Review

Forest responses to climate change in the northwestern United States: Ecophysiological foundations for adaptive management

Daniel J. Chmura [a,*], Paul D. Anderson [b,1], Glenn T. Howe [a,2], Constance A. Harrington [c,3], Jessica E. Halofsky [d,4], David L. Peterson [d,5], David C. Shaw [e,6], J. Brad St.Clair [b,7]

[a] Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall Corvallis, OR 97331-5752, USA
[b] USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331-4401, USA
[c] USDA Forest Service, Pacific Northwest Research Station, 3625 93rd Ave. SW, Olympia, WA 98512-1101, USA
[d] USDA Forest Service, Pacific Wildland Fire Sciences Laboratory, 400N. 34th St., Suite 201, Seattle, WA 98103-8600, USA
[e] Department of Forest Engineering, Resources and Management, Oregon State University, 204 Peavy Hall, Corvallis, OR 97331-5752, USA

ARTICLE INFO

ABSTRACT

Climate change resulting from increased concentrations of atmospheric carbon dioxide ($[CO_2]$) is expected to result in warmer temperatures and changed precipitation regimes during this century. In the northwestern U.S., these changes will likely decrease snowpack, cause earlier snowmelt, increase summer evapotranspiration, and increase the frequency and severity of droughts. Elevated $[CO_2]$ and warmer temperatures may have positive effects on growth and productivity where there is adequate moisture or growth is currently limited by cold. However, the effects of climate change are generally expected to reduce growth and survival, predispose forests to disturbance by wildfire, insects, and disease; and ultimately change forest structure and composition at the landscape scale. Substantial warming will likely decrease winter chilling resulting in delayed bud burst, and adversely affect flowering and seed germination for some species. The extent of these effects will depend on the magnitude of climate change, the abilities of individual trees to acclimate, and for tree populations to adapt in situ, or to migrate to suitable habitats. These coping mechanisms may be insufficient to maintain optimal fitness of tree populations to rapidly changing climate. Physiological responses to climatic stresses are relatively well-understood at the organ or whole-plant scale but not at the stand or landscape scale. In particular, the interactive effects of multiple stressors is not well known. Genetic and silvicultural approaches to increase adaptive capacities and to decrease climate-related vulnerabilities of forests can be based on ecophysiological knowledge. Effective approaches to climate adaptation will likely include assisted migration of species and populations, and density management. Use of these approaches to increase forest resistance and resilience at the landscape scale requires a better understanding of species adaptations, within-species genetic variation, and the mitigating effects of silvicultural treatments.

© 2011 Elsevier B.V. All rights reserved.

Contents

* Corresponding author. Present address: Polish Academy of Sciences, Institute of Dendrology, Parkowa 5, 62-035 Kornik, Poland. Tel.: +48 61 8170 033; fax: +48 61 8170 166.
 E-mail addresses: djchmura@poczta.onet.pl (D.J. Chmura), pdanderson@fs.fed.us (P.D. Anderson), glenn.howe@oregonstate.edu (G.T. Howe), charrington@fs.fed.us (C.A. Harrington), jhalo@u.washington.edu (J.E. Halofsky), peterson@fs.fed.us (D.L. Peterson), dave.shaw@oregonstate.edu (D.C. Shaw), bstclair@fs.fed.us (J. Brad St.Clair).
[1] Tel.: +1 541 758 7786; fax: +1 541 758 7760.
[2] Tel.: +1 541 737 9001; fax: +1 541 737 1319.
[3] Tel.: +1 360 753 7670; fax: +1 360 753 7737.
[4] Tel.: +1 206 543 9138; fax: +1 206 732 7801.
[5] Tel.: +1 206 732 7812; fax: +1 206 732 7801.
[6] Tel.: +1 541 737 2845; fax: +1 541 737 4316.
[7] Tel.: +1 541 750 7294; fax: +1 541 758 7760.

1. Introduction

The Earth's climate is variable, and long periods of both cooler and warmer temperatures have occurred in the past (Jansen et al., 2007). Although large natural climatic changes have occurred over centuries to millennia (Jansen et al., 2007), changes of similar magnitude are now projected to occur over decades to years (Meehl et al., 2007; Trenberth et al., 2007). These unprecedented rates of climatic change may profoundly affect the ability of forests to acclimate or adapt to future conditions.

Forests in the northwestern U.S. (NW) are distinct among the Northern Hemisphere temperate forests in their species composition and high productivity (Waring and Franklin, 1979). Composed mostly of conifers, these forests are adapted to the wet mild winters and warm-dry summers typical of the region (Franklin and Halpern, 2000). There are steep climatic gradients associated with elevation, latitude, distance from the ocean, and proximity to the mostly north–south mountain ranges. Complex topography contributes to substantial climatic variability at a fine scale, often resulting in mosaics of vegetation types within small geographic areas.

The current species composition and age structure of NW forests reflects the variability of ownerships and management objectives within the region, as well as the legacies of past disturbances and management practices. Northwest forests will continue to be an important part of the regional economy and may play a significant role in carbon (C) sequestration and climate change mitigation (Alig et al., 2006; Krankina and Harmon, 2006).

Several reviews have addressed the projected impacts of climate change on forest ecosystem structure, composition and productivity (Peters, 1990; Saxe et al., 1998, 2001; Winnett, 1998; Hanson and Weltzin, 2000; Körner, 2000; Aber et al., 2001; Hansen et al., 2001; Ciais et al., 2005; Easterling and Apps, 2005; Boisvenue and Running, 2006; Mohan et al., 2009), biogeochemical cycles and C sequestration (Malhi et al., 1999, 2002; Gower, 2003; Beedlow et al., 2004; Campbell et al., 2009), air pollution and ecosystem processes (Bytnerowicz et al., 2007), and the production of ecosystem services (Winnett, 1998; Irland et al., 2001). Elevated concentration of atmospheric carbon dioxide – [CO₂], generally warmer temperatures, and changing precipitation regimes will affect the exchange of energy, carbon, water and nutrients between forests and the environment, leading to changes in forest growth, survival and structure. Interactions with biotic and abiotic disturbance agents will also shape future forests.

Ecophysiological processes are the foundation of acclimation and evolutionary adaptation to climate change. Although phenotypic plasticity is substantial for some traits (e.g., timing of bud flush), the existence of among-population genetic variation for bud flush and many other adaptive traits indicates that phenotypic plasticity is insufficient to confer optimal fitness to the range of climates experienced by most species (Rehfeldt et al., 2001; St.Clair and Howe, 2007). Because trees are genetically adapted to their local climates, rapid rates of climate change may challenge the capacity of tree species to adapt in place or migrate to new locations (St.Clair and Howe, 2007; Aitken et al., 2008). To facilitate forest acclimation and adaptation, decision-makers need to understand the potential ecophysiological responses of trees and forests to climate change.

A premise of this review is that the persistence and integrity of forests depend on the acclimation and adaptation of forest trees to future climates. In this review, we identify critical processes, traits and attributes that will underpin this adaptation. Specifically, we (1) review the ecophysiological foundations of forest growth, reproduction and mortality in relation to elevated [CO₂], warmer temperatures, changes in precipitation, and droughts; emphasizing interactions among these factors, and how they interact with disturbances, such as fire, insects and diseases; and (2) identify key adaptations and processes underpinning tree tolerance and resistance to anticipated stresses. It will be important to consider these adaptations when managers design strategies to help forests to adapt to future climates.

We center our attention on forests of the NW – the states of Washington, Oregon, Idaho, the northern parts of California, and western parts of Montana. However, we also cite examples from temperate forests of other regions where appropriate. We will not address the effects of air pollutants (e.g., ozone, SO₂), and refer the reader to recent reviews that cover these topics (e.g., Bytnerowicz et al., 2007; Campbell et al., 2009).

2. Regional climatic limitations and projections of climate change

2.1. Climatic limitations to forest growth and productivity in the NW

Strong climatic gradients are typical of the NW. Environmental severity increases with elevation and distance from the ocean, and is reinforced by the north–south distribution of major mountain ranges (Arno, 1979; Peet, 2000). As a result, regional climatic limitations to forest growth and productivity range from minimal along the coast, where temperatures are mild and moisture is plentiful, to severe in the interior where moisture deficits are common (Arno, 1979; Franklin and Dyrness, 1988; West and Young, 2000; Littell et al., 2008). However, during rare extreme droughts, moisture stress may be greater in the forests west of the Cascade crest, because of their typically greater leaf areas (Zobel, 1974). Within the inte-

rior mountain ranges, moisture and thermal conditions grade from warm and dry in the rain-shadow foothills, to moist and cold at high elevations; and from relatively mesic north-facing slopes, to more xeric south-facing slopes.

