(Middle Rockies, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Ponderosa pine is shade intolerant and drought adapted, occupying low-elevation, dry forests (Minore 1979), and is both an early- and late-seral species, often associated with Douglas-fir and grand fir on moister sites. In the IAP region, Pacific ponderosa pine (var. *ponderosa*) extends from the central mountains of Idaho to the east side of the Sierra Nevada in Nevada. The Rocky Mountain variety (var. *scopulorum*) extends from the eastern mountains of Nevada to the central and northern mountains of Utah. (Note that Washoe pine [*P. p.* subsp. *washoensis*], which is found in a few locations in the Great Basin and northeastern slope of the Sierra Nevada, is no longer considered a discrete

subspecies and is not included in the assessment.) For both the Pacific and Rocky Mountain varieties, moisture typically limits growth, especially in summer, and distribution of ponderosa pine on drier sites is limited by available soil moisture, which, in turn, is affected by soil texture and depth. Ponderosa pine seedlings are susceptible to frost damage, which can exclude this species from low valleys (Shearer and Schmidt 1970). Ponderosa pine tolerates dry soil conditions by efficiently closing stomata to avoid water loss and xylem cavitation (Sala et al. 2005), tolerating intense drought, and drawing groundwater at low soil water potentials.

Cone crop periodicity in ponderosa pine varies greatly, but it is a poor seed producer in some areas. Natural regeneration is sporadic and is best when a heavy seed crop is followed by favorable weather in the next growing season (Heidmann 1983; Shearer and Schmidt 1970). The Rocky Mountain variety is highly inbred, and its vulnerability could be further compromised with limited gene flow between populations (Potter et al. 2015). Soil texture, plant competition, and seedbed conditions reduce seed germination and limit seedling survival and growth, although ponderosa pine can often germinate under moisture stress (Oliver and Ryker 1990). Young seedlings are susceptible to cold night temperatures and deep frosts, and trees occasionally suffer winter desiccation in drying winds.

Disturbance Interactions

Disturbance plays a major role in sustaining ponderosa pine forests. Over 100 species of insects attack the Pacific variety, and over 50 species attack the Rocky Mountain variety. The most damaging of the tree-killing insects are several species of *Dendroctonus* (Oliver and Ryker 1990), followed by ips beetles, both of which are present naturally in all stands. Dwarf mistletoe is widespread but rarely fatal. In the absence of fire or another disturbance that reduces stem density, bark beetles can cause extensive tree mortality. Ponderosa pine has a high capacity to survive fire, better than all of its competitors except western larch (Minore 1979; Ryan and Reinhardt 1988). Thus, wildfire favors the growth of large-diameter ponderosa pine by killing its primary competitors and small-diameter ponderosa pines (Arno 1988; Steele et al. 1986).

Historical and Current Conditions

Wildfire historically promoted ponderosa pine dominance across most low-elevation savannas because of its high resistance to fire, including high-intensity fire. Fire exclusion, mining, timber harvest, and livestock grazing caused major reductions in ponderosa pine forests (Jain and Graham 2005). Changes in fire regime altered the composition and structure of the remaining dry forests (Hann et al. 1997), with area burned by surface fires decreasing (Page and Jenkins 2007), mean fire return interval increasing, and crown fires increasing (Hann et al. 1997). Mid-seral structures have increased, often containing dense stands of small ponderosa pine, Douglas-fir, and grand fir. The proportion of

dry forests occupied by late-seral, single-storied ponderosa pine has declined significantly, and Douglas-fir or grand fir is often common in the understory.

Climate Change Responses

Ponderosa pine is expected to be relatively tolerant of increasing temperatures and longer droughts. The Rocky Mountain variety has relatively high phenotypic plasticity and is therefore better adapted to drought, although regeneration may decrease if precipitation decreases or becomes more variable. Morales et al. (2015) projected an 11 percent increase in the range of ponderosa pine in the western United States, and Nitschke and Innes (2008) used gap modeling to project replacement of dry Douglas-fir with ponderosa pine in British Columbia. Hansen et al. (2001) projected that the range of ponderosa pine will expand in the western United States, whereas most other tree species ranges will decrease. Although species distribution models suggest that the range of ponderosa pine may decrease (Bell et al. 2014; Franklin et al. 1991; Gray and Hamann 2013) and rise in elevation (Crimmins et al. 2011) in a warmer climate, these projections are questionable because they do not consider on-the-ground growth processes and competition.

Advancing competition resulting from fire exclusion, increased wildfire extent and severity, and the potential for increased susceptibility to insects in warmer, drier conditions will dictate the future of ponderosa pine in the IAP region (Hann et al. 1997; Miller and Keen 1960; Negrón and Fettig 2014). If fires are too frequent, regenerating trees will not grow above the lethal scorch height and will not reach maturity. Increasing wildfire severity could also eliminate mature ponderosa pine trees that provide seed sources for populating future burns.

Singleleaf Pinyon (*Pinus monophylla*)

(Great Basin and Semi Desert subregion)

Autecology

Singleleaf pinyon is adapted to a wide variety of sites. It usually grows on pediments; dry, rocky slopes; ridges; and alluvial fans between 4,500 and 7,500 feet elevation (Lanner 1999; Stephenson and Calcarone 1999). It is frost resistant, drought tolerant, and shade intolerant (Lanner 1983), typically growing on shallow, well-drained, low-fertility soils, although it has been found on more productive soils as well (Evans 1988; Gottfried and Severson 1993; Gottfried et al. 1995). Pinyon pine typically grows in association with juniper species, where juniper dominates lower elevations of their range and pinyon the upper. Pinyon-juniper woodlands typically progress toward increased tree density and canopy cover over time (Everett 1985; Meeuwig et al. 1990; Short and McCulloch 1977; West et al. 1975), often expanding into adjacent grass and shrublands (Burwell 1998; West et al. 1975). Understory species make up a small portion of the total biomass in denser stands, although they may be

important forage species and typically persist following disturbance (Everett and Koniak 1981).

Disturbance Interactions

In the Great Basin, there is evidence of both frequent, low-intensity fires carried by once-abundant perennial grasses, and less frequent, local stand-replacement fires during extreme conditions. Fires burned in irregular patterns, producing a mosaic of burned and unburned landscape. On high-productivity sites where sufficient fine fuels existed, fires burned every 15 to 20 years, and on less productive sites with patchy fuels, fire intervals were 50 to 100 years or longer. Fire frequency in singleleaf pinyon communities varies with fuel loads and ignition source, which, in turn, vary with habitat type, aspect, topography, stand history, and climatic conditions (Gruell 1999; Paysen et al. 2000). Cheatgrass has become increasingly common in the understory over the past few decades, continually providing abundant fine surface fuels and increasing the potential for more frequent wildfires (Shinneman and Baker 2009).

Pinyon dwarf mistletoe (*Arceuthobium divaricatum*) can cause extensive damage (Hawksworth and Wiens 1972), leaving trees susceptible to insect attack. Pinyon blister rust (*Cronartium occidentale*) occurs extensively on *Ribes* species in most western States but infects singleleaf pinyon only sporadically (Stillinger 1944), occasionally girdling small trees. Black stain root disease (*Ophiostoma wageneri*) occasionally kills singleleaf pinyon (Smith 1967b; Wagener and Mielke 1961). The disease spreads by root contact, and infection is confined to xylem in the roots and lower trunk. Pinyon ips (*Ips confusus*) is commonly found in pinyon woodlands, with outbreaks occurring when trees are stressed (Chapter 8).

