

forest ecology

Changing Climates, Changing Forests: A Western North American Perspective

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The Earth's mean surface air temperature has warmed by $\sim 1^\circ \text{C}$ over the last 100 years and is projected to increase at a faster rate in the future, accompanied by changes in precipitation patterns and increases in the occurrence of extreme weather events. In western North America, projected increases in mean annual temperatures range from ~ 1 to 3.5°C by the 2050s, and although projected changes in precipitation patterns are more complex to model, more frequent and severe droughts are expected in many areas. For long-lived tree species, because of their relatively slow rates of migration, climate change will likely result in a mismatch between the climate that trees are currently adapted to and the climate that trees will experience in the future. Individual trees or populations exposed to climate conditions outside their climatic niches may be maladapted, resulting in compromised productivity and increased vulnerability to disturbance, specifically insects and pathogens. In western North America, as elsewhere, several recent assessments have concluded that forests are being affected by climate change and will become increasingly vulnerable to mortality as a result of the direct and indirect effects of climate change. Droughts associated with higher temperatures may accelerate levels of tree mortality, for example, because elevated temperatures increase metabolic rates without increasing photosynthesis rates, thus compromising a tree's ability to create defenses against insects and pathogens. Distributions of the climatic niches of some tree species in western North America are predicted to change by up to 200% during this century based on bioclimate envelope modeling. We discuss the science of climate change, the implications of projected climatic changes to forest ecosystems in western North America, and the essential roles of forest managers, policymakers, and scientists in addressing climate change.

Keywords: bioclimatic envelopes, climate change, disturbance ecology, forest ecology, tree physiology

Forests provide vast ecological, economic, and social goods and services (Nelson et al. 2009) including regulation of climate through carbon storage and complex physical, chemical, and biological processes (Bonan 2008). Past climates have

shaped the world's forests (Bhatti et al. 2006), and minor shifts in climate can have significant impacts (Shugart 2003). Even under conservative estimates, future anthropogenic-induced changes to the earth's climate are likely to include further increases in

temperature with significant changes in precipitation patterns in some regions (Intergovernmental Panel on Climate Change [IPCC] 2007). Across western North America, temperature increases are projected to exceed global mean increases, and more frequent extreme weather events are expected (Kharin et al. 2007, Karl et al. 2009, Rodenhius et al. 2009).

A recent global assessment reported 88 unique episodes of increased levels of tree mortality over the last 30 years (Allen et al. 2010). Examples ranged from modest and short-lived local increases in levels of tree mortality to acute, regional-scale episodes often involving large-scale insect outbreaks (e.g., Bentz et al. 2009). The common causal factors in these and other examples (Martinez-Vilalta et al. 2012) are elevated temperatures and water stress, suggesting that the world's forests are increasingly responding to ongoing warming and drying attributed to climate change (Allen et al. 2010, Martinez-Vilalta et al. 2012). Although these episodes are well-documented, the underlying causes of tree mortality are complex and probably involve numerous predisposing,

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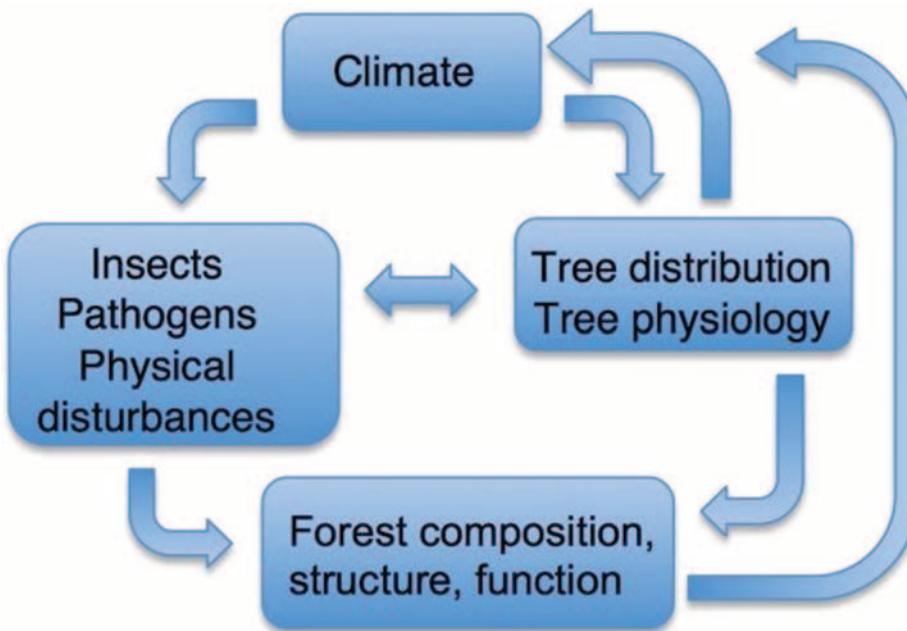


Figure 1. Climate affects the frequency and severity of disturbances (e.g., insects and pathogens) that shape forests, whereas forests influence climate through carbon storage and complex physical, chemical, and biological processes. Many experts conclude that forests are being increasingly affected by anthropogenic-induced changes in the earth's climate that make them more vulnerable to mortality. Forests that were carbon sinks may become carbon sources. Sound policy is needed to address the situation.

inciting, and contributing factors (Manion 1981). These examples raise concern that forests are likely to become increasingly vulnerable to mortality in response to climate change. Here, we discuss the science of climate change, and the potential implications of projected climatic changes to forest ecosystems in western North America. We consider the direct effects of climate on trees as well as indirect effects mediated by insects and pathogens that are in turn influenced directly by climate and indirectly by host tree conditions (Figure 1). The forests of western North America support some of the highest volumes of merchantable trees and stored carbon in the world (Canadian Council of Forest Ministers 2012, USDA Forest Service 2012), making this region of critical economic and ecological importance.

Climate Change

The Earth's mean surface air temperature has warmed by $\sim 1^{\circ}\text{C}$ over the last 100 years (Jones et al. 2012). Most of this warming, particularly in the last 60 years, is believed to result from increases in atmospheric concentrations of greenhouse gases released by human activity (IPCC 2007, Solomon et al. 2007). Changes in precipitation patterns and in the occurrence of ex-

treme temperature and precipitation events have also been documented (IPCC 2007). Temperature changes in western North America are consistent with worldwide trends (Karl et al. 2009, Rodenius et al. 2009). Over the last 60 years, mean annual

surface temperature has increased by $\sim 2^{\circ}\text{C}$ in the northern part of western Canada and by $\sim 1^{\circ}\text{C}$ in the western United States (Karl et al. 2009, Rodenius et al. 2009). Temperature increases have been greater in winter than in summer, and there is a tendency for the increase to be manifested mainly by changes in minimum (nighttime low) temperature (Kukla and Karl 1993). Changes in precipitation patterns are more variable than those observed for temperature with some areas showing small increases and others showing decreases in precipitation during the last 60 years (Karl et al. 2009, Rodenius et al. 2009). In some western forests, warming temperatures have reduced the amount of precipitation that falls as snow, reducing snowpacks and increasing the length of the wildfire season (Westerling et al. 2006). For example, Pederson et al. (2011) reported that late 20th century snowpack reductions are almost unprecedented in magnitude across the northern Rocky Mountains, United States. Both snowpack declines and their synchrony across the region result from springtime warming and shifts in precipitation patterns and form, foreshadowing concerns regarding water supplies because climate change alters not only the amount and type of precipitation, but rates of evapotranspiration, storage, and discharge (Milly et al. 2008, Elsner et al. 2010, Pike et al. 2010).