Climatic gradients influence the natural distributions of NW tree species. For example, the distributions of *Thuja plicata* and *Tsuga heterophylla* are limited to areas that are influenced by moist Pacific Ocean air masses; these species are absent from areas of the northern Rocky Mountains where these air masses fail to reach (Arno, 1979). Transitions to drier conditions within the region are indicated by the presence of more drought-tolerant species, including *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Pinus contorta* (Franklin and Dyrness, 1988). Changes in climate will likely affect future species distributions, forest composition, and forest structure.

2.2. Future climate in the NW

Increases in anthropogenic greenhouse gas concentrations, especially CO_2, are contributing to the warming of the atmosphere (Forster et al., 2007). Since the pre-industrial era, atmospheric $[CO_2]$ increased from about 280 ppm to the current level of about 390 ppm (http://www.co2now.org/), and is likely to reach 540–970 ppm by the end of this century (Prentice et al., 2001). Projected changes in atmospheric $[CO_2]$ at local scales are expected to track changes at the global scale. In contrast, CO_2-induced changes in regional climates will likely differ from the projections at the global scale (Christensen et al., 2007).

Compared to the past three decades, the NW is expected to warm about 0.8–2.9 °C by mid-century (Leung et al., 2004; Duffy et al., 2006; Mote et al., 2008) and 1.6–5.4 °C by the end of the century (Mote et al., 2008). These regional estimates for 2100 are similar to the projected global warming of 1.1–6.4 °C by the end of the century (Meehl et al., 2007). Warming in the NW will probably be greater inland than near the coast (Leung et al., 2004; Duffy et al., 2006), and greater in summer (3.9 °C on average) than in winter (2.7 °C) (Mote et al., 2008). In contrast to this overall regional trend, more warming is projected to occur in winter and spring than in the summer in the Cascade Range and the northern Rocky Mountains (Leung et al., 2004).

Projected changes in regional precipitation are less certain than those for temperature. Except for increases in winter precipitation in northern California, eastern Oregon, and central Idaho, projected changes are not statistically different from historical year-to-year variation (Duffy et al., 2006). Overall, small decreases in summer precipitation and small increases in winter precipitation are projected for the NW (Leung et al., 2004; Mote et al., 2008), but the projected changes in annual and seasonal precipitation typically vary widely among different climate models.

The frequency of heavy precipitation events will likely increase in the NW (Mote et al., 2008; Salathé et al., 2009) and vary among locations and seasons (Leung et al., 2004). Conversely, snowpack and snow cover duration may decrease in the NW in conjunction with a global trend (Hamlet et al., 2005; Meehl et al., 2007; Barnett et al., 2008). A substantially greater relative decrease in snowpack is projected for the Cascades and Sierra Nevada (60–70%) than for the northern Rocky Mountains (20%; Leung et al., 2004).

Future climate projections are uncertain because of intrinsic variability of the climate system, uncertainty in greenhouse gas emissions (IPCC, 2000), and difficulty of representing Earth system processes in climate models (Hegerl et al., 2007; Meehl et al., 2007). In addition, differences in regional climate projections reflect the uncertainty associated with using different general circulation models (GCMs), projection times, and downscaling methods. Projections of future precipitation usually have less precision than those of surface temperatures (Bates et al., 2008).

Despite uncertainty, almost all projections indicate that the NW will be warmer in the future. Warmer temperatures will affect snowmelt, increase summer evapotranspiration, and hasten seasonal depletion of soil moisture (Hobbins et al., 2004; Christensen et al., 2007; Elsner et al., 2009). Thus, the most significant challenge likely facing NW forests is an increase in the frequency, duration, and intensity of droughts (discussed below). Thus, dry summers in the NW may become even drier, which is consistent with recent observations (Luce and Holden, 2009).

Warmer temperatures during the cold season will increase the elevation where rain transitions to snow, cause more precipitation to fall as rain instead of snow, increase the number of rain-on-snow precipitation events, decrease snowpack, and result in earlier snowmelt. Such conditions will increase runoff and the probability of winter and spring floods, soil erosion, and summer water shortages, particularly in areas that depend on water from snowmelt (Barnett et al., 2008; Bates et al., 2008; Adam et al., 2009).

Forest responses to climate change will depend on local site conditions. Warming may be favorable to growth at high elevation sites where the growing season is currently limited by low temperatures or snow cover, but enhance the effects of drought in areas that are currently moisture limited. The amount of water available to trees will depend on the amount and timing of precipitation, as well as the amounts of surface runoff, deep drainage, and evapotranspiration. Underlying geology exerts strong control over subsurface flow and groundwater storage, mediating the response of streamflow to climatic warming in the NW (Tague et al., 2008; Tague and Grant, 2009; Brooks et al., 2010). The risk of floods may increase because of changes in snowmelt hydrology and more intense precipitation (Hamlet and Lettenmaier, 2007; Adam et al., 2009), but the resulting impacts on forests are expected to be relatively small in the NW (see Section 5.3 and Table 1).

Because of the complex topography in the NW, local weather phenomena may decouple fine-scale and regional climate patterns (Daly et al., 2007). Elevation, slope, aspect, soil type and vegetation cover affect local thermal and moisture conditions, making it difficult to predict local climate change from regional trends. Therefore, adaptation strategies must be robust to both regional climatic trends and local, site-specific conditions.

3. Forest adaptation to climate change

Climate change will require trees and forests to cope with new climatic and biotic environments. Populations of trees may cope with new climates by acclimating, migrating to new locations, or evolving in place. If they cannot cope, they may disappear from local ecosystems. Mechanisms of adaptation must be understood to address the capacity of trees and forests to persist and thrive in the future. The word adaptation often has a broad meaning in the climate change literature, where it refers to the "adjustment of natural or human systems to new environments, which moderates harm or exploits opportunities" (IPCC, 2001). The "adjustment of natural systems" includes the acclimation, natural migration, and evolutionary adaptation we describe below. The "adjustment of human systems" includes the management practices applied by humans.

We use the term adaptation as an evolutionary term, referring to the genetic and phenotypic changes that increase population fitness to a particular environment. 'Fitness', or adaptive value, is the relative ability of a group of genotypes to survive and reproduce in a particular environment compared to the optimum set of genotypes. As such, fitness represents a genetic measure of the health of a *population*. In contrast, 'acclimation' refers to the changes that allow *individuals* to better cope with new environments. These

Table 1

Projected responses of trees and forests to climate change in the northwestern U.S. Responses are judged relative to one another based on an aggregate assessment of the expected extent (size of the response and affected area) and confidence in the listed direction and extent (Conf.).