Historical and Current Conditions

Singleleaf pinyon was a source of fuel (charcoal) for the mining industry between the 1860s and 1920s (Young and Budy 1979), and it has been used extensively for firewood and other uses, with local deforestation in some locations. In some lower-elevation locations, pinyon has been removed from the landscape to encourage the growth of grasses and forage for livestock grazing. Persistent woodlands of pinyon pine or juniper species, or a mixture of both, are found where local soils and climate are favorable, and wildfire has been infrequent (Romme et al. 2009). Pinyon-juniper savannas are found where local soils and climate are suitable for both trees and grasses, and low-intensity fires have been relatively frequent. Large increases in junipers have occurred in portions of pinyon-juniper woodlands (Romme et al. 2009). Damage to cryptobiotic crusts has caused erosion in some pinyon-juniper woodlands.

Climate Change Responses

Singleleaf pinyon is drought tolerant, and reduced soil moisture is not expected to have a significant effect on its abundance and distribution, although its growth may decrease over time. It is not as drought tolerant as the juniper

species with which it is associated, and may decrease in abundance where the species compete. However, it may be able to outcompete ponderosa pine at higher elevations.

The future of singleleaf pinyon will largely depend on spatial and temporal patterns of wildfire, which is expected to increase in frequency (Floyd et al. 2004). Pinyon is only moderately fire tolerant and is easily engaged in crown fires because of low crowns and high concentrations of volatile chemicals. After an initial fire, accumulation of surface fuels and tree regeneration is likely to be slow (unless Gambel oak [*Pinus gambelii*] is present) because of moisture limitations, resulting in a sparse canopy and disconnected fuels (Rocca et al. 2014). If fire frequency is high in areas where pinyon is codominant with ponderosa pine, the latter species will become more common and pinyon will become less common. The long-term condition of juniper is complicated by nonnative annual grasses, which increase surface fuels and fire frequency. Insects, especially pinyon ips, will also be an important stressor, especially during extended droughts.

Twoneedle Pinyon (Pinus edulis)

(Plateaus subregion)

Autecology

Pinyon-juniper woodlands are found between the low plains covered by grassland, desert shrub, or chaparral vegetation and the high mountains just below the zone dominated by either submontane shrubs or ponderosa pine. They grow best on higher, wetter sites of the woodland zone, just below ponderosa pine (Fowells 1965; Jameson et al. 1962). Twoneedle pinyon grows in semiarid to arid climates, often associated with oneseed juniper (*Juniperus monosperma*) and Utah juniper. Pinyon is drought tolerant and shade intolerant, and seedlings require extra moisture or shade until their elongating taproots reach deeper substrates (Mitchell 1984). The extensive root system of established pinyons and relatively rapid rate of root elongation, especially of young seedlings, enhance the ability of pinyon to survive in dry environments.

Disturbance Interactions

Small pinyon pines are sensitive to fire and may be killed by low-intensity fire (Floyd et al. 2000; McCulloch 1969), whereas larger trees tend to be somewhat resistant to surface fire because foliage is high enough above the ground to avoid crown scorch or other damage (Dwyer and Pieper 1967; Wittie and McDaniel 1990). Cheatgrass has become increasingly common in the understory over the past few decades, continually providing abundant fine surface fuels and increasing the potential for more frequent wildfires (Shinneman and Baker 2009). Foliage diseases include needle casts (*Elytroderma deformans*, *Bifusella saccata*) and needle rusts (*Coleosporium jonesii*, *C. crowellii*) (Fowells 1965; Hepting 1971). Pinyon blister rust and pinyon dwarf mistletoe damage stems; the latter species is considered the major pathogen of pinyon.

Historical and Current Conditions

Pinyon-juniper woodland expansion since the time of settlement has been attributed to several factors, including a warming climate, fire exclusion, increased populations of seed-dispersing birds and mammals, and reduced competition from grasses resulting from overgrazing by livestock (Everett 1987; Jameson 1970). In the absence of wildfire, fuels have accumulated in some stands, especially in more mesic sites, increasing the possibility of crown fire. Hazardous fuels reduction, including prescribed burning, has been used in some locations.

Climate Change Responses

Twoneedle pinyon is drought tolerant, and reduced soil moisture is not expected to have a significant effect on its abundance and distribution, although its growth may decrease over time. It is not as drought tolerant as juniper, and may decrease in abundance where the species co-occur. However, it may outcompete ponderosa pine at higher elevations. Since 2000, twoneedle pinyon at low-elevation sites in northern New Mexico has suffered significant mortality associated with extended drought and pinyon *Ips* (Breshears et al. 2009) (Chapter 8), and although similar mortality has not been widespread in Utah, it may be possible during long droughts. If pinyon mortality increases in the future, juniper would probably become more dominant.

The future of twoneedle pinyon will largely depend on spatial and temporal patterns of wildfire, which is expected to increase in frequency (Floyd et al. 2004). Pinyon pine is only moderately fire tolerant, and it is easily engaged in crown fires because of low crowns and high concentrations of volatile chemicals. After an initial fire, accumulation of surface fuels and tree regeneration will probably be slow (unless Gambel oak is present) because of moisture limitations, resulting in a sparse canopy and disconnected fuels (Rocca et al. 2014). If fire frequency is high in areas where pinyon pine is codominant with ponderosa pine, the latter species will become more common and pinyon pine will become less common. The long-term condition of juniper is complicated by nonnative annual grasses, which increase surface fuels and fire frequency. Insects, especially pinyon *Ips*, will also be an important stressor, especially during extended droughts.

Western White Pine (Pinus monticola)

(Great Basin and Semi Desert subregion)

Autecology

Western white pine occupies the extreme western Great Basin portion of the IAP region and is typically associated with other conifer species. It is limited by moisture at lower elevations and by temperature at higher elevations. Western white pine grows on a variety of sites, but is more common along moist creek bottoms, lower benches, and northerly slopes. Seedling establishment is favored by

partial shade in severe sites (Graham 1990) but minimal shade on northern slopes. Once established, it grows best in full sun. Seedlings have low drought tolerance, and first-year seedlings are subject to mortality from high surface temperatures on exposed sites. White pine attains dominance only after wildfire or in silvicultural systems that favor it. A generalist species with broad climate and environmental tolerances (Devine et al. 2012), western white pine adapts to different conditions through phenotypic plasticity and selective genetic differences.

Disturbance Interactions

Historically, white pine forests originated from wildfires, especially stand-replacing burns, but they were also maintained by frequent low-intensity fires (Barrett et al. 1991). When mature, white pine has thick bark and a high crown, which make it tolerant of fire. White pine blister rust has greatly decreased survival and vigor of white pine (Fins et al. 2002; Harvey et al. 2008), virtually eliminating this species in some locations. Armillaria root rot causes foliar chlorosis and root mortality, as well as reduced growth. Annosus root disease and laminated root rot also cause reduced vigor and some mortality. Bark beetles attack western white pine, killing groups of trees in mature forests, especially those weakened by blister rust (Chapter 8).

Historical and Current Conditions

Western white pine stands were previously more dominant in western North America (Harvey et al. 2008). It is much less abundant in mixed conifer forests as a result of logging, fire exclusion, and blister rust (Fins et al. 2002). This decline will probably continue to reduce abundance, and in some cases, cause local extirpation in the absence of assertive restoration.

Climate Change Responses

Western white pine may be well adapted to a warmer climate in some portions of its range (Loehman et al. 2011). It can disperse seeds into burned areas, which are likely to increase in the future, and a warmer climate may increase its productivity in some locations. However, the prevalence of white pine blister rust will make it difficult for white pine to persist in most forests (Fins et al. 2002; Harvey et al. 2008), and it is expected to continue to decline throughout much of its range.