Projections of future climates are based

Management and Policy Implications

The earth's climate is changing and will continue to do so at a faster rate than in recent history due to anthropogenic-induced increases in concentrations of greenhouse gases, primarily carbon dioxide (CO_2). Climate change poses a significant challenge for society because it is unlikely that efforts to control greenhouse gas emissions will eliminate the risk of anthropogenic-induced climate change. A sound forest carbon policy informed by the best available science represents an important part of the solution because forests have the potential to assimilate, accumulate, and sequester large amounts of carbon from the atmosphere, thus reducing one of the primary drivers of climate change. Alternatively, large amounts of CO_2 are released when forests are killed, burned, defoliated, or deforested, and carbon may be lost when forests are converted to other systems (e.g., shrublands) that have smaller carbon pools. Individual trees or populations exposed to climate conditions outside their climatic niches may be maladapted, resulting in compromised productivity and increased vulnerability to disturbance. Tree distributions and plant associations, as we know them today, will change. Although forest managers, policymakers, and scientists have been working to develop and implement strategies that increase the resistance and resilience of forests to climate change in western North America, much of this work has not been well-coordinated. By collaborating with scientists, managers can implement adaptive strategies based on the best available science, which in turn informs forest policy. We encourage flexible management approaches that promote learning and sharing and recognize the need for a more collaborative approach, in which managers, policymakers, and scientists of broad expertise from various disciplines and across political borders work to address climate change.

2050s – Change in mean annual precipitation 2050s – Change in mean annual temperature

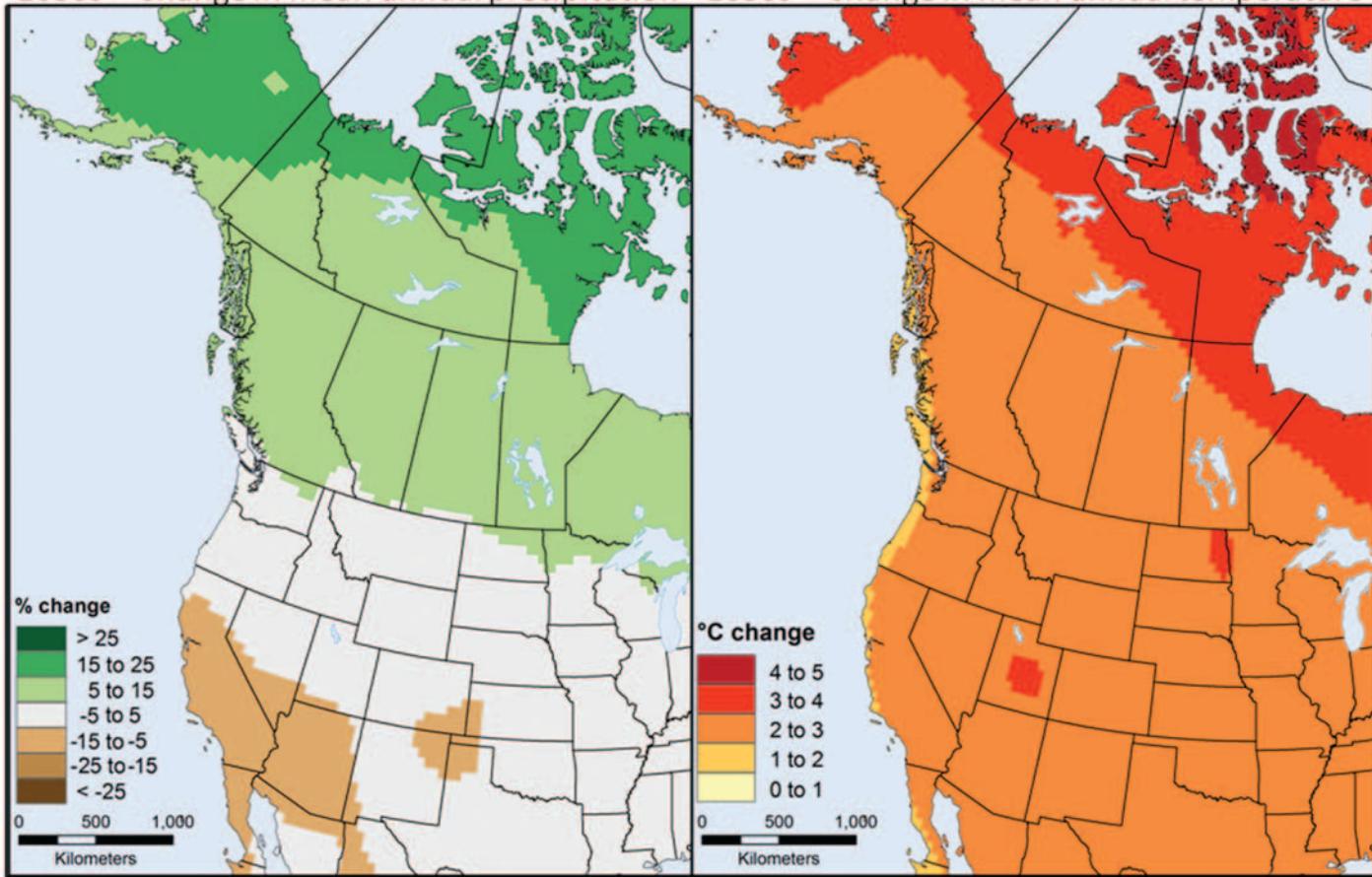


Figure 2. Median change in mean annual precipitation (left panel) and mean annual air temperature (right panel) from 1961 to 1990 normals based on projection by 13 global climate models and the A2, A1B, and B1 emission scenarios. The range around these median values is discussed in the text. (Produced by the Pacific Climate Impacts Consortium 2011.)

on assumptions about future anthropogenic greenhouse gas emissions and simulations using sophisticated global climate models (GCMs; Solomon et al. 2007). Differences in the formulation and resolution of these models and the different emission scenarios¹ result in a wide range of projections. However, all forecast a warmer climate than what we experience today in western North America. For example, projected increases in mean annual and seasonal temperatures for British Columbia, Canada, range from ~ 1 to 4°C by the 2050s (Figures 2 and 3) and increases to ~ 2 to 7°C by the 2080s compared with the 1961–1990 climatic normal period² (Rodenhuis et al. 2009). The period 1961–1990 is commonly used for comparisons regarding anthropogenic-induced changes to the earth's climate and also represents a period of limited departure in temperature compared with the 1904–1980 mean for western North America (Wahl and Smerdon 2012). For the western United States, increases range from ~ 1.5 to 3.5°C

by the 2050s (Figures 2 and 3) and ~ 2 to 6°C by the 2080s (Karl et al. 2009, Mote and Salathé 2010). Depending on the scenario and location, winter precipitation is projected to increase by 10–30% in western Canada and the northern part of the western United States by the 2050s and decrease by up to 20% in the southern part of the western United States (Figure 4). In summer, precipitation is projected to increase in the northern part of western Canada by 5–20% and to decrease in the southern part of western Canada and the western United States by ~ 10 –30% (Figure 4). Warming temperatures will exacerbate recent decreases in the winter snowpack, produce earlier snowmelt and alter streamflow regimes (Elsner et al. 2010, Pike et al. 2010), and increase the risk of weather-related forest disturbance (Karl et al. 2009, Haughian et al. 2012).