Nature of change			Tree and forest responses					
Direction	Conf.[a]	Spatial scale[b]	Process or effect	Direction[c]	Effect size[d]	Conf.[e]	Primary areas impacted	Relative importance[f]
1. Atmospheric CO_2 Increase	VH	G	1. Tree and stand growth	+	M	M/H	Areas not limited by water or nutrients	M
			2. Water-use efficiency	+	L/M	H	All areas	L
			3. Drought hardiness	0/+	VL	M/H	Areas limited by water	L
			4. Nutrient availability	−	L	VL	Nutrient-poor sites	VL
			5. Regeneration success	+	L	L	Unknown	L
2. Temperature Increase	VH	G	1. Heat injury	+	L	M/H	Areas with warm summer temperatures	L
			2. Evapotranspiration	+	H	M/H	All areas	H
			3. Timing of germination	A/D[*]	M	L	Areas with mild winters	L
			4. Timing of bud flush	A/D[*]	H	H	Areas with mild winters	M/H
			5. Spring frost injury	+/−[*]	M	L	Unknown	M
			6. Timing of bud set	D	L/M	M	Areas not limited by water	L/M
			7. Fall frost injury	+/−[*]	M	L	Unknown	M
			8. Growing season length	+/−[*]	M	L	Areas not limited by water; Areas limited by temp.	L
3. Precipitation Increase/decrease/ changed intensity	M	R/S	1. Physical damage (e.g.	+	L	L	Prone sites	L
			2. Physiological damage (e.g.	+	L	L	Prone sites	L
4. Drought Increase	H	R/S	1. Tree and stand growth	−	H	VH	Areas limited by water	VH
			2. Drought injury	+	H	VH	Areas limited by water	H
			3. Mortality	+	H	H	Areas limited by water	H
			4. Regeneration success	−	H	H	Areas limited by water	H
5. Wildfire Increase	VH	R	1. Fire injury	+	M	H	Fire prone environments	VH
			2. Tree and stand growth	−	M	H	Fire prone environments	VH
			3. Mortality	+	M	H	Fire prone environments	VH
			4. Forest structure and composition	Change	M	M	Areas with infrequent fires and large fuel loads	H
			5. Landscape structure	Change	M	M	Areas with infrequent fires and large fuel loads	H
6. Epidemics of insects and diseases Increase	M	R	1. Tree and stand damage	+	M	M	Predisposed stands and landscapes	VH
			2. Tree and stand growth	−	M	M	Predisposed stands and landscapes	H
			3. Mortality	+	M	M	Predisposed stands and landscapes	H
			4. Landscape structure	Change	M	M	Predisposed stands and landscapes	H

[a] Confidence, using the IPCC scale, that the direction of change will be as indicated: VH is very high, H is high, M is medium, L is low, and VL is very low.

[b] Spatial scale of the change: G is global, R is regional (NW), and S is local or site-specific.

[c] Projected direction of change of the process or effect: + is an increase, − is a decrease, and +/− is either an increase or decrease, A is an advance in timing, and D is a delay in timing.

[d] Effect size: VH is very high, H is high, M is medium, L is low, and VL is very low.

[e] Confidence that the direction of response and the effect size will be as indicated: VH is very high, H is high, M is medium, L is low, and VL is very low.

[f] Relative importance given the nature of the change, projected tree and forest responses, areas impacted, and confidence levels.

[*] Separation with a slash (/) indicates variation in response to warming: with slight warming, an A or + response is expected; with substantial warming, a D or − response is expected.

changes may be biochemical (e.g., changes in gene expression), physiological, morphological, or developmental. The ability of an individual to acclimate, or alter its phenotype, is its phenotypic plasticity.

Climate-related phenotypic plasticity is common and often dramatic in forest trees. The timing of fall growth cessation, bud set, cold acclimation, and dormancy induction varies from year to year because of variation in the onset of cold temperatures,

which interact with short days to control these adaptive responses (Howe et al., 2003). Similarly, spring bud burst varies depending on the amount of chilling and warming during the winter and spring (Timmis et al., 1994; Harrington et al., 2010). Acclimation to drought may occur in response to low soil moisture (Kozlowski and Pallardy, 2002). Because trees tend to be long-lived, phenotypic plasticity will be important for existing trees to cope with climate change. However, long-term provenance tests and genecological studies suggest that phenotypic plasticity alone will be insufficient for maintaining healthy and productive tree populations in the future (Wang et al., 2006; St.Clair and Howe, 2007). Thus, migration or *in situ* evolution may be required to maintain sufficient population fitness in the face of climate change.

Given time, tree species may be able to cope with climate change by migrating into new areas (i.e., range shifts) or by exchanging genes among genetically distinct populations. The first form of migration, which involves dispersal and colonization by seeds or vegetative propagules, is facilitated by disturbance. For example, locally adapted populations at the poleward (northward in the NW) limits of a species' range may be able to track the poleward movement of climatic conditions to which they are adapted. Nonetheless, these migration rates will probably be too slow to keep pace with climate change, at least for some forest trees (McLachlan et al., 2005; Aitken et al., 2008; Mohan et al., 2009; Gugger et al., 2010). Species may also migrate to higher elevations, but with sufficient warming, these locally available habitats may eventually disappear. In contrast, the second form of migration also occurs via pollen. Although pollen can travel much farther than seeds and vegetative propagules, differences in flowering phenology between source and recipient populations may limit the rate of effective pollen migration between climatically distinct areas (Silen, 1963; Slavov et al., 2005).

Alternatively, populations may be able to adapt via *in situ* evolution; that is, within-population changes in the frequencies of alleles and phenotypes that increase mean fitness. New alleles may enter existing populations via mutation (the ultimate source of new alleles), and adaptive changes in allele frequencies can occur from one generation to the next via natural selection imposed by the climate. In practice, this strict form of *in situ* evolution will be augmented by gene immigration, primarily via pollen. Nonetheless, individual populations contain large amounts of adaptive genetic variation – often 50% or more of total genetic variation (Howe et al., 2003); and this can contribute substantially to the potential for *in situ* evolution. Traits that have been modified by natural selection to confer adaptation to local climatic conditions include survival, height growth, diameter growth, growth phenology, cold hardiness, drought hardiness, chilling requirements, and seed stratification requirements (Howe et al., 2003; St.Clair et al., 2005). Other traits, such as flowering phenology, seed production, and fundamental physiological processes may belong to this group as well, but have not been well studied at the population level.

In situ evolution may be sufficient to track climate change in species with short to modest generation times (i.e., months to years; Jump and Peñuelas, 2005; Smith and Beaulieu, 2009). This may not be the case for most forest trees, however, because they do not begin flowering until age 10–15 (Bonner and Karrfalt, 2008), and the actual generation interval is often much longer (e.g., hundreds of years) because of infrequent stand-replacing disturbances. Barring large-scale disturbances, the long-lived conifers of the NW will probably be regenerating in a climate that is substantially different from the present. Increased knowledge of important ecophysiological traits, including their inheritance and genetic architecture, will allow us to make better inferences about the future of our forests.

4. Ecophysiological modeling of climate change impacts

Models have proved very useful for projecting effects of climate change on trees and forests, because they can incorporate changes in many parameters. Mechanistic models of tree ecophysiology are important components of process-based species distribution models (Coops et al., 2009; Keenan et al., 2011), systems for mapping and monitoring changes in forest productivity and carbon sequestration (Turner et al., 2007; Coops et al., 2010), and may become important components of climate-sensitive, hybrid growth and yield models (Weiskittel et al., 2010). Process-based models function at scales ranging from single leaves to biomes (e.g. Farquhar and von Caemmerer, 1982; Wang and Jarvis, 1990; Aber et al., 2001; Coops et al., 2001; Turner et al., 2007), but those providing information on stands, species, and ecosystems will be especially useful for informing regional mitigation or adaptation strategies.

Both statistical and mechanistic approaches have been used to explain current species distributions and to predict how these distributions might change in response to climate change (Kearney and Porter, 2009). Statistical approaches (e.g., 'environmental envelope' or 'ecological niche' models) use correlations between species occurrence and environmental characteristics (e.g., climate, soils, and topography) to understand current distributions and predict where suitable habitat may be found in the future (Heikkinen et al., 2006; Elith and Leathwick, 2009). However, they may inaccurately predict future species distributions (future realized niches) because they rarely account for other relevant factors such as biotic interactions, fire, [CO_2], and migration ability. Nonetheless, these statistical models are valuable for uncovering key relationships between environmental variables and the adaptive characteristics of species and populations (Heikkinen et al., 2006; St.Clair and Howe, 2007). These relationships will be particularly important to include in ecophysiological process models. Information on ecophysiological adaptations and responses to climate are the foundation of mechanistic species distribution models (Kearney and Porter, 2009). Although the necessary ecophysiological information is unavailable for most species, successful mechanistic models should have a greater ability to extrapolate species distributions into no-analog and non-equilibrium conditions. Genetic variation and phenotypic plasticity are implicitly accounted for in statistical species distribution models, but unless migration is modeled, the ability of genetically adapted populations to migrate with suitable habitat is unknown. In contrast, population-level genetic variation must be explicitly included in mechanistic models via population specific parameters, but this is rarely done.