Whitebark Pine (*Pinus albicaulis*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front subregions)

Autecology

Whitebark pine is an important component of upper subalpine forests in the IAP region (Arno and Hoff 1990). It supports unique components of floral and faunal

diversity and promotes community development and stability (Tomback and Achuff 2010; Tomback et al. 2001). It is a long-lived tree, tolerates moderate shade (Minore 1979), grows slowly, and tolerates long periods of drought (Callaway et al. 1998). In the absence of wildfire, whitebark pine is replaced by subalpine fir and Engelmann spruce in some locations (Arno and Hoff 1990). Whitebark pine has a mutualistic relationship with Clark's nutcracker, which caches and disperses seeds (Tomback 1982, 1983). Whitebark pine is genetically diverse (Keane et al. 2012), allowing it to exist across many environments.

Disturbance Interactions

Whitebark pine fire regimes are complex and variable in space and time (Morgan et al. 1994b). Most fires in the upper subalpine zone burn in mixed-severity patterns that facilitate long-term survival of the species (Keane et al. 1994). Mountain pine beetle can damage mature stands, often causing high mortality. White pine blister rust is also damaging, preventing tree development and often causing mortality. Whitebark pine has some resistance to white pine blister rust, and although efforts at developing rust-resistant seed for regenerating burned and treated areas hold promise, restoration will need to occur at large spatial scales to be effective.

Historical and Current Conditions

Whitebark pine, a candidate species for listing under the U.S. Endangered Species Act (USFWS 2011), has been declining since the early 20th century from the combined effects of mountain pine beetle-caused mortality, fire exclusion, and spread of white pine blister rust (Schwandt 2006; Tomback and Achuff 2010) (fig. 6.4). Within the last decade, outbreaks of mountain pine beetle and increasing damage and mortality from blister rust have resulted in cumulative whitebark pine losses that have altered high-elevation community composition and ecosystem processes throughout much of western North America.

Climate Change Responses

Although whitebark pine was able to persevere through climatic variability in the past, it will be highly exposed to future climate change because of its confined distribution to upper subalpine environments. It is expected to continue to decline in abundance and vigor in a warmer climate, not because it is poorly adapted to an altered climate, but because it is experiencing so much stress from blister rust and mountain pine beetle that regeneration capability is greatly reduced (Bartlein et al. 1997; Bentz et al. 2016; Devine et al. 2012). In some cases, whitebark pine populations are so low that Clark's nutcracker is acting more as a seed predator than a seed disperser (Keane and Parsons 2010; Leirfallom et al. 2015). A warmer climate is expected to exacerbate this decline in most locations.



Figure 6.4—Whitebark pine. This species, which has been subjected to mortality from white pine blister rust for decades, may be more susceptible to mountain pine beetles in a warmer climate (photo: J. Beck, National Park Service).

Blue Spruce (*Picea pungens*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

The shallow roots of blue spruce restrict it to moist sites where water is close to the surface (Lanner 1983). Blue spruce occurs at middle elevations on montane streambanks, well-drained floodplains, first-level terraces, ravines, intermittent streams, and gentle slopes (Fechner 1985; Hess and Alexander 1986; Lanner 1983). Spruce grows in cool climates that are sub-humid to humid and characterized by low summer temperatures and low winter precipitation. It is a pioneer species in riparian communities that are subject to periodic disturbances, such as scouring and flooding (Baker 1990; Fechner 1990; Szaro 1990). It is a shade-tolerant, mid- to late-seral species in montane and subalpine zones (Baker 1988; Schmidt and Larson 1989).

Disturbance Interactions

Blue spruce is easily killed by fire (Jones 1974; Wright and Bailey 1982). Insects and disease reduce growth, viability, and vigor of spruce (Fechner 1985; Walters 1978) (Chapter 8). Heart and root rots, cone

rusts, nematodes, snow molds, canker, and tip blight can reduce the vigor of spruce (Fechner 1990; Nelson and Krebill 1982) and can cause mortality in older, low-vigor trees.

Historical and Current Conditions

Because blue spruce is located at high elevation and has no commercial value for timber, it has been relatively free of human influence, except in stands where it may have been associated with harvest of other species, such as Engelmann spruce. Western spruce budworm has killed patches of spruce and often other species in some locations, but this appears to be a normal occurrence in older, low-vigor stands.

Climate Change Responses

Climate change may reduce the functionality of riparian and wet meadow locations where blue spruce is commonly found. Therefore, its distribution and abundance could decrease locally if growth and vigor decline over time. Wildfire is currently uncommon in blue spruce communities, but if it becomes more frequent in a warmer climate, blue spruce will decrease in abundance because of fire. If fire frequency is high enough, spruce may not achieve dominance in the overstory.

Engelmann Spruce (*Picea engelmannii*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Engelmann spruce is widely distributed and is a major component of high-elevation forests in the IAP region (Alexander and Shepperd 1990). It occupies very cold environments in some locations. It is shade tolerant, although not as much as its common associate subalpine fir. This species is not drought tolerant, especially as a seedling (Alexander and Shepperd 1990), but tolerates frost and seasonal standing water. Pure Engelmann spruce is found in wet areas, but the species is usually mixed with other conifer species in upland locations. Seeds germinate in a variety of substrates, including litter and decomposed humus. Following establishment, survival is favored by adequate soil moisture, cool temperatures, and some shade.

Disturbance Interactions

Engelmann spruce is highly susceptible to fire injury and death, but some large spruce can survive severe burns (Bigler et al. 2005; Wadleigh and Jenkins 1996). It survives fire better than its primary associate, subalpine fir (Ryan and Reinhardt 1988). Surviving spruce can provide abundant seed in burned areas, although the subsequent forest may or may not be dominated by both spruce and

other species (e.g., subalpine fir) (Pfister et al. 1977). Engelmann spruce is susceptible to windthrow, especially after timber harvest and thinning. Several insect species are associated with Engelmann spruce (Chapter 8).

Historical and Current Conditions

Recent trends in Engelmann spruce forests across the IAP region are unclear. Advancing succession during many decades of fire exclusion has probably increased spruce abundance in subalpine and upper subalpine landscapes. But logging and fire have reduced spruce at lower elevations, where it occurs in seasonally wet areas and frost pockets. Several locations throughout the IAP region with mature Engelmann spruce have sustained extensive mortality from spruce beetle (*Dendroctonus rufipennis*) outbreaks.

Climate Change Responses

Some losses of Engelmann spruce are likely in drier portions of its range, especially in seasonally moist sites that will be drier in the future. Some mortality may have already occurred from recent drought (Liang et al. 2015). Higher temperatures can increase growth in some locations (Luckman et al. 1984) and reduce growth in other locations (Alberto et al. 2013). If wildfire frequency increases, it will probably reduce the extent of mature spruce, although it readily establishes following wildfire. Spruce beetle can cause greater stress in a warmer climate, especially in mature stands (Bentz et al. 2010). Although Engelmann spruce is sensitive to climate, it will probably persist in high-elevation landscapes, because of its genetic capacity to adapt to climatic variability by taking advantage of suitable microsites (Jump and Peñuelas 2005).

Quaking Aspen (*Populus tremuloides*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Quaking aspen is abundant in the IAP region, with its distribution limited by water availability and growing-season temperature. Aspen stems are relatively short lived and maintained by disturbance (Mueggler 1985; Rogers 2002), although belowground genets of aspen clones can survive for millennia. It is shade intolerant and sprouts aggressively following disturbance (usually fire), which kills most of the live stems, thus stimulating vegetative propagation (suckering) (Bartos 1978) and facilitating rapid reoccupation of the site. This species has substantial phenotypic variation, as evidenced by varied foliar morphology, stem morphology, and phenology among different clones.