Changes in the frequency of extreme weather conditions will accompany the mean changes discussed above. For example, an increase of 2°C in mean temperature (as

may be seen in parts of western North America by the 2050s) may result in what is currently a 1 in 20-year event becoming a 1 in 5-year event (Kharin et al. 2007). Extreme cold events will become less frequent or, depending on location, no longer occur. Extreme precipitation events are projected to exhibit similar changes in frequency with 1 in 20-year events becoming 1 in 10-year events or perhaps more frequent (Kharin et al. 2007). Dry periods during the summer in southern Canada and the western United States will probably become more intense (Karl et al. 2009, Mote and Salathé 2010, Haughian et al. 2012).

Climate change projections in impact assessments and vulnerability analyses need to recognize the large range of possible future climates (IPCC-Task Group on Data and Scenario Support for Impact and Climate Assessment [TGICA] 2007, Murdock and Spittlehouse 2011). Most projections are at a relatively coarse spatial scale (e.g., $50,000 \text{ km}^2$), but managers usually desired

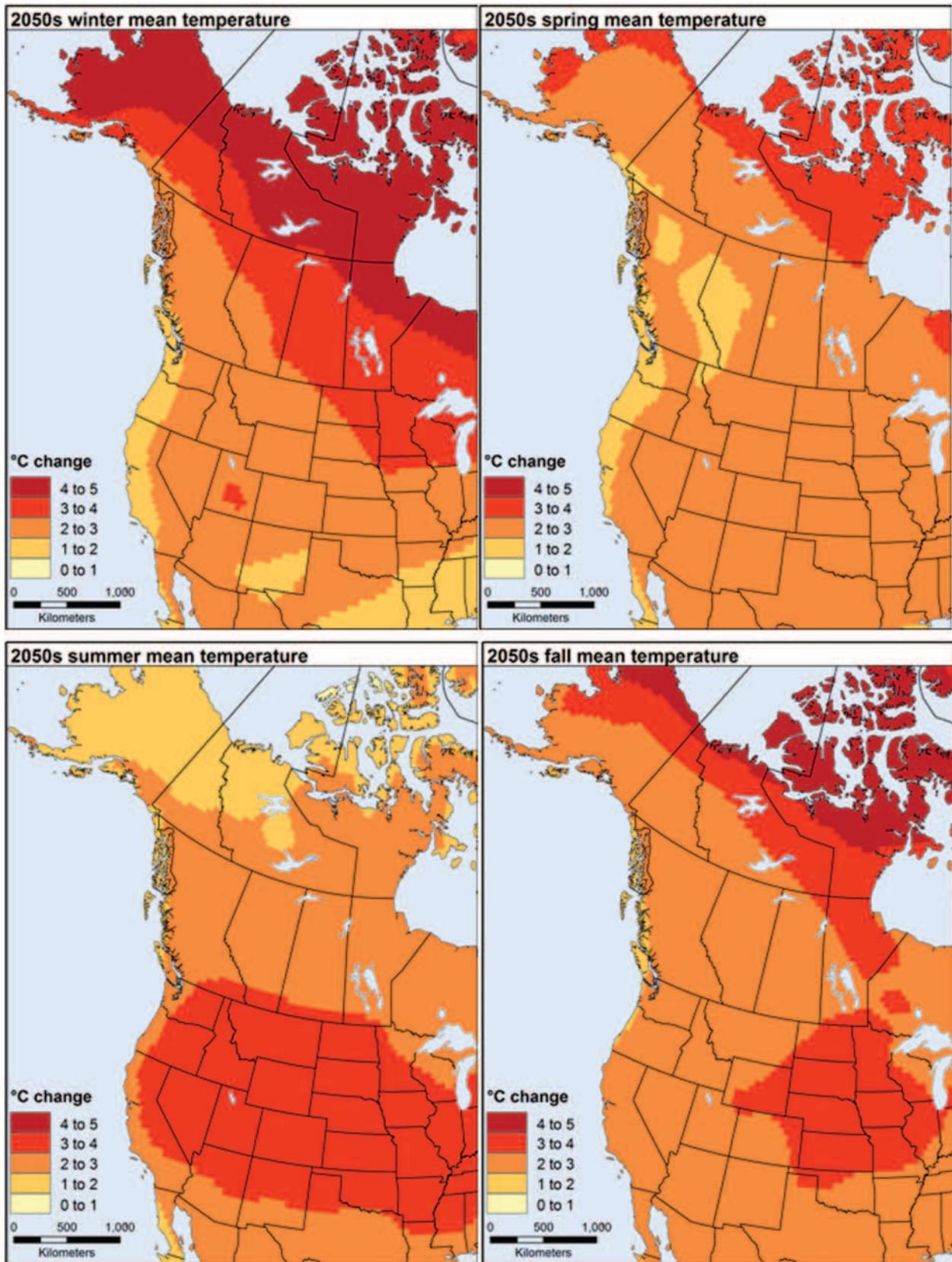


Figure 3. Median change in mean air temperature by season from 1961 to 1990 normals based on projection by 13 global climate models and the A2, A1B, and B1 emission scenarios. The range around these median values is discussed in the text. (Produced by the Pacific Climate Impacts Consortium 2011.)