Forest gap models are valuable for predicting landscape level responses to climate change because they model competitive interactions and successional trends of forests over decades to centuries (Norby et al., 2001). Gap models (e.g., FORCLIM, FOREL, JABOWA, LINKAGES, ZELIG, FORSKA, GUESS) are individual tree models that simulate forest dynamics on patch-sized areas of land, that are then scaled to stands and landscapes. These models come in many forms – some are predominantly empirical, whereas others are based on mechanistic process functions. Gap models form the foundation of some dynamic global vegetation models (Smith et al., 2001; Robinson et al., 2008). Gap models use climate and other environmental information in combination with species-specific parameters that describe key ecophysiological processes. Although information is scarce for many species, accounting for within-species genetic variation in these parameters could improve gap models. Use of gap models to study climate change is limited by the difficulty of modeling how carbon allocation patterns may change in response to changes in climate and associated stressors (Wullschleger et al., 2001). Furthermore, these models should account for changes in the length of the growing season and potential acclimation of growth to new conditions (Norby et al., 2001).

Some gap models allow for simple management practices such as harvesting, site preparation, managed fire, and N-fertilization (Robinson et al., 2008). Although these models could be used to study regional management options (Lasch et al., 2005), they fall short in their capacity to predict how management activities will influence forest responses to climate change on a site-specific basis.

5. Impacts of climate change on trees and forests in the NW

Elevated [CO_2], warmer temperatures, and changed moisture regimes will interact to affect future trees and forests. It is difficult to discern the interactive and possibly nonlinear responses of forests to multiple stresses, particularly using historical data or retrospective studies. Multi-factor manipulative experiments and modeling are invaluable for examining the possible responses to climate change, and for identifying the interactive "surprises" that are impossible to discern from single-factor studies (Norby and Luo, 2004). Long-term ecological studies and eddy-flux measurements also provide evidence that forest have responded to recent changes in climate (Franklin et al., 1990; Falk et al., 2008). Therefore, whenever possible, we focus the following discussion on evidence from these types of experiments to infer the responses of trees and forest to climate change.

5.1. Elevated [CO_2]

Elevated [CO_2] will impact forests both indirectly and directly. As a greenhouse gas, CO_2 will exacerbate changes in the energy fluxes driving changes in climatic variables. Elevated [CO_2] may influence tree growth, reproduction, and mortality by impacting assimilate supply via direct effects on physiological processes of photosynthesis, respiration, and transpiration. Over the past three decades, the direct effects of elevated [CO_2] have been studied at increasingly larger scales (e.g., potted seedlings, small-scale field trials of young trees, and microcosms), allowing inferences to be extended from tissues, to whole-plants, to groups of trees, and from short durations, to seasons, and years. State-of-the-art free-air CO_2 enrichment (FACE) studies expose small areas of relatively intact vegetation to controlled concentrations of atmospheric CO_2, thus avoiding some of the limitations of chamber-based exposure systems (Ainsworth and Long, 2005). Inferences from forests growing near natural CO_2 springs have been used to examine the effects of [CO_2] gradients and long-term exposure (Hattenschwiler et al., 1997; Tognetti et al., 1999). Although scale limitations persist, we can make reasonable predictions of the potential effects of elevated [CO_2] on trees and forests, but interactions with other climatic changes may be missed. Process-based models that integrate changes in climate with plant responses through functional relationships may be the best means for addressing these interactions.

Tree growth was generally enhanced in elevated [CO_2] in both short- and long-term studies (Ceulemans and Mousseau, 1994; Curtis and Wang, 1998; Norby et al., 1999; Hamilton et al., 2002; Nowak et al., 2004; Ainsworth and Long, 2005; DeLucia et al., 2005; Finzi et al., 2006, but see Körner et al., 2005; Norby et al., 2010), and the response may be modulated by other stresses (Curtis and Wang, 1998). At the individual tree level, increased growth results from physiological adaptations that optimize photosynthetic C acquisition and allocation (Eamus and Jarvis, 1989; Pushnik et al., 1995). The leaf area of individual trees and stands (i.e., leaf area index, LAI) may increase under elevated [CO_2] (Ceulemans and Mousseau, 1994; Ainsworth and Long, 2005), but the maximum LAI is typically similar in ambient and elevated [CO_2] (Norby et al., 2003b; DeLucia et al., 2005). Many studies found increases in the production and standing crops of tree roots under elevated [CO_2], and

increases in the amount and depth of fine-root growth were particularly noticeable (Allen et al., 2000; Tingey et al., 2000; Lukac et al., 2003; Norby et al., 2004; Pritchard et al., 2008, but see Johnson et al., 2006; Bader et al., 2009). Nonetheless, there have been no life-cycle assessments of these growth responses, and for some multi-year exposures, enhanced growth has been transitory (e.g., Asshoff et al., 2006; Norby et al., 2010).

It is unclear whether elevated [CO_2] will alter tree allometry, such as changes in root:shoot ratios (Callaway et al., 1994; Ceulemans and Mousseau, 1994; Norby et al., 1999; Tingey et al., 2000; McCarthy et al., 2010). In separate FACE studies, the deciduous tree *Liquidambar styraciflua* allocated most of the extra carbon it assimilated in the elevated [CO_2] treatment into non-woody fine roots (Norby et al., 2004), whereas the evergreen *Pinus taeda* allocated most of its additional carbon into woody biomass (Hamilton et al., 2002). Because fine roots have rapid turnover, these differences may have ramifications for C cycling and overall productivity (DeLucia et al., 2005).

It is also unclear whether elevated [CO_2] will interact with warmer temperatures (C × T interaction) to affect biomass growth or allocation. In a *P. menziesii* mesocosm experiment, warming affected seasonal growth patterns and seedling height, but stem diameter, whole seedling biomass, and biomass allocation were unaffected by warming, [CO_2], or their interaction (Olszyk et al., 1998a,b, 2003). In seedlings of *Acer rubrum* and *Acer saccharum*, the dry mass of stems was reduced by warming, but this effect was greater in ambient than in elevated [CO_2] (Norby and Luo, 2004). However, these species differed in their response to elevated [CO_2], and their final biomass was determined by multiple processes that were differentially affected by the combination of warming and [CO_2] (Norby and Luo, 2004).

Elevated [CO_2] directly affects plant physiological processes. Most trees are C_3 plants in which CO_2 and oxygen (O_2) compete for the active site of the primary enzyme involved in photosynthesis, Rubisco. When CO_2 is used as the substrate, CO_2 assimilation occurs via photosynthesis (P_s), but when O_2 is the substrate, CO_2 is produced as an outcome of photorespiration. Elevated [CO_2] increases the CO_2 concentration in leaves and at the active sites of Rubisco, and can enhance light-saturated photosynthetic rates in woody plants by 2–280%, depending on species and environmental conditions (Curtis and Wang, 1998; Norby et al., 1999; Nowak et al., 2004; Ainsworth and Rogers, 2007). Over time, though, stimulation of P_s in elevated [CO_2] may decline as a result of biochemical adjustments in leaves (Stitt, 1991; Bowes, 1993; Tissue et al., 1999) or changes in sink activity, competition, or other stresses (Ceulemans and Mousseau, 1994; Saxe et al., 1998). Acclimation is not universal, however, and even when the declines in photosynthetic capacity occur, the rates of P_s may be greater in elevated than in ambient [CO_2] (Norby et al., 1999; Nowak et al., 2004). Although plants fix C via photosynthesis, they also evolve CO_2 through respiration (R_d). In general, respiration decreases at elevated [CO_2] (Drake et al., 1997; Curtis and Wang, 1998), but results vary and no consistent picture has emerged (Norby et al., 1999; Hamilton et al., 2001). Overall, our understanding of respiration at the cellular level is incomplete, and we cannot use information at the cellular level to predict the effects of elevated [CO_2] on respiration of whole-trees or ecosystems (Drake et al., 1999; Valentini et al., 2000).

The simultaneous impact of elevated [CO_2] and warming may be important because they affect the efficiency of photosynthesis, and hence plant C balance, in contrasting ways. Elevated [CO_2] tends to decrease photorespiration and mitochondrial respiration, but warmer temperatures generally increase these processes (Long, 1991; Bowes, 1993; Saxe et al., 1998; Norby et al., 1999). Thus, the relative stimulation of P_s by elevated [CO_2] should be enhanced in warmer temperatures (Long, 1991). This prediction was supported by observations in seedlings of *P. taeda* (Lewis et al., 1996), but

not in other tree species (Tjoelker et al., 1998). No significant C × T interactions were found in a *P. menziesii* mesocosm study for photosynthetic and respiration parameters at the leaf level (Lewis et al., 1999, 2001, 2002; Apple et al., 2000), but these factors were not independent in the long-term, or at the whole-system level (Tingey et al., 2007). When both factors were acting together, canopy P_s and R_d were not significantly different from those in current ambient conditions.