Disturbance Interactions

Browsing of post-disturbance suckers by ungulates—including elk (*Cervus elaphus*), moose (*Alces alces*), and cattle—frequently damages seedlings and sprouted stems (Eisenberg et al. 2013; White et al. 1998), and in some cases mature trees, thus increasing susceptibility to insects and pathogens. Wildfire can kill aboveground stems (Bartos 1998) but also promotes new seedlings and suckering by eliminating conifers (Campbell and Bartos 2001; Shepperd et al. 2001). Following disturbance, aspen dominates a site for 40 to 80 years; thinning from insects and disease and succession (shading) by conifers eventually reduce aspen abundance (Mueggler 1985; Rogers 2002). Hypoxylon canker (*Hypoxylon mammatum*) causes significant damage in some locations (Perala 1990). Young trees can be killed by small rodents and mammals (Eisenberg et al. 2013).

Historical and Current Conditions

Since around 1970, aspen has been in a period of general decline that may be at least partly attributed to wildfire exclusion, allowing plant succession to proceed toward conditions that ordinarily exclude aspen (Campbell and Bartos 2001; Frey et al. 2004). Recent episodes of aspen dieback (“sudden aspen decline”) have been superimposed on this general decline; the epidemiology begins with death of branch tips and progresses to death of mature trees and eventually death of entire clones (Frey et al. 2004). Dieback is suspected to be caused by periods of drought (Worrall et al. 2013). The worst symptoms are generally found at lower elevations.

Climate Change Responses

Seral aspen communities will respond to a warmer climate differently than mature aspen communities (Rice et al. 2017). Aspen on warmer sites could suffer high mortality because of increasing water deficit (Hogg and Hurdle 1995; Ireland et al. 2014). Extreme droughts (Frey et al. 2004) and high temperatures (Perala 1983) are of special concern, especially at the margins of aspen distribution at low elevation, and may weaken trees enough that insects and pathogens can cause tree mortality (Rice et al. 2017). Increased wildfire frequency, particularly on moist sites, is likely to favor aspen regeneration in the future by removing conifers. If future wildfires are severe, however, they may kill shallow root systems and locally extirpate aspen. In some locations, declining stands may have little regeneration because of ungulate herbivory (Rogers et al. 2013).

Fremont Cottonwood (*Populus fremontii*)***(Southern Greater Yellowstone, Uintas and Wasatch Front subregions)******Lanceleaf Cottonwood (*Populus x acuminata*)******(Great Basin and Semi Desert subregion)******Narrowleaf Cottonwood (*Populus angustifolia*)******(Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)******Balsam Cottonwood (*Populus balsamifera*)******(Middle Rockies subregion)****Autecology*

The four cottonwood species in the IAP region—Fremont cottonwood, lanceleaf cottonwood, narrowleaf cottonwood, and balsam cottonwood—grow primarily in seasonally wet to moist open-canopy sites, typically along streams and rivers. Cottonwood often dominates riparian communities on alluvial sites from 4,000 to 6,000 feet elevation, with other hardwood species, shrubs, and grasses in the understory. Cottonwood is shade and drought intolerant, requiring access to the water table during most of the growing season (Rood et al. 2003). High streamflows facilitate seedling establishment through scouring and deposition of alluvial sediments for germination of windborne seeds. High numbers of seedlings often become established after a flood, but thin over time. Seedlings and saplings are frequently injured and sometimes killed by early or late frosts (DeBell 1990).

Disturbance Interactions

Cottonwood is somewhat fire tolerant owing to its thick bark and high branches. It is a weak stump sprouter, but rarely regenerates from suckers (Brown 1996). Cottonwood can resprout and survive low-intensity fires in the short term (Gom and Rood 1999), but fire injuries can introduce diseases that weaken and sometimes kill trees (Borman and Larson 2002). Several insects attack cottonwood. Many fungal species cause decay in cottonwood, but only brown stringy heart rot (*Spongipellis delectans*) and yellow laminated butt rot (*Pholiota populnea*) cause significant damage. Russian olive (*Elaeagnus angustifolia*) and saltcedar (*Tamarix* spp.) are aggressive nonnative trees that can out-compete cottonwood in some locations, particularly during or after drought (Shafroth et al. 2002).

Historical and Current Conditions

Cottonwood species are well distributed within their respective habitats in the IAP region, although degradation of riparian areas by grazing and other land uses have damaged some trees and the functional integrity of the riparian system. Russian olive and saltcedar have displaced cottonwoods in many locations, thus altering local hydrological function, because the nonnative species take up more water than native species. Biological control releases of the nonnative northern tamarisk beetle (*Diorhabda carinulata*) in the Southwest, starting in the 1990s, have caused rapid mortality and decline in vigor in many saltcedar populations (Sher and Quigley 2013; Tracy and Robbins 2009).

Climate Change Responses

As snowpack declines and melts earlier with warming temperatures, there will be reduced, attenuated river flows, along with a possible shift in timing of peakflows. These shifts may decrease germination and establishment of young cottonwoods, depending on the relative timing of floods and seed production (Whited et al. 2007). Altered hydrological flow, which can also be caused by withdrawal for human use, will affect both floodplain interaction and water available to cottonwoods, which, in turn, can affect recruitment and establishment of seedlings (Auble and Scott 1998; Beschta and Ripple 2005). Upland conifers can potentially establish in the riparian zone if the local water table has dropped, increasing competition with cottonwoods. Long-term transport of seeds provides cottonwood with an effective mechanism for regeneration across large landscapes, conferring some resilience to future climate.

Sitka Alder (*Alnus viridis* subsp. *sinuata*)***(Middle Rockies subregion)******Thinleaf Alder (*Alnus incana* subsp. *tenuifolia*)******(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)******White Alder (*Alnus rhombifolia*)******(Middle Rockies subregion)****Autecology*

Sitka alder and thinleaf alder are small, deciduous trees or shrubs found on a wide range of soils and wide range of elevations. Sitka alder is usually multistemmed and bushy, forming dense thickets. White alder is a deciduous, medium to large tree found on a variety of soils typically near permanent streams at low to mid-elevations. All species are found on moist, cool sites, typically riparian areas or other locations where a reliable water

source is available; for example, Sitka alder is often located in avalanche tracks. These species are associated with other hardwood and shrub species, mixed with or intermittent with overstory conifer species. All species are moderately shade tolerant (Haeussler and Coates 1986). Seeds require a moist mineral soil for germination, which normally takes place in the spring. Thinleaf alder can also propagate by cloning (Hall 1973). All alder species fix nitrogen through their association with actinomycetes.

Disturbance Interactions

Many sites occupied by alder species are subject to periodic flooding. Although tops may be damaged or killed, all species can sprout from root crowns. Wind-dispersed seeds readily germinate on alluvial soils exposed by floods or covered by sediment, and on bare soil created by wildfire, avalanches, and soil slumps. Alders have thin bark, and stems are easily killed by fire. Although alder can be killed by severe fire (Barro et al. 1989), it can also sprout following top kill by fire (Fischer and Bradley 1987). Although alder wood is resilient and somewhat limber, avalanches can damage Sitka alder and thinleaf alder, which often reproduce by sprouting (Oliver et al. 1985).

Historical and Current Conditions

Alders have rarely been disturbed by human activity because they have no timber value. They have been subjected to some stress in riparian areas that have been disturbed by water withdrawals or livestock grazing.