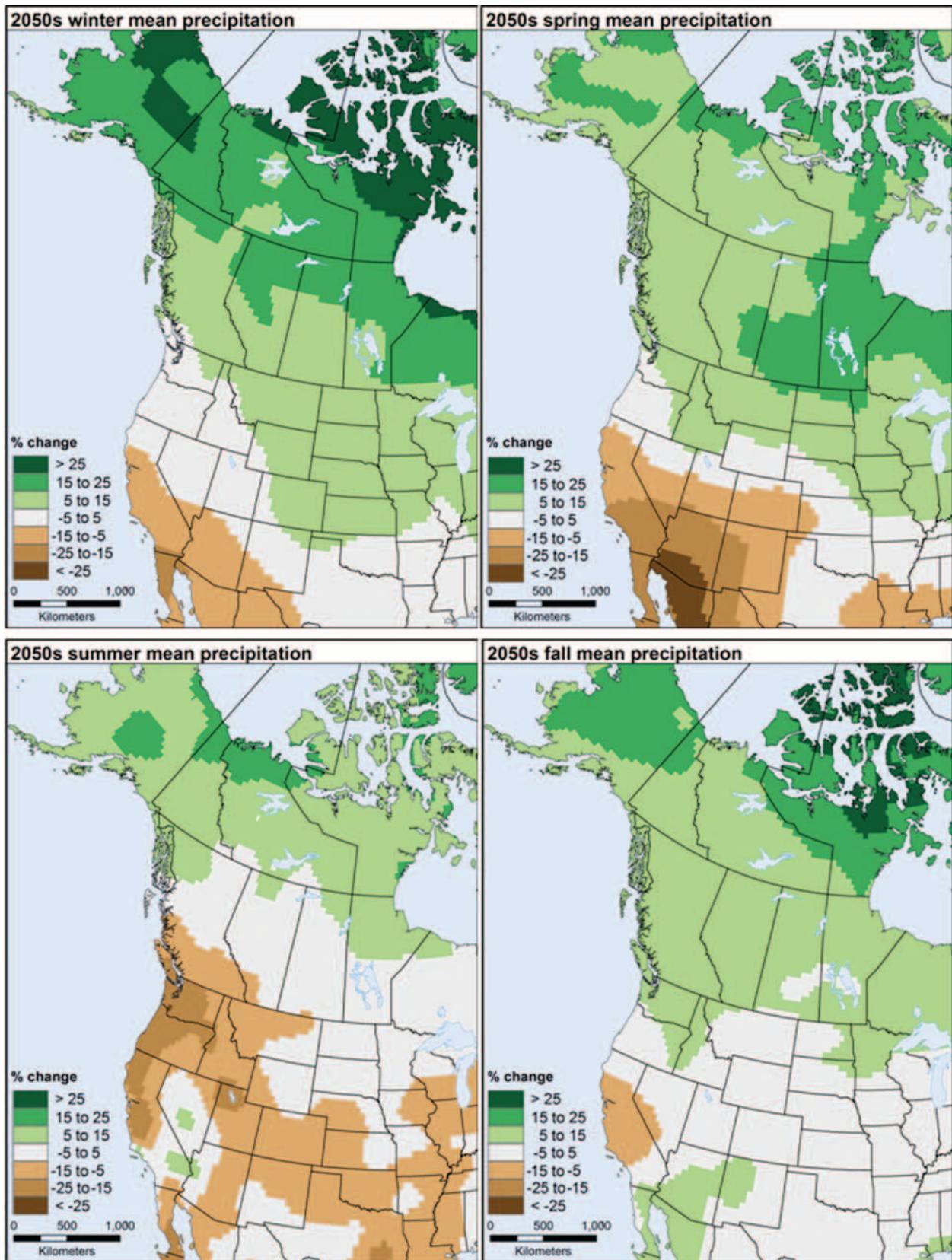


Figure 4. Median change in mean precipitation by season from 1961 to 1990 normals based on projection by 13 global climate models and the A2, A1B, and B1 emission scenarios. The range around these median values is discussed in the text. (Produced by the Pacific Climate Impacts Consortium 2011.)

information at a more local level. Various methods to downscale data (increase resolution) are available but introduce uncertainty into the downscaled climate projections (Wilby et al. 2004, Bürger et al. 2012). The range of projected climates can be addressed by basing analyses on a suite of projections from a range of GCM/emissions combinations (IPCC-TGICA 2007, Murdock and Spittlehouse 2011). Furthermore, projections of changes in means and extremes are usually based on a 30-year window of data. In using these data, we must recognize the large interannual and interdecadal variability superimposed on the data.

Climate change projections can be obtained from a variety of sources. These range from the extremely large gridded data sets to software and websites that provide subsets of these data tailored to users with limited technical skills (Girvetz et al. 2009, McKenney et al. 2011, Wang et al. 2012b). There are also publications illustrating future changes (Joyce et al. 2011, Price et al. 2011) and recommendations on selecting and using climate change data (Murdock and Spittlehouse 2011, Levinson and Fettig 2013). The data referenced in these publications are all based on simulations done for the Fourth Assessment Report of the IPCC (IPCC 2007). Projections of change produced for IPCC's Fifth Assessment (Taylor et al. 2012) are based on a wider range of climate forcing (i.e., agents or factors that cause climate change)³ and were produced using GCMs with higher resolution and physical complexity. However, the projected changes in climate show the same trends as those of IPCC's Fourth Assessment. Consequently, although variability and uncertainty in climate projections must be recognized, there is enough consensus in the major trends that we should anticipate these changes and proceed to address their ecological consequences.

Climate Change Impacts on Forests

Climate is one of the primary factors regulating the geographic distributions of forest trees (Woodward 1987, McKenney and Pedlar 2003). Forest tree species are adapted to a range of climatic conditions, which is often referred to as their "climatic niche." Because the climatic niche of a tree species is unlikely to change (Peterson et al. 1999), at least not in the short term (Ackerly 2003, Wiens and Graham 2005), changes in

climate will cause shifts in the geographical distribution of the climatic niche. In fact, shifts have already been documented for a large number of plant and animal species (Parmesan 2006). Based on meta-analysis, Parmesan and Yohe (2003) reported an average boundary shift of 6.1 km per decade northward (or 6.1 m in elevation upward) associated with climate change for 99 species of birds, herbs, and insects. For long-lived tree species, because of their slow rates of migration, climate change will probably result in a mismatch between the climate to which trees are currently adapted and the climate that trees will experience in the future (Aitken et al. 2008). Individuals or populations exposed to climate conditions outside their climatic niches may be maladapted, resulting in compromised productivity and increased vulnerability to disturbances, such as insects and pathogens (Aitken et al. 2008, Bentz et al. 2010, Sturrock et al. 2011). However, there will be exceptions as many tree species have been grown successfully far outside their native geographic ranges (i.e., realized climatic niches). For example, Monterey pine (*Pinus radiata*), native to certain areas of the coast of California, United States, has become the staple softwood in Chile, New Zealand, Australia, and the Cape Province of South Africa (Clapp 1995). Efforts to model the climatic niche of forest tree species and associate forest ecosystems and to project their shifts under future climates have proliferated in recent years.

Projections of changes in tree species distributions are achieved with niche-based bioclimate envelope models⁴ or process-based mechanistic models. Because of limited knowledge on the biophysiological processes of tree species and the computational complexity, bioclimate envelope models (also referred to as "ecological niche models") have been used more widely than process-based mechanistic models (Rehfeldt et al. 2006, McKenney et al. 2007, Wang et al. 2012a). These models are built on the basis of the relationships between observed presence of a species (or a forest ecosystem) and values of climate variables at those sites. Because they rely on actual distribution of the target species, they model the realized niche (i.e., resulting from abiotic and biotic constraints, such as interspecific competition) as opposed to the fundamental niche (i.e., solely based on the species' abiotic requirements). However, it is important to emphasize that these models predict the shift in

distribution of the climatic niche of a species (or a forest ecosystem) rather than the shift in distribution of the species per se. The fate of any tree species will depend on genetic variation, phenotypic variation, fecundity and dispersal mechanisms, and their resilience to a multitude of disturbances (Levinson and Fettig 2013).

Substantial shifts in geographical distributions of bioclimatic envelopes have been projected for some tree species and forest ecosystems. Based on consensus projections integrating individual projections derived from 20 climate change scenarios in British Columbia, Wang et al. (2012a) forecasted increases in the geographical distributions of bioclimatic envelopes for interior cedar-hemlock (*Thuja-Tsuga*), interior Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) ecosystem zones of 80–200% by the 2050s. Meanwhile the bioclimatic envelope for interior spruce (*Picea*) is projected to contract substantially. Through modeling of the biomes in North America, Rehfeldt et al. (2012) reported a considerable contraction of climates for Canadian taiga biome and northward expansion of climates suitable for Great Plains grassland and temperate deciduous forests biomes into Canada. For individual tree species, McKenney et al. (2007) projected an average decrease in the size of species climate envelopes by 12–58%, depending on dispersal scenarios, by the end of this century. Rehfeldt et al. (2006) suggested that ~48% of the western United States landscape is likely to experience climate profiles with no contemporary analog for the current coniferous vegetation by the end of this century. Projections showed that the distributions of grassland, chaparral, and montane forest would increase largely at the expense of subalpine forest, tundra, and Great Basin woodland (Rehfeldt et al. 2006). Shifts are expected to be most rapid along ecotones, particularly in semiarid landscapes (Allen and Breshears 1998).