Tree and forest responses to elevated [CO_2] will interact with water availability. Plant water-use efficiency (WUE) is expected to increase under elevated CO_2 (Table 1) due to reduced stomatal conductance (g_s), increased carbon assimilation (P_s), or both (Drake et al., 1997). However, WUE is usually assessed at the leaf level (instantaneous WUE defined either as P_s/transpiration or P_s/g_s), and individual-leaf measures may not be indicative of whole-plant or canopy responses (Wullschleger et al., 2002a). Unfortunately, the more appropriate integrated measure of WUE – the "biomass water ratio" (biomass production/transpiration) (Morison et al., 2008) – is rarely reported in trees, making it difficult to evaluate the importance of WUE for plant water status during drought (Wullschleger et al., 2002b). Also, few studies have investigated how plant water-use under elevated [CO_2] affects the soil water content in forests. Compared to ambient [CO_2], there may be no change in soil water content (Ellsworth, 1999), or significant water savings in the top soil horizons (Hungate et al., 2002; Leuzinger and Körner, 2007), except after a long drought (Leuzinger et al., 2005). Thus, trees growing under elevated [CO_2] may conserve soil moisture and prolong active growth during mild water stress, as long as the water is not used by other plants or evaporated from the surface. However, these positive effects on water retention may be unrealized if drought intensity increases in the future (Heath, 1998; Wullschleger et al., 2002a).

Although elevated [CO_2] may increase WUE (particularly at the leaf level), there may be no associated increase in drought hardiness (tolerance or resistance) or tree growth under water stress (Guehl et al., 1994; Dixon et al., 1995; Tschaplinski et al., 1995; Beerling et al., 1996; Saxe et al., 1998). During the eight-year experiment in the Duke Forest FACE, basal area increment (BAI) was greater in the elevated [CO_2] treatment than in the control, and the relative stimulation of BAI was greatest during a severe drought (Moore et al., 2006). Nonetheless, the BAI in both treatments was lower in this drought year than in any other year. In other seedling experiments, leaf-level WUE was greater under elevated [CO_2], but biomass accumulation during drought was either lower or not different from trees growing under well-watered ambient [CO_2] conditions (Guehl et al., 1994; Tschaplinski et al., 1995; Anderson and Tomlinson, 1998). Thus, elevated [CO_2] may ameliorate but not eliminate the adverse effects of drought (Table 1). Much more research is needed to understand how elevated [CO_2] interacts with droughts and other stresses to affect tree and stand growth.

Nutrient availability, particularly nitrogen (N), may determine whether forests benefit from elevated [CO_2] because there may be little response on nutrient-poor sites (Table 1; Curtis and Wang, 1998; Oren et al., 2001; McCarthy et al., 2010). Furthermore, increases in C assimilation may increase the demand for N to support additional plant growth, and increase the sequestration of C and N into long-lived pools (e.g., plant biomass and soil organic matter). This may lead to a subsequent decline in growth due to "progressive nitrogen limitation" (Luo et al., 2004). Although NPP (net primary production) increased under elevated [CO_2] at four forest FACE sites (Norby et al., 2005; Finzi et al., 2006; Moore et al., 2006; McCarthy et al., 2010), these responses may be transient and limited by the availability of N and other resources (McCarthy et al., 2010; Norby et al., 2010). Even at the N-limited FACE sites, however, the typical response was an increase in N uptake, not an increase in nitrogen-use efficiency, and this contrasts with most biogeochemi-

cal models (Finzi et al., 2007). Nonetheless, responses of NW species and forests may differ because N deposition rates are mostly lower in the NW than in the eastern US (Fenn et al., 1998, 2003; Sparks et al., 2008) where the forest FACE sites are located. The long-term consequences of interactions between elevated [CO_2], increased NPP, N uptake, and N availability need further study (Hyvonen et al., 2007; McCarthy et al., 2010).

Increased nutrient demands should be partly alleviated by faster decomposition of organic matter and greater mineralization rates in warmer climates (Rustad et al., 2001). Because elevated [CO_2] should stimulate microbial activity and increase total biomass (i.e., because of increased inputs of soil carbon), much of the mineralized N may be immobilized by microbes and not available for trees (Saxe et al., 2001). This prediction, however, has not been supported by experimental results (Zak et al., 2003). Changes to litter chemical composition under elevated [CO_2] may affect decomposition rates and the release of nutrients (Olszyk et al., 2003; Körner et al., 2005, but see Finzi et al., 2001). The interaction between temperature and soil moisture will also be important because decomposition and mineralization rates are slower in both dry and saturated soils (Prescott, 2005). An increased demand for nitrogen may be partly alleviated by N deposition (Fenn et al., 1998; Pregitzer et al., 2008).

Elevated [CO_2] may increase the amount of carbon allocated to reproduction (Jablonski et al., 2002). Under elevated [CO_2], *P. taeda* trees matured earlier, flowered in greater numbers, and produced more pollen, cones, and seeds in the Duke FACE experiment (LaDeau and Clark, 2001, 2006a,b). Seeds produced in elevated [CO_2] were heavier, had greater lipid contents, germinated faster, and germinated at a higher percentage than those developed under ambient [CO_2]. Although the resulting seedlings had longer roots and more needles, total biomass was unaffected (Hussain et al., 2001). Similar results were observed for *Betula papyrifera* in another FACE study (Darbah et al., 2007). These findings suggest that elevated [CO_2] could reduce the time to flowering, increase seed production, and improve seed quality, leading to improved seedling emergence (Table 1). Recruitment rates, however, may respond differently. Mohan et al. (2007) examined below-canopy survivorship of early- and late-successional species in the Duke Forest FACE experiment. Overall, seedling survivorship was slightly higher in elevated [CO_2], but species differences were large, and mostly associated with shade tolerance and previous year's growth (Mohan et al., 2007). Interactions between elevated [CO_2], temperature and water availability have been shown to affect seedling emergence and establishment in three early-successional tree species in an old-field (Classen et al., 2010). Soil moisture was the best predictor of seedling establishment, but the magnitude of the effect varied according to species seed phenology (Classen et al., 2010). Consequently, interactions with other stresses and disturbances will probably affect regeneration success, and ultimately forest composition and structure, more than will the direct effects of elevated [CO_2] (see Section 5.5).

Elevated [CO_2] will probably favor some plants over others. For example, it should provide more growth benefits to C_3 compared to C_4 plants. Although C assimilation in C_3 plants may saturate at high CO_2 concentrations (above 450 ppm), saturation of P_s is not straightforward, because high CO_2-grown plants may exhibit higher CO_2-saturation points (Sage et al., 1989). Among C_3 plants, however, responses to elevated [CO_2] vary widely among studies, genera, species, and genotypes (Tolley and Strain, 1984; Rogers et al., 1994; Houpis et al., 1999; Anderson et al., 2003; Ainsworth and Long, 2005). In forest trees, there have been relatively few studies of within-species variation in responses to elevated [CO_2]. Of western North American species, intra-specific variation has been evaluated in *P. ponderosa*, but these studies involved relatively few families (≤ 20), provenances (3–7) or distinct ecotypes (2) (Surano et al., 1986; Houpis et al., 1988, 1999; Callaway et al.,

1994; Delucia et al., 1994; Pushnik et al., 1995, 1999; Anderson et al., 2003). For example, seedlings of *P. ponderosa* from the Sierra Nevada increased their height and volume growth in elevated [CO_2] more than did seedlings from the Rocky Mountains (Surano et al., 1986; Houpis et al., 1988). In another study, half-sib seedlings originating from three native maternal sources varied in stem growth responses to increasing [CO_2], but displayed similar physiological responses – increased photosynthetic rate, decreased pigmentation and decreased light-use efficiency (Anderson et al., 2003). Unlike responses to temperature and moisture (discussed below), responses to [CO_2] are unlikely to vary substantially among populations (i.e., because of within-species genetic variation). This is because among-population genetic variation is strongest when there are large differences in environmental conditions among locations, and when adaptations in some environments, are disadvantageous in others (i.e., tradeoffs exist; Howe et al., 2003), which is not the case for [CO_2].