Climate Change Responses

In general, higher temperatures are not expected to have significant direct effects on alder species because alders are usually located in riparian areas that are buffered from temperature increases. However, smaller riparian areas may become drier in a warmer climate, especially if they rely on adjacent snowpack. Lower levels of soil moisture could reduce the vigor of alder and other species. Increased frequency of wildfire may be a significant stressor for white alder because it may not sprout vigorously after fire (Fryer 2014), possibly making associated species more competitive. Sitka alder and thinleaf alder can sprout after wildfire, so increased disturbance will probably not affect their distribution and abundance.

Velvet Ash (*Fraxinus velutina*)

(Uintas and Wasatch Front, Plateaus subregions)

Autecology

Velvet ash (also called desert ash or Arizona ash) is a deciduous tree with spreading branches and a rounded crown (if it has sufficient sunlight) that grows up to 30 feet tall when mature. It is found in riparian areas in canyons and along streambanks in desert mountains of

southern Utah and southern Nevada above 3,000 feet elevation. Velvet ash grows in a variety of substrates, including alkaline soils. The presence of this species in the desert generally indicates a permanent underground water supply. It is shade intolerant, regenerates through wind dispersal of winged seeds, and can sprout from the base when damaged.

Disturbance Interactions

Velvet ash is easily top-killed by fire, but stumps can sprout vigorously following fire and mechanical damage and can attain prefire heights in 8 years (Winkel and Syzdek 2015). North American ash populations are at substantial risk from the introduction of emerald ash borer (*Agrilus planipennis*), which has now reached as far west as Colorado. Large-scale mortality of ash trees, as a result of borer infestations, would probably result in significant modifications in the composition and successional dynamics of many natural forests (MacFarlane and Meyer 2005) (Chapter 8).

Historical and Current Conditions

Little is known about the historical distribution or uses of velvet ash. It has no commercial value for timber but may have been used for firewood in some locations. Its populations are probably mostly intact, except where riparian areas have been modified.

Climate Change Responses

As soil moisture declines in a warmer climate, marginal riparian sites for velvet ash may become less favorable for regeneration and survival of young trees. With increases in fire frequency, there are likely to be increased vegetative regeneration and decreased production of seedlings following fire; fire would probably kill seeds on or near the soil surface, restricting seedling recruitment to surviving seed-producing trees. Low-intensity fires may promote regeneration by thinning stands and stimulating sprouting. Increased temperatures may promote ash seedling and mature tree growth by increasing soil temperatures. Browsing pressure on ash may increase with increased drought, as upland grasses and forbs desiccate and senesce earlier, or are replaced by less palatable species.

Water Birch (*Betula occidentalis*)

(Middle Rockies, Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Water birch is primarily a riparian species, occurring near waterways, wet swales, marshes, ravines, bogs, and moist woodlands (Arno and Hammerly 1977; Welsh et al. 1987). Water birch is common along streams in steep

areas of the IAP region, especially in coarse-textured, moist to wet soils (Sutton and Johnson 1974). Although common in semiarid climates (Arno and Hammerly 1977), water birch is not particularly drought tolerant (Merigliano 1996) but is moderately shade tolerant and flood tolerant. In the Great Basin, riparian habitats with water birch are found in upland habitats ranging from mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana*) shrublands (Manning and Padgett 1989) to fir forests (Lanner 1983).

Disturbance Interactions

Water birch often forms clumps by sprouting from the base of the trunk (Harrington 1964). Sprouts can develop after top kill by flooding or other physical injury (Hansen et al. 1995; Skinner et al. 2006) or without aboveground damage (Lanner 1983). This species can regenerate quickly following damage and disturbance.

Historical and Current Conditions

Little is known about the historical distribution and use of water birch. It has little commercial value but is sometimes used for firewood and fence posts. Birch is used as browse by ungulates, including livestock, to some extent. Birch stems may have increased in some areas where American beaver (*Castor canadensis*) populations were reduced or extirpated.

Climate Change Responses

Water birch adapts well to a wide range of climate and water availability (Disalvo and Hart 2002). As soil moisture declines with a warmer, drier climate, marginal riparian sites for birch may become less favorable for regeneration and survival of young trees. With increased fire frequency, there are likely to be better vegetative regeneration and decreased production of seedlings following fire events. Fire would probably kill seeds on or near the soil surface, restricting seedling recruitment to surviving seed-producing trees. Low-intensity fires may promote regeneration by thinning stands and stimulating sprouting. Birch productivity may benefit from increased temperatures because seedling and mature tree growth may increase with increasing soil temperatures. Browsing pressure may increase with increased drought, as upland grasses and forbs desiccate and senesce earlier, or are replaced by less palatable species.

Boxelder (*Acer negundo*)

(Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus subregions)

Autecology

Boxelder is a fast-growing and fairly short-lived hardwood that grows in riparian and palustrine communities. It generally grows on moist sites along lakes and streams,

on floodplains, and in low-lying wet places where its shallow root system can find abundant moisture (Lanner 1983). Resilient to climate extremes (Preston 1948), boxelder is drought tolerant once established and can withstand short periods of flooding (Sutton and Johnson 1974). It is moderately shade tolerant but does not reproduce in its own shade. Boxelder roots are shallow and spreading, except in deep soils (Preston 1948; Sutton and Johnson 1974). It tolerates a wide range of soils but grows more vigorously in well-drained soils (Medina 1986).

Disturbance Interactions

Boxelder grows on moist bottomland sites, which are seldom subject to burning. This thin-barked species is easily injured by fire (Van Dersal 1938), regenerating via sprouting and seeds. It produces large annual crops of wind-dispersed seeds that germinate on a wide variety of soils. It also sprouts from the root crown, stump, or exposed roots following top kill by mechanical damage (Hansen and Hoffman 1988; Nix and Cox 1987). Verticillium wilt (*Verticillium albo-atrum*) is the only notable disease that kills boxelder, although it is also susceptible to stem canker caused by eutypella canker (*Eutypella parasitica*). Boxelder bugs (*Boisea trivittata*) infest boxelder trees and other maples, but do not cause significant damage.

Historical and Current Conditions

Boxelder was used for windbreaks and erosion control in many parts of the West. It has no commercial value but is sometimes used for firewood. It is used as browse by ungulates, and although it is unpalatable to livestock, the animals may damage stems while seeking shade. It is possible that boxelder stems have increased in some areas where American beaver populations were reduced or extirpated (Dieter and McCabe 1989). It is probably mostly intact from an ecological perspective.

Climate Change Responses

Boxelder exists across a broad range of soils and topographic locations, but as soil moisture declines in a warmer climate, marginal riparian sites may become less favorable for regeneration and survival of young trees. With increased fire frequency, there are likely to be increased vegetative regeneration and decreased production of seedlings following fire. Fire is likely to kill seeds on or near the soil surface, restricting seedling recruitment to surviving seed-producing trees. Low-intensity fires may promote regeneration by thinning stands and stimulating sprouting. Boxelder productivity may benefit from increased temperatures because seedling and mature tree growth may increase with increasing soil temperatures. Browsing pressure on boxelder may increase with increased drought, as upland grasses and forbs desiccate and senesce earlier, or are replaced by less palatable species.



Figure 6.5—Gambel oak sprouts vigorously following wildfire, as shown in both the foreground and background. The distribution and abundance of this species may increase in a warmer climate, replacing conifers as a dominant species in some locations (photo by Heath Haussamen, used with permission).