Although tree species as a whole can be characterized by their bioclimatic envelopes, populations within a tree species vary in their response to climate (Matyas 1994, Rehfeldt et al. 1999, Wang et al. 2006, 2010), and local adaptation has been demonstrated along climatic gradients (Epperson 2003, Howe et al. 2003). For example, peripheral populations of lodgepole pine (*Pinus contorta*) from cold environments at the northern limit of its distribution grow much slower under favorable temperatures for this

species than central populations (Wang et al. 2006). This finding suggests that localized northern populations would be unable to take full advantage of warming temperatures attributed to climate change, whereas some populations in the South are likely to be growing outside their bioclimatic envelopes (Rehfeldt et al. 1999, Wang et al. 2006). Therefore, climate change will also cause climate mismatches at the population level within a tree species.

The magnitude of projected shifts in bioclimatic envelopes for tree species, populations, and ecosystems suggests that climate mismatch will be a serious matter. Forest scientists, managers, and policymakers need to develop new management strategies to effectively address these concerns. Assisted migration (also referred to as “facilitated migration” or “assisted colonization”)⁵ has been proposed and discussed at the species level (Andalo et al. 2005, Rehfeldt et al. 2006, Iverson et al. 2011) and population level (Rehfeldt et al. 1999, Wang et al. 2006). In western North America, long-term field experiments have been established to explore the potential of assisted migration for commercial tree species (O’Neill et al. 2011) and for whitebark pine (*Pinus albicaulis*; McLane and Aitken 2012). Different approaches have been explored (Rehfeldt and Jaquish 2010, Ukrainetz et al. 2011). The challenge lies with the uncertainty in the timing and magnitude of climatic changes, coupled with the longevity of trees, ranging from decades to centuries. To that end, assisted migration is a contentious issue. Proponents advocate that the undesirable consequences of projected changes (e.g., localized extinctions of some tree species) warrant such intervention applied at broad spatial scales. Others are concerned about the unintended consequences. McLachlan et al. (2007) argued that assisted migration is necessary despite the potential risks, which can be minimized through proper monitoring and adaptive management and that further delays in policy formulation and implementation are unacceptable. Perez et al. (2012) provided a hierarchical decision-making system that considers 10 criteria useful for implementing successful projects involving assisted migration.

Climate Change Impacts on Tree Physiology

For locally adapted tree populations, climate change tests the adaptive limits of

tree physiology, productivity, and defensive mechanisms (Bokhorst et al. 2009, van Mantgem et al. 2009, Allen et al. 2010, Carnicer et al. 2011, Peng et al. 2011). Increases in atmospheric CO₂ may stimulate plant growth through enhanced photosynthesis and/or indirectly through increased water use efficiency, but tree growth has not increased as expected (Peñuelas et al. 2011), suggesting that other factors compete with the potential growth benefits of elevated CO₂. Plant defenses to insect attacks and pathogen infections are energy intensive (e.g., Bolton 2009), and therefore compromised physiological function and reduced productivity often lead to higher vulnerability to such disturbances (e.g., Larsson 1989, Larsson and Björkman 1993). However, despite decades of research on plant responses to climate, the physiological mechanisms by which plants succumb under climatic stress are still under debate (Schaberg et al. 2008, Adams et al. 2009, McDowell and Sevanto 2010, Sala et al. 2010, Anderegg et al. 2012).

During the growing season, most of western North America is expected to be warmer and drier than in the recent past (Figures 3 and 4). The general response of plants to drought is to close the stomata (i.e., pores in the leaf epidermis that regulate vapor exchange) to avoid excessive water loss and consequent wilting. This, however, inherently leads to reduced productivity because stomatal closure also prohibits CO₂ uptake and therefore photosynthesis (Figure 5). The balance between avoidance of excessive water loss and reduction in productivity has led to current hypotheses of tree mortality mechanisms. Plants that readily close their stomata during drought develop a negative carbon balance (i.e., respiration exceeds photosynthesis) and may die of carbon starvation under prolonged drought, whereas plants that keep their stomata open risk mortality via hydraulic failure in the form of uncontrollable runaway cavitation and consequent loss of conductivity of the xylem tissue (McDowell et al. 2008). There is evidence that xylem structure and susceptibility to cavitation are linked to the timing of stomatal closure during drought (e.g., Tyree and Sperry 1988, Jones and Sutherland 1991, Schultz 2003), but what determines the dominant mortality mechanism in individual cases and how these are linked with insect attacks and pathogen infections is still relatively unknown (McDowell 2011, S. Sevanto, unpublished data). Hydraulic

failure and carbon starvation may also be coupled via the need of carbohydrates for controlling loss of hydraulic conductivity (McDowell 2011, Secchi et al. 2011, Secchi and Zwieniecki 2011). Drought and stomatal closure also slow and ultimately hamper water and carbohydrate transport in forest trees (S. Sevanto, unpublished data). This could accelerate both carbon starvation and hydraulic failure and reduce availability of plant defenses as redistribution of resources ceases (McDowell and Sevanto 2010, Sala et al. 2010). Drought also reduces growth (e.g., Orwig and Abrams 1997, Klos et al. 2009) and respiration rate (S. Sevanto, unpublished data), both of which may initially decrease more rapidly than photosynthesis, leading to a temporary increase in carbohydrate reserves at the onset of drought (Sala et al. 2010, McDowell 2011).

Increasing temperature generally increases plant maintenance respiration rate (Ryan 1991) as well as evaporative demand, the latter speeding up stomatal closure (e.g., Farquhar 1978, Franks and Farquhar 1999). Indeed, there is evidence that droughts occurring during warm periods are more damaging to plants than those during cool periods (Breshears et al. 2005, Adams et al. 2009), but the combined effect of increased temperature and drought on carbohydrate consumption and its link with plant susceptibility to specific insects or pathogens remains to be fully determined. Reduced carbohydrate reserves or hydraulic conductivity will also affect recovery of the surviving trees and could lead to fatal insect attacks or pathogen infections years after the drought has ceased because the structural defense mechanisms (e.g., size of resin ducts and thickness of cell walls) might have been compromised during drought and remain in this condition (Ogle et al. 2000, Gaylord et al. 2012).