To summarize, increases in atmospheric [CO_2] should be somewhat favorable for trees and forests, resulting in increased growth, vigor, regeneration, and survival. However, increases in [CO_2] will not occur in isolation, but are expected to occur in combination with warmer temperatures and increased drought stress. Elevated [CO_2] enhances WUE at the leaf level, but this is unlikely to translate into large increases at the tree or stand levels, or substantially increase drought hardiness. Consequently, the adverse effects of these other climatic changes will probably be much larger than the positive effects of higher [CO_2]. Therefore, rather than focusing on the direct effects of CO_2 alone, it is important to understand whether elevated [CO_2] will mitigate the adverse effects of other climatic stressors. Unfortunately, we have only limited information on these interactions, and how they might differ by developmental stage or among species or functional groups. Ultimately, these interactions must be realistically integrated into physiological process models to confidently predict ecosystem responses to climate change.

5.2. Elevated temperatures

Temperature affects forest ecosystems at scales ranging from the chemistry of fundamental physiological processes to plant development to biogeochemical cycles. Recent warming has already resulted in earlier flowering and vegetative bud burst in forest trees (Badeck et al., 2004; Menzel et al., 2006; Parmesan, 2007; Körner and Basler, 2010). These trends are expected to continue in both the NW and elsewhere, at least for moderate increases in temperature. Genetic differences in the timing of bud burst, bud set, and flowering indicate that species and populations are generally adapted to their local temperature environments (Howe et al., 2003). Thus, elevated temperatures will directly affect adaptability of trees and forests via effects on plant phenology and growth, and indirectly through interactions with other stressors and disturbances that will affect species distributions, forest composition, and forest structure.

Warmer temperatures tend to enhance plant biochemical and physiological processes as long as optimum temperatures are not exceeded and moisture is adequate. In the short term, moderate warming tends to increase rates of P_s and R_d (Saxe et al., 2001), but these rates may decline after prolonged exposure to elevated temperatures (Tjoelker et al., 1998, 1999; Teskey and Will, 1999; Gunderson et al., 2000; Atkin and Tjoelker, 2003; Way and Sage, 2008). This acclimation suggests that long-term C fluxes in response to warming will differ from those predicted from the instantaneous, short-term responses. Because warming stimulates photorespiration in C_3 plants, net C gain may be lower in the future. However, higher CO_2 concentrations may counteract the increase in photorespiration (Long, 1991; Drake et al., 1997, see Section 5.1).

In addition to the effects on biochemical and physiological processes, warming may result in more frequent and severe heat events (IPCC, 2007) that expose trees to temperatures above their threshold for heat injury (Table 1). High temperatures may directly damage cell membranes and disrupt structure and function of proteins, leading to a number of harmful metabolic changes (Levitt, 1980; Nilsen and Orcutt, 1996). Exposure to high temperatures at the soil surface often results in cambial girdling in open-grown seedlings (Helgerson, 1990), but exposure to heat in excess of 40 °C may lead to other injuries and mortality (Seymour et al., 1983; Seidel, 1986). Abnormalities in bud development were observed when *P. menziesii* seedlings were exposed to temperatures exceeding 40 °C (Apple et al., 1998). Although this was reversible, it was associated with irregularities in bud burst, probably resulting from heat shock or insufficient chilling (Apple et al., 1998). Increased transpiration reduces leaf temperatures, but may also lead to increased drought injury associated with warming (Table 1; Levitt, 1980); on the other hand, stomatal closure reduces transpiration but also increases leaf temperatures, which may increase respiration or damage foliage.

The consequences of warming must be evaluated based on limitations at specific sites. For example, growth limitations for *Tsuga mertensiana* at high elevations in the NW arise from short growing seasons associated with low temperatures and long durations of snow cover; and at warmer locations in southern Oregon, from high summer temperatures and low water availability (Peterson and Peterson, 2001). Similar degrees of spring and summer warming would have distinctly different consequences for trees in these two settings. In areas with adequate moisture, slight warming will probably increase growth by extending the duration of temperatures favorable for growth. However, where moisture is limited, warming will probably cause growth to cease earlier in the season, and increase evaporative demand, thus exacerbating the negative effects of drought stress (reviewed in Allen et al., 2010, see also Section 5.4). Based on long-term provenance tests, the growth of *P. contorta* is expected to increase if temperatures increase about 1.5 °C, then decline thereafter (Wang et al., 2006). These initial increases in growth probably result from the positive effects of moderately warmer temperatures in the cold-limited environments inhabited by this species.

Climatic warming may affect the timing and success of seed germination and, thus, regeneration success in naturally regenerated forests (Table 1). NW forest trees have a wide range of seed dormancy – from none to complex (Farmer, 1997; Finch-Savage and Leubner-Metzger, 2006; Bonner and Karrfalt, 2008). As long as future climates continue to satisfy seed chilling (stratification) requirements for species with some level of physiological seed dormancy, warmer spring temperatures may be favorable for seed germination and recruitment. Warmer fall temperatures may affect germination of non-dormant seeds. In *T. plicata*, for example, warmer conditions may cause fresh seed to germinate in the fall (Burns and Honkala, 1990; C.A. Harrington, unpublished results), thereby increasing winter mortality. In oaks, warm and dry falls may reduce germination because of desiccation and mortality of acorns. In general, we have insufficient information on the long-term consequences of climatic warming for all phases of plant regeneration – from flower bud differentiation through pollen shed, fertilization, seed development, seed dispersal, dormancy release, germination, and early seedling growth. The processes beyond seed germination will likely determine regeneration success in future climates.

Winter dormancy is an important adaptive strategy because it prevents trees from flushing during short warm periods in the winter. Dormancy induction and release may limit the ability of trees to take advantage of longer periods of favorable temperatures in the future. Temperature plays a dual role in the release of dormancy

(Linkosalo et al., 2006). Cold temperatures slightly above freezing help satisfy chilling requirements for rest completion. Once critical chilling requirements are met, warm temperatures then accelerate bud burst. Based on studies of these processes, scientists have developed quantitative models to predict the timing of flowering and vegetative bud burst under different winter and spring temperature regimes (Chuine, 2000; Saxe et al., 2001; Linkosalo et al., 2006; Hänninen and Kramer, 2007; Harrington et al., 2010). These models will be important components of process-based growth and species distribution models (Chuine, 2010).

Phenological responses to climate change will depend on the amount and timing of warming and its impact on the ability of species and populations to meet their chilling and flushing requirements (Morin et al., 2009). Many observations (Menzel et al., 2006; Linkosalo et al., 2009) and modeling studies (Hänninen, 1991; Linkosalo et al., 2000) indicate that bud burst will advance with moderate warming, given that chilling requirements have been satisfied. Warming of about 2–3 °C is expected to hasten bud break in *P. menziesii*, but with greater warming, bud burst may be delayed because of insufficient chilling (Guak et al., 1998; Harrington et al., 2010). With more substantial warming (>3 °C), chilling may be insufficient in other species as well, resulting in delayed bud burst and poor growth (Worrall, 1983; Cannell and Smith, 1986; Murray et al., 1989; Morin et al., 2009). For example, species from mild maritime climates often have higher chilling requirements (Cannell and Smith, 1983; Hannerz et al., 2003) that may not be met under substantial warming. Populations within species also differ in their chilling requirements (Campbell and Sugano, 1979; Leinonen, 1996; Hannerz et al., 2003). In some species, warmer temperatures during dormancy induction in the fall may also increase chilling requirements and delay bud burst in the spring (Heide, 2003; Junttila et al., 2003; Søgaard et al., 2008). Thus, dormancy release and bud burst may be unaffected, occur earlier, or occur later in future climates, depending on the chilling requirement of the species and population, as well as the degree and timing of warming (Table 1). Interactive influences of temperature and [CO$_2$] on phenology may be minor with warming being the dominant driver (Murray et al., 1994; Repo et al., 1996; Ceulemans, 1997; Guak et al., 1998; Olszyk et al., 1998a; Norby et al., 2003a; Slaney et al., 2007).