Gambel Oak (*Quercus gambelii*)

(Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Gambel oak is a small deciduous tree or large shrub that is widespread in foothills and lower mountain locations of the IAP region. The tree typically grows at between 3,000 and 10,000 feet elevation, where average annual precipitation is 10 to 24 inches. Oak height is typically 10 to 30 feet depending on soil type and water availability. Branches are irregular and crooked, making them flexible enough to bend without breaking when covered with snow. Deep roots, xeromorphic leaves, and efficient water transport contribute to the high drought tolerance of Gambel oak (Kolb and Stone 2000), which grows in both pure stands and associated with ponderosa pine, pinyon pine, and other hardwood tree and shrub species. In most of its range, Gambel oak regeneration depends more on sprouting than establishment from seed (Clary and Tiedemann 1986; Larsen and Johnson 1998).

Disturbance Interactions

Gambel oak responds to fire by vegetative sprouting from its lignotuber and rhizomes, and even the stems can survive low-intensity fires (Harper et al. 1985) (fig. 6.5). Fire frequency in oak stands depends on accumulation of fuels by both oak and associated species (Mitchell 1984).

Following wildfire, sprouts continue to grow, and natural thinning occurs, adding dead stems to the fuel bed. In the absence of fire, sprouts form young poles. At the pole stage, fires cause 100 percent stem mortality, either creating openings within stands for resprouting or cycling back to a grass-forb stage. In the absence of fire, Gambel oak stands reach maturity in 60 to 80 years. Dense understories of oak may serve as ladder fuels that carry fire to overstory conifers, increasing fire risk to adjacent species. Fire in some ponderosa pine stands can convert to thickets of Gambel oak, initiating a Gambel oak successional stage after the competing ponderosa pine overstory is removed (Dick-Peddie and Moir 1970). Late-spring frosts that kill oak leaves can cause extreme fire behavior later in the summer; the dead leaves tend to cling to the stem and act as dry aerial fuels (Jester et al. 2012). Many insects and diseases are associated with Gambel oak.

Historical and Current Conditions

Gambel oak acorns have been an important food for Native Americans for thousands of years, and the species is widely used for firewood. Oak density has been reduced in some areas with herbicides, mechanical treatments, and prescribed burning, typically to reduce fire hazard and protect overstory species such as ponderosa pine. In some areas where multiple wildfires have occurred in the past 30 years, oak appears to be increasing in dominance through sprouting and mortality of conifers (e.g., Adams and Dockter n.d.) combined with slow regeneration of the overstory.

Climate Change Responses

Gambel oak is very tolerant of low soil moisture, providing an advantage in a warmer climate with more droughts. Oaks sprout readily following wildfire, and with an expected increase in fire in the future, oaks may retain dominance or codominance in most locations. Being adapted to both drought and fire will improve the competitive status of oak with co-occurring tree species such as ponderosa pine and pinyon pines and probably with other shrub species, except at the lowest elevations where shrub-steppe systems dominate. Therefore, it is likely that Gambel oak will increase in abundance and possibly distribution in a warmer climate with more fire.

Curl-Leaf Mountain Mahogany (*Cercocarpus ledifolius*)

(Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Curl-leaf mountain mahogany is a drought-tolerant, somewhat shade-tolerant, slow-growing tree or tall shrub (Lacey and Mosley 2002; Lanner 1983) found at 4,000 to 8,000 feet elevation in the IAP region (Brotherson 1990), typically in scattered patches and in extensive pure stands on dry, rocky slopes between conifer and desert steppe communities (Munz 1973; Stubbendieck et al. 1992). The root system is shallow and spreads widely (Sutton and Johnson 1974), typically in shallow to deep, well-drained, low-fertility sandy loam soils (Davis 1990; Hickman 1993).

Disturbance Interactions

Wildfires usually cause mortality of curl-leaf mountain mahogany, although older plants with thick bark may survive low-intensity fires (Gruell et al. 1985; Martin and Johnson 1979). Postfire regeneration is primarily by seedling establishment (Gruell et al. 1985), and sprouting after fire is rare (Tisdale and Hironaka 1981). Several species of insects, including mountain-mahogany looper (*Iridopsis clivinaria*), feed on mountain mahogany, but do not generally cause significant damage.

Historical and Current Conditions

Curl-leaf mountain mahogany was used by Native Americans to make bows and other small implements. Euro-Americans first used it as fuel for mining in the 1860s. The species provides forage for ungulates and wildlife. Livestock can damage productivity where grazing is heavy (Smith 1967a). Fire exclusion has facilitated increased mountain mahogany abundance and successful regeneration in some locations (Gruell 1982; Kay 2003), allowing it to compete with more fire-adapted species. Mountain mahogany is occasionally killed with herbicides,

mechanical removal, or prescribed fire to improve range quality or reduce fuel bed continuity.

Climate Change Responses

Curl-leaf mountain mahogany is drought tolerant, so it should continue to be productive in a warmer climate with more droughts, especially compared to other species. However, if wildfire frequency and extent increase as expected, it will be at a disadvantage because it is not fire tolerant and does not regenerate by sprouting. If wildfire is sufficiently frequent, new seedlings may be successively killed, thus reducing the abundance of mountain mahogany across fire-prone landscapes.

Bigtooth Maple (*Acer grandidentatum*)

(Uintas and Wasatch Front, Plateaus, Great Basin and Semi Desert subregions)

Autecology

Bigtooth maple is an important component of montane riparian communities in the IAP region (Fitzhugh et al. 1987; Moir 1982), typically located in canyons, in ravines, along mountain streams, and on lower slopes (Alexander et al. 1984; Cronquist et al. 1997) at 4,000 to 7,000 feet elevation. It is more abundant in the bottom than in the top of snowmelt drainages. In Idaho, it grows on hillsides, below springs and seeps, and on secondary floodplains of narrow canyon drainages (Hall and Hansen 1997). It is found on upper slopes in the Wasatch Mountains, although it is more common on mesic, north-facing slopes than on drier south-facing slopes (Dina and Klikoff 1973; Ehleringer et al. 1992). Bigtooth maple is drought tolerant (Sorenson et al. 1984; Sutton and Johnson 1974) and cold hardy, and tolerates summer temperatures above 100 °F (Sorenson et al. 1984).

Disturbance Interactions

Although bigtooth maple can be top-killed by fire, plants can survive by sprouting from the root crown (Bradley et al. 1992; Harper et al. 1992). In a severe burn, this species is likely to be killed (Harper et al. 1992). Smaller stems are more likely to be killed by fire, clearing areas for new tree seedlings and sprouts from surviving larger trees.

Historical and Current Conditions

Little is known about the historical distribution and use of bigtooth maple. It has no economic value except as firewood. The species is used for forage and cover by native ungulates and for cover by livestock (Hall and Hansen 1997). Bigtooth maple is useful for restoration of sites where vegetation has been denuded because it establishes deep roots, even in infertile soils (Barker 1977).

Climate Change Responses

Because bigtooth maple is drought tolerant, its productivity may be relatively stable in a warmer climate, especially because it is located in canyons and other places where water is typically present. As soil moisture declines in a warmer climate, marginal riparian sites for maple may become less favorable for regeneration and survival of young trees. With increased fire frequency, there are likely to be increased vegetative regeneration and decreased production of seedlings in some locations. Low-intensity fires may promote regeneration by thinning stands and stimulating sprouting. Browsing pressure on maple could increase with increased drought, as grasses and forbs desiccate and senesce earlier, or are replaced by less palatable species.