With the projected increase in winter and spring temperatures (Figure 3), more frequent warm spells followed by below-freezing temperatures and warm springs may have different consequences on plant survival. An overall increase in winter temperature tends to increase respiration rates (Vesala et al. 2010) and could lead to reduction of carbohydrate reserves in both dormant deciduous trees and conifers in the far north where photosynthetic capacity and solar radiation is low during winter (Sevanto et al. 2006, Vesala et al. 2010). Frequent freeze-thaw cycles also cause cavitation and loss of xylem conductivity (e.g., Martinez-Vilalta

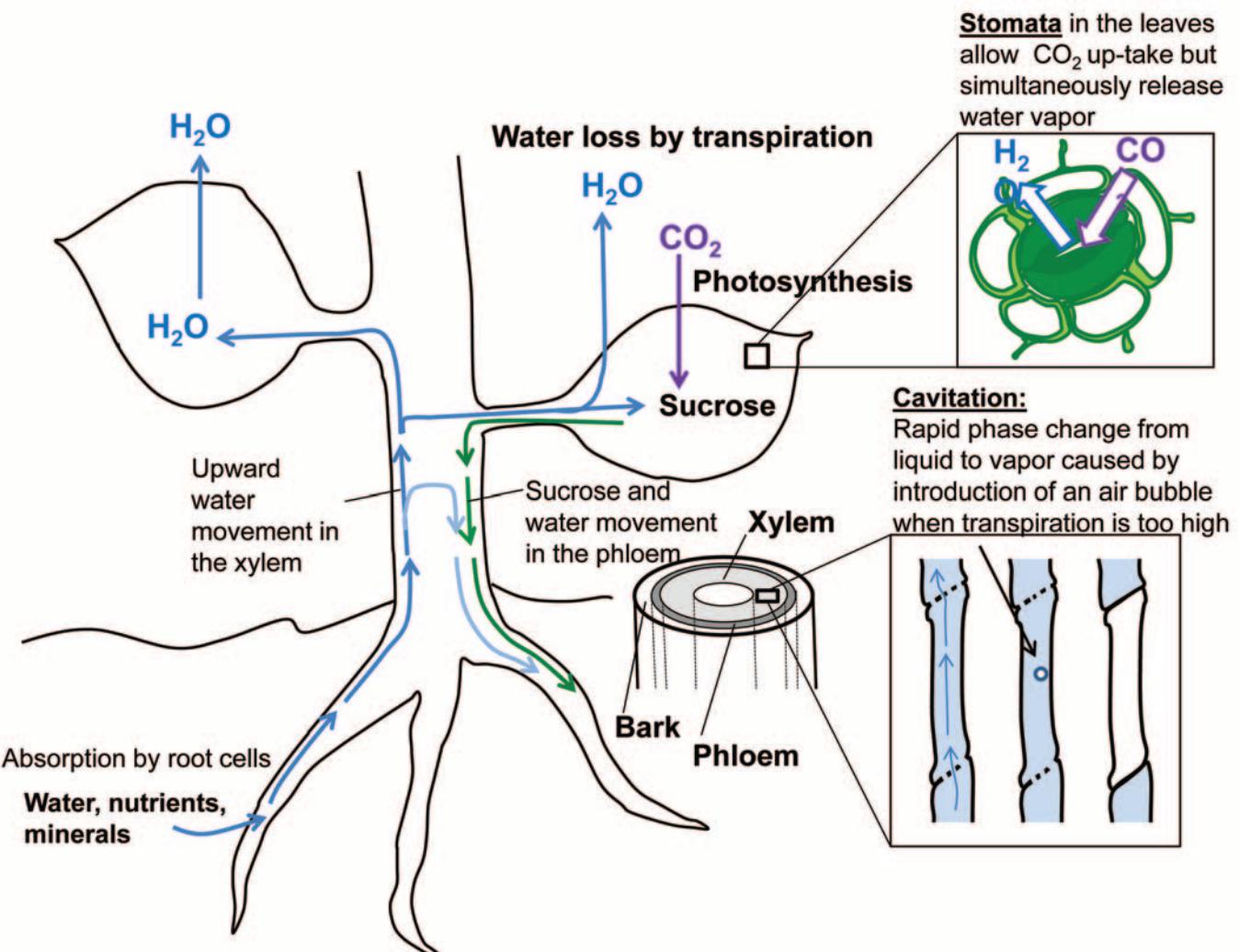


Figure 5. Illustration of plant function. While taking CO_2 from the air for photosynthesis, trees lose water through the stomata. If water lost to transpiration is not replaced by soil water uptake, the water flow in the xylem can be interrupted by gas bubble formation (cavitation). Unrepaired, this can lead to hydraulic failure of the xylem and plant mortality. Stomatal closure during drought constrains transpiration but may promote carbon starvation as stomatal closure also prevents CO_2 from entering the leaf. Repairing gas-filled conduits requires sugars, but movement of sugars requires water. How climate-induced suppression of this interaction between water and carbon transport and use in plants affects plant defenses to insects and pathogens is still relatively unknown.

and Pockman 2002, Pittermann and Sperry 2006, Mayr et al. 2007) and could deplete carbohydrate reserves during warm spells because xylem conductivity has to be repaired to avoid spring drought mortality (Hacke and Sauter 1996). In many trees, roots are more vulnerable to cavitation than the bole (Kavanagh et al. 1999), and, therefore, any reductions in snow cover could lead to spring drought responses even in springs of normal precipitation (Hacke and Sauter 1996, Pockman and Sperry 1997). Melting of snow and subsequent freezing and thawing of soil also affect soil nutrient content, and leaching could leave plants nutrient deprived during the growing season (Larsen et al. 2002, Joseph and Henry 2008). Similar to midwinter warm spells, warming in the

early spring could affect the cold hardening⁶ of trees, and direct frost damage could result in loss of tissue and reduced resources, leading to a higher susceptibility to insects and pathogens. The results of these events may be seen the following summer, or they could lead to cumulative reduction of tree vigor and productivity and ultimately to large-scale tree mortality over several years (Saxe et al. 2001, Gu et al. 2008).

The sensitivity of different trees to climatic stress depends on how susceptible the tree is to the stress and whether it will be able to recover once conditions improve. Currently, few data that would assist us in determining a threshold of recovery versus no recovery exist, but some predictive arguments can be made based on our current under-

standing of tree physiology and wood anatomy (Engelbrecht et al. 2007, Brodrribb and Cochard 2009, Coops and Waring 2011). In general, trees that have narrow xylem conduits (gymnosperms) can maintain physiological function and recover from more severe droughts than trees exhibiting wide xylem conduits (most angiosperms; Brodrribb and Cochard 2009). Similarly, trees with narrow conduits are less vulnerable to freeze-thaw cycles than those with wide conduits (Sperry and Sullivan 1992). Early spring frost or warm autumns could affect angiosperms more than gymnosperms, because of their wide xylem conduits and temperature-sensitive leaf phenology (Polgar and Primack 2011). The effects of warm autumns could be expected to be

especially damaging to ring-porous species (e.g., oaks [*Quercus*] and ash [*Fraxinus*]) because they rely on developing a new layer of conduits before budbreak to supply the developing leaves with nutrients and water (Hinckley and Lassoie 1981). If carbohydrate reserves have been depleted during a warm autumn, as a result of increased respiration, resources for building new cells before leaf development may be reduced. Diffuse porous trees (e.g., birches [*Betula*], maples [*Acer*], aspens [*Populus*], and alder [*Alnus*]), may need fewer carbohydrates for recovery after winter because some of their large conduits may be protected from freezing/thawing by their location far inside the tree bole (Sevanto et al. 2012).