Paradoxically, warming may lead to increased spring frost damage if increased temperatures hasten dehardening. Large-scale frost damage to vegetation in the eastern U.S. and northeastern Ontario in the spring of 2007 illustrates the possible consequences (Gu et al., 2008; Man et al., 2009). However, it is difficult to judge the future risk of frost damage because of uncertainty in projecting the timing of spring frosts and in the phenological responses to complex patterns of warming (Hänninen, 1991, 2006; Murray et al., 1994; Kramer et al., 1996, 2000; Linkosalo et al., 2000; Hänninen et al., 2001; Jönsson et al., 2004). If moderate warming occurs without an increase in temperature variability, the probability of frost events may stay the same or decrease (Table 1); however, if frost occurs, the consequences may be more severe, at least for tree populations adapted to current climates.

Climatic warming will probably delay bud set and growth cessation in the fall (Table 1), but the effect may be small because the duration of seasonal growth is constrained by photoperiodic and endogenous controls (Hänninen and Kramer, 2007), as well as seasonal moisture deficits (Aitken et al., 2008). Low night temperatures hasten bud set (Junttila, 1980; Downs and Bevington, 1981), and in some very northern clones of *Populus*, bud set can be induced using low temperatures alone (i.e., under a 24-h photoperiod; G.T. Howe, pers. observation). Thus, in the absence of low temperature cues, growth cessation may be delayed. Bud set and growth cessation are also associated with temperature sums during the growing season, but because temperature sums and developmental stages are confounded, this may actually result from developmental differences in sensitivity to photoperiod (Partanen, 2004). Although low, near-freezing temperatures are important for inducing cold acclimation (Levitt, 1980), a delay in cold acclimation due to climatic warming should not have a major adverse effect as long as damaging fall frosts are delayed as well (Table 1). Thus, climatic warming is expected to lengthen the duration of favorable growing temperatures, but trees may not be able to begin growing earlier in the spring (e.g., if chilling requirements are unmet) or grow later into the fall (e.g., if growth is constrained by photoperiod, drought, or endogenous controls). For species and populations with good experimental data, we can examine the consequences of alternative climate change scenarios using phenological process models, but for other species, it is difficult to predict the magnitude, or even direction, of change in the duration of seasonal growth in the long-term (Table 1).

The effects of climate change will be influenced by genetic variation in growth phenology among populations. Genetic differences in phenology may result from variation in chilling requirements (Perry and Wu, 1960; Hannerz et al., 2003; Junttila et al., 2003), flushing requirements (Beuker, 1994), or both (Campbell and Sugano, 1979). Genetic differences in growth phenology and cold hardiness, which reflect local adaptations to cold temperatures, have been found in many NW species, including *Alnus rubra* (Cannell et al., 1987), *P. menziesii* (Campbell and Sorensen, 1973; Rehfeldt, 1978; St.Clair et al., 2005), *P. contorta* (Rehfeldt, 1988), *P. ponderosa* (Rehfeldt, 1986a,b), *Picea sitchensis* (Cannell et al., 1985), *T. heterophylla* (Kuser and Ching, 1980), and *Larix occidentalis* (Rehfeldt, 1982), but less so in *Pinus monticola* (Rehfeldt, 1979; Rehfeldt et al., 1984; Chuine et al., 2006). In addition to differentiation among populations, there is substantial genetic variation among trees within populations (cf. Campbell, 1979; Rehfeldt, 1983), indicating some potential for *in situ* evolution.

Future species distributions and forest compositions will reflect new competitive relationships among species that result from the different ways species respond to warming. For example, some treelines have advanced during the 20th century (Parmesan and Yohe, 2003; Harsch et al., 2009), and the optimum locations for some species have moved to higher elevations (Lenoir et al., 2008). Plant migration rates, population structures, and forest health will depend partly on the direct effects of warming on flowering, seed production, dispersal, germination, recruitment, and competitive interactions. However, the indirect effect of warming on water balance and drought stress will probably have greater consequences for many forest ecosystems (Adams et al., 2009; Allen et al., 2010; see Section 5.4). A better evaluation of the simultaneous effects of warming, elevated [CO$_2$] and drought on plant physiology and ecosystem processes is needed.

5.3. Precipitation

Although projections of future precipitation are less certain than those for temperature, projected decreases in snowpack, earlier snowmelt, and increases in the frequency of heavy precipitation events, may increase the frequency of flood-related injuries (Table 1; Hamlet and Lettenmaier, 2007). Flooding causes physical damage to plants and soils through mechanical stresses, soil erosion and sediment deposition. Inundation also affects soil structure, depletes soil oxygen, and causes physiological injuries that often lead to growth reductions and plant mortality (Dreyer et al., 1991; Gardiner and Hodges, 1996; Pezeshki et al., 1996; Kozlowski, 1997; Jackson, 2002; Kreuzwieser et al., 2002, 2004). The consequences of flooding, however, will depend on the timing and duration of the flood, and the quality of water (Glenz et al., 2006). During active tree growth, flooding may cause both physiological and physical damage (Table 1), but during the dormant season, it may have lit-

tle effect on tree physiology (Kozlowski, 1997). Future flooding risks in the NW will be associated primarily with the effects of warmer midwinter temperatures on watershed hydrology (Hamlet and Lettenmaier, 2007). Within watersheds, however, the impacts will be mostly localized toward the flood-prone sites (e.g., riparian forests), poorly drained soils susceptible to waterlogging, and slopes susceptible to debris flow (i.e., landslides or mudslides) (Table 1). At a broader scale, projected increases in the frequency and severity of droughts will probably have greater consequences for forests.

5.4. Drought

Droughts adversely affect multiple processes in trees and forests, including gas exchange, C allocation, growth, survival, and regeneration (cf. Fritts, 1966; Hsiao et al., 1976; Hinckley et al., 1979; Lawlor and Cornic, 2002; Ciais et al., 2005; Breda et al., 2006; Flexas et al., 2006; Rennenberg et al., 2006; McDowell et al., 2008). Adaptations to drought are evident from the changes in species composition and drought hardiness that occur along moisture gradients in the NW (Franklin and Dyrness, 1988). Droughts affect trees directly and predispose forests to damage by insects, diseases and wildfires, potentially leading to shifts in species distributions and large-scale changes in forest community composition and structure (e.g. McDowell et al., 2008; Breshears et al., 2009). Projected increases in temperatures may exacerbate future droughts (Adams et al., 2009; Allen et al., 2010).

Growth is more sensitive than many other plant processes to moisture stress (Boyer, 1970; Hsiao et al., 1976). Depending on the seasonality of drought, shoot growth and leaf area may be affected differently for species with seasonally determinate versus seasonally indeterminate shoot growth. Younger trees of many NW species are capable of free growth as long as environmental conditions are favorable (Cline and Harrington, 2007); therefore, height growth may be curtailed by mid- and late-season droughts in these species. Furthermore, if these droughts are broken while photoperiod is still permissive for growth, multiple flushing could become more common, with possible negative impacts on stem form and log quality. Late-season droughts may limit diameter growth, but have little effect on height growth and leaf area development in seasonally determinate species, because these processes are usually completed earlier in the growing season. However, in five deciduous tree species, severe late-season droughts had little impact on diameter growth (Hanson et al., 2001). Emerging seedlings are highly sensitive to drought during germination, and because shoot growth typically continues later into the growing season, late-season droughts may impact seedlings much more than they affect mature trees. In contrast, water stress increases with foliage height within a tree because of the effect of gravity on the water column that reduces turgor and likely limits cell division and expansion, and thus, growth (Woodruff et al., 2004, 2008). Droughts may also reduce leaf area by limiting the production or expansion of leaf primordia, or by causing premature shedding of leaves (Tyree et al., 1993; Breda et al., 2006). Although growth will be impacted (Table 1), it is difficult to predict which growth components will be most affected by droughts in future climates.

The effects of drought on tree growth and biomass allocation may affect tree competitive status. Tree growth may be limited because of reduced nutrient uptake under water stress. This limitation is a result of reduced root growth, greater root mortality, shrinkage of roots and soil, slower decomposition and mineralization, and restricted mass flow of nutrients in dry soil, and altered kinetics of nutrient uptake (Bloom et al., 1985; Gessler et al., 2004; Prescott, 2005). During low-severity drought, root growth may decrease relatively less than shoot growth, leading to an increase in the root:shoot ratio (Kramer and Boyer, 1995). This response is usually more pronounced in seedlings than in mature trees (Joslin et al., 2000), although it may be species-dependent (Leuschner et al., 2001).