Crack Willow (*Salix fragilis*)

(Southern Greater Yellowstone, Uintas and Wasatch Front, Plateaus subregions)

Autecology

Crack willow is native to Europe and western Asia, where it is found in riparian habitats, usually growing beside rivers and streams and in marshes and wet meadows. It grows in similar habitats in the IAP region. The tree grows rapidly to a height of 30 to 60 feet, occasionally reaching 90 feet. Stem fragments are spread by water, and suckers spread locally. Crack willow outcompetes native species in riparian sites and forms dense, often pure stands along channels (Czarapata 2005), in some cases causing blockages, flooding, and structural changes in waterways (Weedbusters n.d.). This species is susceptible to wind, ice, and snow damage.

Disturbance Interactions

Crack willow responds favorably to periodic flooding. Broken twigs and branches can take root readily, enabling the species to colonize new areas as broken twigs fall into waterways and can be carried some distance downstream. Crack willow is assumed to respond to wildfire like most willow species, by sprouting from the root crown following top kill.

Historical and Current Conditions

Crack willow is now well established in many riparian areas in the IAP region. It was planted for erosion control and water uptake in some locations where rapid plant growth was desired. Although a nonnative species, crack willow is not listed as a noxious weed in any State in the IAP region, and it provides habitat for native bird species.

Climate Change Responses

As soil moisture declines in a warmer climate, marginal riparian sites for crack willow may become less favorable for regeneration and survival of young trees. With increased fire frequency, there are likely to be increased vegetative regeneration and decreased production of seedlings in some locations. Even if this species is inhibited somewhat by a warmer climate, it is unclear whether native species could outcompete it.

Saltcedar (*Tamarix spp.*)

(Uintas and Wasatch Front, Plateaus subregion)

Autecology

Saltcedar (five species) is a nonnative, shrub-like tree with numerous large basal branches and a deep, extensive



Figure 6.6—Saltcedar.

This species has caused widespread damage in riparian areas, although the recently introduced tamarisk beetle is a promising biocontrol (photo: M. Mejia, Bureau of Land Management).

root system that extends to the water table and is capable of extracting water from unsaturated soil layers. Saltcedar is found on lakeshores, in riparian floodplain habitats, on seasonally submerged sites, and in fine fluvial substrates (Diggs et al. 1999; Welsh et al. 1987). It is competitively superior to most native species under dry, saline conditions (Stromberg 1998; Vandersande et al. 2001), and few species can tolerate the understory environment (Brotherson and Winkel 1986) (fig. 6.6). Saltcedar is less sensitive to changes in ground-water availability than native riparian trees with which it is commonly associated. Greater tolerance of water stress can lead to saltcedar dominance on relatively dry riparian sites (Horton et al. 2001; Smith et al. 1998; Stromberg 1998). Seedlings establish as flood waters recede, leaving moist deposits of bare soil along riparian corridors. Its small, wind- and water-dispersed seeds make it ideally suited as a pioneer species on these sites. Saltcedar is also early seral after fire (Busch and Smith 1993; Stuever et al. 1997). It is listed as a noxious weed in Nevada.

Disturbance Interactions

Evidence for specialized adaptation to wildfire in saltcedar remains unclear, despite its efficient postfire recovery—it is usually top-killed by fire but sprouts readily from the root crown (Busch 1995). Flammability increases with accumulation of dead and senescent woody material within the plant. When plants burn under high fuel loads, fire tends to be more severe, increasing the likelihood of killing the root crown of some individuals (Hohlt et al. 2002). Saltcedar plants can have many stems and high rates of stem mortality, resulting in a dense accumulation of dead, dry branches. Fire hazard peaks in tamarisk stands at 10 to 20 years of age (Ohmart and Anderson 1982). With a combination of flood suppression, water stress, and invasion by saltcedar, wildfires have replaced floods as the primary disturbance factor in many southwestern riparian systems.

Historical and Current Conditions

Saltcedar was introduced in North America in the 1800s, spreading rapidly in the southwestern and intermountain western United States in the 1920s, and altering the ecology and hydrology of riparian areas in this broad region. Control of saltcedar has proven to be challenging. Cutting, burning, and herbicides have been used in various combinations to reduce saltcedar populations, but treatments need to be conducted at large spatial scales to make a significant difference (Racher and Mitchell 1999). Biological control releases of the nonnative northern tamarisk beetle in the Southwest, starting in the 1990s, have caused rapid mortality and decline in vigor in many saltcedar populations (Sher and Quigley 2013; Tracy and Robbins 2009). The success of the beetle as a biological control agent is aiding the recovery of previously suppressed native riparian species. However, because the endangered southwestern willow flycatcher (*Empidonax traillii extimus*) now uses saltcedar as habitat, concern exists about beetles causing the loss of flycatcher

habitat, and introduction of beetles has been restricted in some locations.

Climate Change Responses

Saltcedar is more drought tolerant and more efficient at obtaining water than most native species with which it is associated in riparian areas, so it is not expected to be vulnerable to a warmer climate. It also sprouts readily after wildfire, so it will be able to persist in a warmer climate with more fire. Despite efforts to control saltcedar, it would appear to be a permanent fixture in many riparian systems regardless of climate change.

Climate Change Assessment for Forest Vegetation Types

Vegetation types are broad species assemblages used to identify the geographic distribution of vegetation in the USFS Intermountain Region (table 6.1). These types are used to characterize broad landscapes for mapping, planning, and various aspects of vegetation management, but do not have specific spatial definitions. Here we describe the likely response of forest vegetation types to climate change, based on the preceding species descriptions (box 6.3).

Subalpine Pine Forest

Subalpine forests dominated by whitebark pine will be highly vulnerable in a warmer climate, primarily because this species is already subjected to considerable stress from white pine blister rust and mountain pine beetle (Chapter 8). As a result, populations are in decline and reproductive capacity is limited, even when germination conditions are suitable. In areas where wildfire has been excluded for many decades, subsequent fuel loading may create intense future fires that lead to mortality of mature trees. Decline in whitebark pine would have cascading effects on other species that eat its seeds, especially Clark's nutcracker. Subalpine forests in which bristlecone pine is a major component are mostly in dry locations that could become increasingly stressed by low soil moisture, which would reduce growth.

Other subalpine forests are expected to be moderately affected by a warmer climate. Limber pine, subalpine fir, Engelmann spruce, and white fir may all have increased growth in the upper subalpine zone because of a longer, snow-free growing season. These species may migrate to higher elevations where conditions are suitable, although this would be a slow process over many decades. If wildfire increases in the subalpine zone, especially where it has been excluded in the past, crown fires may be prevalent, quickly eliminating mature trees across the landscape. Limber pine is challenged by mountain pine beetle and white pine blister rust (Chapter 8). Quaking aspen found in subalpine forests will be minimally affected by a warmer climate, especially compared to aspen at lower elevations.

Subalpine Spruce-Fir Forest

Spruce-fir forest will be moderately vulnerable to a warmer climate. Subalpine fir, Engelmann spruce, and blue spruce may all have increased growth in the upper subalpine zone because of a longer, snow-free growing season, so overall productivity could increase. These species may migrate to higher elevations where conditions are suitable, although this would be a slow process over decades to centuries. If wildfire increases in the subalpine zone, especially where it has been excluded in the past, crown fires may be prevalent, quickly eliminating mature trees across the landscape.

Often a seral species in spruce-fir forests, lodgepole pine is a host of mountain pine beetle. Bark beetle outbreaks in Engelmann spruce and lodgepole pine are often severe and can accelerate succession in areas of high tree mortality (Chapter 8). Most subalpine species are fire intolerant, but because most lodgepole pine populations have serotinous cones and the potential for rapid, dense regeneration, it is likely to persist in high-elevation landscapes. Quaking aspen in subalpine forests will be minimally affected by a warmer climate, especially compared to aspen at lower elevations. Where Douglas-fir is a seral species, it could increase in distribution and abundance where sufficient soil water is available. In addition, Douglas-fir is more fire tolerant than any of its associates, so it may become more common if fire increases.