In addition to differences in xylem structure and leaf phenology, trees can be divided into roughly two groups (isohydric and anisohydric) based on the stomatal response to drought (Tardieu and Simonneau 1998). Isohydric trees tend to close their stomata earlier than anisohydric species during drought. Interestingly, gymnosperms and angiosperms, as well as evergreens and deciduous trees, exist in each group, precluding broad generalizations among them. It has been hypothesized that isohydric trees are less vulnerable to severe droughts of shorter duration, whereas anisohydric trees would better survive prolonged droughts (McDowell et al. 2008). This hypothesis seems to be true and is supported by recent data from large-scale tree mortality events in the southwestern United States (Allen et al. 2010). Isohydric and anisohydric species coexist in many forests, and therefore drought could alter not only structure but also species composition in dramatic ways. However, rates of tree mortality depend not only on tree physiological differences but also on tree age (Chazdon et al. 2005), stand density (Savage 1997, Allen and Breshears 1998), soil depth and composition (Peterman et al. 2012), and aspect (Plaut et al. 2012), among other factors. Therefore, making predictions about where and when forest mortality is likely to occur and which tree species are going to suffer the most is prone to failure without a comprehensive understanding of associated interactions, including the influences of climate change on common disturbances. Predictions of susceptibility are further complicated by the potential of resprouting, which is more common in angiosperms than in gymnosperms (Del-Tredici 2001).

Climate Change Impacts on Forest Insects and Pathogens

Insects and pathogens will be the primary biotic catalysts for changes in the structure and composition of forests in western North America (Levinson and Fettig 2013). Outbreaks of forest diseases caused by native and introduced pathogens are generally thought to become more frequent and severe as a result of climate change (Sturrock et al. 2011). However, diseases caused by pathogens directly affected by climate (e.g., needle blights) are predicted to have a reduced impact under warmer and drier conditions. These groups of pathogens may cause disease in healthy hosts if the environmental requirements of the pathogen, many of which require moist conditions, are met (Sturrock et al. 2011). For example, *Cronartium ribicola*, the fungus that was introduced from Asia in the early 1900s, which causes white pine blister rust, requires high humidity and temperatures $<20^{\circ}\text{ C}$ for germination and needle infection to occur (Van Arsdel et al. 1956). Infection by *C. ribicola* has had a significant impact on white pines throughout much of western North America, but climate is thought to currently limit its distribution in the southwestern United States, and less rust infection is expected as a result of climate change (Kinloch 2003, Sturrock et al. 2011). Thus, the timing of a pathogen's life cycle with respect to projected seasonal changes in temperature and precipitation (Figures 3 and 4) will be critical.

Insects are major components of forest ecosystems, representing most of the biological diversity and affecting virtually all processes (Mattson 1977). Because temperature is a major driver of their physiological processes, all insect species will be affected in some way by climate change. As an example, we consider the mountain pine beetle (*Dendroctonus ponderosae*), a native bark beetle species for which climate effects have been studied most extensively (Carroll et al. 2004, Aukema et al. 2008, Safranyik et al. 2010), and an important disturbance in western coniferous forests. Recent outbreaks of the mountain pine beetle have been severe, long-lasting, and well-documented (Bentz et al. 2009). Since 2001, >25 million ha of lodgepole pine forest have been affected (Figure 6). The mountain pine beetle ranges throughout British Columbia and Alberta, Canada, in most of the western United States, and into northern Mexico and colo-

nizes several pine species, most notably, lodgepole pine, ponderosa pine, sugar pine (*Pinus lambertiana*), limber pine (*Pinus flexilis*), western white pine (*Pinus monticola*), and whitebark pine.

In addition to the effects of temperature and precipitation on host distributions and tree physiology (as described above), temperature directly influences several important mountain pine beetle life history traits, including developmental timing (Bentz et al. 1991) and mortality (Safranyik and Linton 1998, Bentz and Mullins 1999), which collectively influence the population dynamics of this species (Bentz et al. 2010, Safranyik et al. 2010). The range of mountain pine beetle is limited by climate rather than host tree distribution (Carroll et al. 2004), and today successfully breeding populations can be found in locations of western North America with no published record of outbreak populations since monitoring began ~ 100 years ago. For example, a new Nebraska state collection record recently documented its presence in several western counties in that state (Costello and Schaupp 2011), and mountain pine beetle populations have been found in Alberta in areas that are not considered part of the historical distribution of this insect (Cudmore et al. 2010, de la Giroday et al. 2011). Several temperature-dependent life history traits play a role in mountain pine beetle population success and, when combined with attributes of host tree condition and landscape configuration (Fettig et al. 2007, Hicke and Jenkins 2008), contribute to the positive feedback necessary for range expansion and epidemic populations to occur (Raffa et al. 2008, Bentz et al. 2010, Safranyik et al. 2010). In short, outbreaks occur when favorable climatic and forest conditions coincide in time and space.

Mountain pine beetle uses cues of declining temperature to cold harden, and larvae can survive extreme winter cold, although significant mortality occurs after cold snaps when the acclimation process is disrupted (Bentz and Mullins 1999). Parent adults also cold harden to survive winter (Lester and Irwin 2012), thereby potentially contributing to sister broods, an important life history trait that can influence population growth (DeLeon et al. 1934). In areas where cold has historically limited mountain pine beetle population growth, warm temperatures associated with climate change have had a positive influence on population success (Sambaraju et al. 2012). Even if cold



Figure 6. Bark beetles are important disturbance agents in forests of western North America, and climate effects have been studied most extensively in the mountain pine beetle (*Dendroctonus ponderosae*). Recent outbreaks have been severe (red or faded trees), long-lasting, and well-documented. In many areas, these outbreaks have been linked to climate change and an abundance of susceptible hosts. There is evidence that mountain pine beetle outbreaks and associated levels of tree mortality affect the subsequent risk and severity of wildfire, another major disturbance in western forests.

temperature survival has not been a limiting factor, warm temperatures can increase the synchrony of emergence and consequent population success by enabling mass attack of trees (Bentz et al. 1991, Powell and Bentz 2009).

With use of process-based models, the phenology of mountain pine beetle (Bentz et al. 1991, Logan and Bentz 1999, Régnière et al. 2012), acclimation to decreasing fall temperature (Régnière and Bentz 2007), and beetle-host interactions (Safranyik et al. 1975) have been described. Based on climate change projections of temperature, simulation results from these models suggest that climatic suitability for mountain pine beetle expansion across the boreal forest of North America in future decades will be highest in central British Columbia and western Alberta and moderate in central Alberta east to Saskatchewan, Canada and decrease eastward (Bentz et al. 2010, Safranyik et al. 2010). Therefore, the likelihood of mountain pine beetle range expansion into the eastern United States via the boreal forests of central Canada appears low (Bentz et al.

2010) despite recent concerns. High-elevation forests will become more suitable for population success (Sambaraju et al. 2012). Similar to tree species, local adaptation of mountain pine beetle along climate gradients in the western United States has resulted in substantial genetic differences and phenotypic plasticity in developmental rates and thresholds (Bentz et al. 2011). Phenotypic plasticity has allowed the species to be successful in variable and new thermal habitats, but this success may be limited without further adaptation. Mismatches within a population could occur as thermal conditions move beyond the current limits of plasticity. However, with much shorter lifecycles than forest trees, insects and pathogens have a greater potential for adaptation to changing climatic conditions. Community associates and trophic interactions, including avian predators and insect parasitoids and predators, will undoubtedly be influenced by climate change as well, although little is known about these relationships (Bentz et al. 2010).