Mesic Mixed Conifer Forest

The composition of mesic mixed conifer forest varies greatly across the IAP region, with site conditions and species assemblages determining vulnerability to climate change. In general, late-seral forests may become increasingly susceptible to wildfire, especially where fire has been excluded for many decades and fuel loads are elevated. Shasta red fir has some fire tolerance, but other firs and lodgepole pine are subject to high mortality from intense fires. The firs are intolerant of low soil moisture, so as snowpack declines and summer temperature increases, growth and productivity will probably decrease, except on north aspects.

Douglas-fir, ponderosa pine, and Jeffrey pine have high tolerance to fire and can survive mixed-severity fires. Therefore, if wildfire extent and intensity increase in the future (Chapter 8), these species may become relatively more common, and late-seral species may become less common. Douglas-fir, ponderosa pine, and Jeffrey pine are all tolerant of dry soils, so they are likely to persist across the landscape, but their growth rates will probably decrease. Lodgepole pine and quaking aspen, which are also common in this forest type, both respond to wildfire with rapid, abundant regeneration and are expected to persist across the landscape, possibly with increased stress from insects and pathogens (Chapter 8).

Dry Mixed Conifer Forest

The composition of dry mixed conifer forest varies across the IAP region, with site conditions and species assemblages determining vulnerability to climate change. Located in lower-elevation montane sites, often on steep slopes and shallow soils, this forest type contains some of the most drought-tolerant species in the region. Common seral species include ponderosa pine, which is fire tolerant and regenerates well after fire, and quaking aspen, which sprouts heavily and reproduces after fire. The woodland species curl-leaf mountain mahogany, Gambel oak, and bigtooth maple are drought tolerant, and the latter two sprout vigorously after fire. Therefore, a major component of mixed conifer forest is expected to be able to cope with both drier soils and increased wildfire.

Twoneedle pinyon and singleleaf pinyon are drought tolerant, and although intense fire typically kills them, they can usually regenerate successfully if competition is minimal. Singleleaf pinyon at its lowest elevational extent in northern New Mexico has undergone significant mortality from prolonged drought and pinyon engraver beetles during the past 15 years (Floyd et al. 2009) (Chapter 8), so this species may be susceptible to increasing drought in the future. Limber pine, which is considered late seral in these forests, is drought tolerant, but may be challenged by mountain pine beetle, white pine blister rust, and increasing (usually fatal) wildfire (Chapter 8).

Other species such as Douglas-fir and white fir are not nearly as drought tolerant as other mixed conifer species. Their growth will probably decrease in a warmer climate, and although Douglas-fir has relatively high fire tolerance, white fir tolerates fire only when it has large-diameter and thick bark. In a warmer climate with more fire, it will be increasingly difficult for these conifer species to compete with early-seral and woodland species that are more tolerant of both drought and fire. Therefore, it is likely that early-seral species will become more dominant in the future, and late-seral species will become less common and perhaps confined to north aspects and valley bottoms.

Aspen-Mixed Conifer Forest

The composition of this forest type is diverse, distinguished by the prominent role of quaking aspen as an early-seral species, often in combination with other conifer and woodland species. Response to climate change will depend on associated species, ranging from high to low elevation, and from north to south aspects. Increased wildfire frequency and extent will be the primary factor determining future composition and structure of aspen-mixed conifer forests.

Most of the higher-elevation, late-seral species in this forest type (firs, Engelmann spruce) are readily killed by fire, especially when immature. If wildfire reaches into the subalpine zone, it is likely that mature spruce-fir forests will become less common, or will persist only on northern slopes and in valley bottoms. Therefore, early-seral species,

especially aspen, will attain increasing dominance because of their ability to resist fire or regenerate after it occurs. This will also be true at lower elevations in this forest type, where species such as ponderosa pine can readily survive intense fires, and other species such as aspen and Gambel oak sprout aggressively after fire. Productivity in these systems will probably be lower in a warmer climate with more fire. But the more fire-tolerant species will persist, especially in drier locations, where they can outcompete species that are susceptible to drought and fire.

Persistent Aspen Forest

Quaking aspen can persist for many decades in some forests in the IAP region, where productivity is relatively low and conifer species do not compete well. Succession proceeds slowly in persistent aspen forests, even in the absence of wildfire, especially at the higher elevations of the subalpine zone. The late-seral species in this forest type (firs, spruces) are readily killed by fire, especially when immature. Consequently, if wildfire reaches into the subalpine zone, it is likely that mature spruce-fir forests will become less common, or will persist only on northern slopes and in valley bottoms. Therefore, aspen will maintain dominance because of its ability to sprout aggressively after fire.

This will also be true at lower elevations in this forest type, where species such as ponderosa pine can readily survive intense fires, and other species such as aspen and Gambel oak sprout aggressively after fire. Douglas-fir will probably persist at some locations on the landscape because it has relatively high drought tolerance and fire tolerance. Productivity in these systems will probably be lower in a warmer climate with more fire. But the more fire-tolerant species will persist, especially in drier locations, where they can outcompete species that are susceptible to drought and fire.

Montane Pine Forest

Ponderosa pine is a dominant species in drier montane locations throughout much of the IAP region. Several other conifer species are included in this forest type, but are rarely as abundant as ponderosa pine, except in wetter locations (north aspects, valley bottoms). Ponderosa pine is persistent in these systems because it is tolerant of drought and very tolerant of fire. Consistently drier soils will cause this species to grow slower, but mortality will be rare unless drought lasts for several consecutive years and biotic agents cause additional stress (Chapter 8).

The expected increase in frequency and extent in a warmer climate will favor ponderosa pine over its less fire-tolerant competitors, thus ensuring dominance in most forests. But limber pine and bristlecone pine will probably persist at higher elevations, where fuel loads are typically low. An exception might be in areas where fire exclusion has increased stand density and fuel loads conducive to crown fires, but even then, regeneration of ponderosa pine will probably be sufficient to maintain dominance after fire. If

insects become more prevalent in a warmer climate (Chapter 8), they could increase stress and mortality in pine species, especially during drought periods.

Riparian Forest

Riparian forests are distributed throughout the IAP region, adjacent to lakes, streams, seeps, springs, and high water tables. Vegetation is extremely diverse, including a broad range of conifer and hardwood species. Many of these species occur only in riparian systems, providing habitat for numerous wildlife species. In some lower-elevation, drier locations, nonnative saltcedar and Russian olive have been present, and, in some cases, dominant for many decades, displacing native species and reducing available groundwater.

Riparian systems will be one of the most vulnerable vegetation types in a warmer climate because they depend on reliable water supply. Higher temperatures will accelerate evapotranspiration as soils dry faster and as vegetation takes up water earlier and faster during the growing season. Both surface and subsurface water flows will decrease if snowpack decreases and melts earlier, precluding recharge during dry summers (Chapter 4). At a minimum, this will alter vegetation dominance to species that are more tolerant of seasonal drought, including ponderosa pine and other deep-rooted conifers. Hardwood species that rely on periodic high water levels for regeneration could become less common. Riparian forests associated with small or transient water sources (e.g., springs) will be more susceptible than forests near large water sources (e.g., rivers). Low-elevation riparian forests near small water sources will be more susceptible than high-elevation forests that have long duration of snowpack.

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