Conclusion

Our climate is changing and will continue to do so at a faster rate than in recent history. There is an aspirational goal that global emission reduction should be large enough to maintain a global temperature change of $\leq 2^{\circ}$ C by 2100. However, recent computer simulations suggested that a 60% reduction in greenhouse gas emissions is required to achieve such a goal (Weaver et al. 2007), and that the earth will continue to warm into the 22nd century unless we reduce emissions by an even greater amount. As a result, it is unlikely that efforts to control anthropogenic-induced greenhouse gas emissions will eliminate the risk of climate change. To that end, a sound forest carbon policy informed by the best available science represents an important part of the solution because forests have the potential to assimilate, accumulate, and sequester large amounts of carbon from the atmosphere, thus reducing one of the primary drivers of climate change (Bonan 2008). Young, healthy forests tend to be carbon sinks; however, as many forests mature, they become carbon neutral or sources of carbon as net primary productivity declines (but see Luyssaert et al. 2008). Furthermore, large amounts of CO₂ are released when forests are killed, burned, defoliated, or deforested (Kurz and Apps 1999), and carbon may be lost when forests are converted to other systems (e.g., shrublands) that have smaller carbon pools. In these cases, forests that were once carbon sinks may become carbon sources (Kurz et al. 1995, 2008, Stocks et al. 1996), causing further warming and influencing land use (Figure 1).

There are well-recognized tools available to increase the resiliency of forests to common disturbances exacerbated by climate change, such as bark beetle outbreaks (Fettig et al. 2007) and wildfire (Stephens et al. 2012). Stephens et al. (2012) concluded that treatments, such as prescribed fire and mechanical fuel reduction treatments (e.g., thinning of small-diameter trees), which are implemented to create more fire-resistant forests probably create forests that are also more resistant and resilient to changes imposed on them by climate change. Others have reported that fuel reduction treatments and forest restoration treatments are also prudent approaches for reducing risks associated with bark beetle infestations in some western forests (Hayes et al. 2009), although thinning prescriptions applied to specifically

reduce the susceptibility of forests to bark beetles would differ (Fettig et al. 2007). Tools are also available to identify where the probability of disturbance is likely to have the greatest negative impact (e.g., Stocks et al. 1998, Aukema et al. 2008, Bentz et al. 2010). Resource managers can intervene and reduce some of the negative impacts of climate change through adaptation⁷ (Peterson et al. 2011). For example, as previously discussed, some suggest that assisted migration in large-scale reforestation programs could be a potent and cost-effective adaptation strategy for some tree species (Gray et al. 2011). Research and monitoring programs should be implemented to determine how disturbances affect forests and to continually update our understanding of how climate change is influencing disturbances that shape forests (Dale et al. 2001). Through collaboration with scientists, managers can implement adaptive management based on the best available science, which in turn should be used to inform forest policy. (See Franklin and Johnson [2012] for a relevant example involving restoration in the Pacific Northwest, United States.) For this reason, it is appropriate to create a diversity of forest structures and compositions and to learn about their resistance and resilience to climate change. Others have encouraged flexible approaches that promote reversible and incremental steps and that favor ongoing learning and the capacity to modify decisions and direction (Millar et al. 2007). We agree with these approaches. Decision-support tools that help transform complex scientific concepts into management options are available (e.g., Morelli et al. 2012). The Climate Change Resource Center (2012) is a valuable resource for managers addressing climate change in forest plans and during project implementation. We encourage use of this resource. Furthermore, we emphasize that forest management decisions implemented today must consider any potential unintended consequences in the future and the direct and indirect effects of prevailing climates for the entire life cycle of trees.

Numerous interagency and international efforts have been initiated over the past 3 decades to analyze several aspects of the earth's climate and to develop options that have the potential to aid in addressing climate change. The most well-known of these is IPCC, formed by the United Nations in 1988 to help address the scientific, economic, and policy aspects of global cli-

mate change. Despite these efforts, climate change poses a significant, if not daunting, challenge to forest managers and policymakers. Climate science is complex and often difficult to understand. The body of science is rapidly evolving, challenging even the most informed to remain knowledgeable of recent advances. Projections of future climates contain inherent uncertainty and require understanding of complex assumptions (scenarios) and use of sophisticated models. Assessing the extent to which recent changes in climate have affected forests is difficult, and predicting future ecological impacts is even more so. Of necessity, studies in this area are primarily correlational rather than experimental, and, as a result, assignment of causation is inferential (Parmesan and Yohe 2003). This may lead to skepticism despite experimental research (e.g., on the effects of temperature and precipitation on target species) serving as the foundation for this inference. Although this skepticism is understandable, we readily acknowledge the influence of past climates on current tree species and forest distributions. For example, the downslope expansion of juniper (*Juniperus*) into more xeric sites in the northern Great Basin, United States, is commonly recognized and associated with a wetter period 1900–4000 years ago (Miller and Wigand 1994). Despite these challenges and limitations, there is enough consensus in the major trends concerning projections of future climates and changes in tree species and forest distributions that we should anticipate these changes and proceed to address them (McLachlan et al. 2007).

The IPCC stated that "In the long-term, a sustainable forest management strategy aimed at maintaining or increasing forest carbon stocks, while producing an annual sustained yield of timber, fiber, or energy from the forest, would generate the largest sustained mitigation benefit" to climate change and that "Forestry can make a very significant contribution to a low-cost global mitigation portfolio that provides synergies with adaptation and sustainable development" (Metz et al. 2007, p. 543). Malmesheimer et al. (2011) provided a useful framework for managing forests for carbon over time as well as for the numerous other benefits provided by forests (Nelson et al. 2009). Their framework includes the following three aspects: keeping forests as forests through active management to increase resiliency; recognizing that substantial quantities of carbon can be stored in wood

products for lengthy periods of time; and promoting wood products as a substitute for other building materials (e.g., aluminum, concrete, and steel) that do not provide the associated carbon benefits of wood (Malmesheimer et al. 2011). Although managers, policymakers, and scientists have been working to develop and implement strategies that increase the resiliency of forests to climate change in western North America, much of this work has not been well-coordinated. We recognize the need for a more collaborative approach, in which managers, policymakers, and scientists of broad expertise from various disciplines and across political borders work to address one of the most important issues facing our society. Our communities, tribes, industries, nongovernmental agencies, and local, state, and federal agencies need to be involved and engaged.

Endnotes

1. Projections of climate change depend on assumptions (scenarios) based on changes in human populations, technology, land use, and global gross domestic production, which in turn influence greenhouse gas emissions. There are six families of scenarios discussed in the Fourth Assessment Report (AR4). A brief summary is available online at www.ipcc.ch/PDF/assessment-report/ar4/wg1/ar4-wg1-spm.pdf.
2. Climatic "normals" are used to compare current or future climatological trends with past observations. A normal is defined as the mean of a climate element (e.g., temperature) over a 30-year period. This period of time is thought to be long enough to filter out any interannual variation or anomalies, but short enough to be able to show emerging climatic trends.
3. Most notable are changes in atmospheric concentrations of greenhouse gases (primarily carbon dioxide [CO₂], but also other gases such as methane [CH₄], nitrous oxide [N₂O], and halocarbons) and variations in solar activity that affect radiation and climate.
4. Bioclimate envelope models require present-absent data (where the trees grow and where they do not) to determine the realized climatic niche of a particular tree species as well as high-resolution climate data that reflect climatic conditions where the species is present or absent and a powerful modeling approach that can effectively capture the relationship between the species occurrence and climate variables.
5. The practice of planting tree species outside of their current distribution due to anticipated changes in the climatic niche.
6. Cold hardening is a process that plants and insects use to prevent injury due to chilling and freezing, although the physiological mechanism differs (Salt 1961).

- An adjustment in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities (IPCC 2007).

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