In trees, dehydration avoidance is typically more common than dehydration tolerance (Pallardy, 1981; Oliver, 1996; Chaves et al., 2003). Therefore, traits that allow trees to withstand droughts by minimizing water loss or maximizing water uptake will be important in future, drought-prone climates. These adaptations must be balanced by the need to acquire CO_2. Water and carbon balance are tightly linked in trees, and both are affected by water stress. Transpirational water loss inevitably accompanies carbon assimilation. With increasing evaporative demand, stomatal aperture decreases, restricting water efflux, and preventing excessive dehydration. However, stomatal closure also limits CO_2 diffusion into the leaf and, thus, photosynthesis (Cornic, 2000; Yordanov et al., 2000; Chaves et al., 2002). Water stress may also decrease P_s via direct effects on the photosynthetic machinery (Tezara et al., 1999; Flexas et al., 2004), or indirectly through alterations of growth and sink capacity. In drought-stressed plants, respiration is usually less affected than P_s (Kramer and Boyer, 1995), leading to a net loss of C (Lawlor and Cornic, 2002; Flexas et al., 2006). However, much is unknown about the response of R_d to water stress (Rennenberg et al., 2006; Loreto and Centritto, 2008).

Stomata respond to a host of correlated environmental stimuli, including light, temperature, and vapor pressure deficit. Stomatal function is also affected by CO_2 (Jarvis and Davies, 1998; Jarvis et al., 1999), and the internal balance of nutrients (Kramer and Boyer, 1995) and growth regulators (Wilkinson and Davies, 2002; Dodd, 2003). Hormonal and hydraulic signals for stomatal closure seem to be integrated in nature (Tardieu and Davies, 1993; Comstock, 2002). Although regulation of stomatal function is complex, an integrated view of plant hydraulic architecture and stomatal response to drought is needed for greater insight into tree and forest adaptability to drought (Lovisolo et al., 2010).

Because hydraulic architecture governs the movement of water from roots to leaves (Tyree and Ewers, 1991; Cruiziat et al., 2002; McCulloh et al., 2010), it may provide insights into the potential of trees to adapt to future drier climates. For example, species native to xeric habitats tend to have greater xylem conductivity and resistance to embolism than those found in mesic habitats (Cochard, 1992; Pockman and Sperry, 2000; Maherali et al., 2004). Strongly negative xylem water potentials that develop during drought cause embolism and xylem dysfunction (Table 1; Sperry and Tyree, 1988, 1990) that may lead to plant hydraulic failure in extreme cases (Tyree and Sperry, 1988). Embolized conduits can refill and restore hydraulic conductance (Tyree et al., 1999; Holbrook et al., 2001), but more research is needed to elucidate the mechanisms of embolism repair (Zwieniecki and Holbrook, 2009) and to understand their contribution to drought resistance, particularly in tall trees (Meinzer et al., 2001). Consequently, mechanisms for preventing xylem embolism, such as stomatal regulation of transpiration and, thus, xylem water potential, are important components of drought hardiness (Jones and Sutherland, 1991; Cochard et al., 1996; Cruiziat et al., 2002).

In addition to drought avoidance mechanisms, some adaptations allow trees to tolerate droughts. Many trees exhibit osmotic adjustment – a trait that contributes to the maintenance of cell turgor and gradients of water potential necessary for the movement of water into and through the plant (Abrams, 1988; Kozlowski and Pallardy, 2002). However, in the foliage of NW conifers, osmotic adjustment seems to be passive and a result of foliage maturation (Teskey et al., 1984; Woodruff et al., 2004; Meinzer et al., 2008). Thus, osmotic adjustment operates most efficiently when droughts develop slowly (Gebre et al., 1994); during a rapid drought, adjustments in cell elasticity may be more effective than osmotic adjustments for maintaining turgor (Saito and Terashima,

2004; Lambers et al., 2008). Maintenance of turgor will be an important component of stress resistance because turgor affects oleoresin pressure and therefore the ability of trees to respond to insect and pathogen attacks.

Biochemical changes in response to water stress include the regulation of specific proteins. Dehydrins (Close, 1996; Yordanov et al., 2000; Allagulova et al., 2003), heat shock proteins (Schoffl et al., 1998; Wang et al., 2003), and aquaporins (Bohnert et al., 1995; Alexandersson et al., 2005; Luu and Maurel, 2005; Maurel et al., 2008) are up-regulated in response to drought. Aquaporins facilitate movement of water and solutes across membranes and are involved in water uptake in roots, cell elongation, short-distance water transport, and stomatal movement (Kaldenhoff et al., 2008; Maurel et al., 2008). Other compounds may be involved in stabilizing enzyme complexes and membrane structures to facilitate recovery of cellular function after dehydration (Hoekstra et al., 2001; Allagulova et al., 2003). Research is needed to better understand the regulation and function of these compounds, regulatory variation among and within species, and whether patterns of gene expression or markers in associated genes provide useful indicators of relative drought hardiness.

Drought, in combination with warming and other mortality agents, may be responsible for recent increases in tree mortality in the western U.S., Canada, and around the globe (Hogg et al., 2008; Worrall et al., 2008; van Mantgem et al., 2009; Allen et al., 2010). Drought-related mortality in trees has been alternatively attributed to either carbon starvation or hydraulic failure (Martínez-Vilalta et al., 2002; McDowell et al., 2008). Decreased stomatal conductance during long-term droughts, especially droughts associated with warming, may result in depleted carbon reserves (McDowell et al., 2008; Adams et al., 2009), although the carbon starvation hypothesis has been disputed (Leuzinger et al., 2009; Sala, 2009; Sala et al., 2010). On the other hand, if trees maintain high stomatal conductance during drought, transpiration rates may exceed the cavitation threshold, leading to "runaway embolism" and hydraulic failure (Tyree and Sperry, 1988). Thus, inherent stomatal behavior may predispose a species to damage or death from carbon starvation or hydraulic failure (Table 1; McDowell et al., 2008). Species differences in mortality in the semiarid forests of the southwestern U.S. appear to result from these different mechanisms and their interactions with biotic agents operating at the ecosystem scale (Allen and Breshears, 1998; Breshears et al., 2005; Mueller et al., 2005; McDowell et al., 2008; Adams et al., 2009). In particular, massive mortality of *Pinus edulis* and only limited mortality of co-occurring *Juniperus monosperma* was observed after an unusually warm drought in 2000–2003, called a "global change-type drought" (Breshears et al., 2005, 2009; McDowell et al., 2008). Although the specific cause of regional mortality of *P. edulis* was a bark beetle infestation (Breshears et al., 2005), this illustrates the impact of interactions among multiple stressors on tree vigor and survival, and potential future trends (Table 1; Allen et al., 2010).

Water stress may promote or inhibit flowering, depending on the tree's physiological status as well as the timing, duration, and severity of stress. For example, dry summers often precede the production of abundant seed crops in late-successional masting species (Piovesan and Adams, 2001; Selas et al., 2002; Koenig and Knops, 2005). Water stress or root pruning has been widely used to induce flowering in temperate conifers (Dewers and Moehring, 1970; Ross et al., 1985; Pharis et al., 1987, but see Ross, 1991; Dohrenbusch et al., 2002). However, it is uncertain how the directional change in climate and water availability will affect flowering and other reproductive processes in the longer term. It is likely that drought-related regeneration failures will increase in future climates because of increased seedling mortality (Table 1). However, many unknowns remain in relation to climate change effects on forest regeneration. Will more frequent droughts induce trees to flower more

often or more abundantly? Will seed development be affected? Will trees experience additional stress as more resources are allocated to reproduction as compared to growth and defense (Bloom et al., 1985; Obeso, 2002)? How will future recruitment rates be affected by altered water regimes, especially water deficits interacting with other disturbances such as wildfires and insect outbreaks? These are important but unanswered questions for naturally regenerated and planted forests.

In addition to drought acclimation (phenotypic plasticity), evolutionary adaptation to drought is evident from the genetic differences in drought hardiness that have been found among species, varieties, and populations (Pallardy, 1981; Abrams, 1990, 1994; Martinez-Vilalta et al., 2004). In the NW, differences in drought hardiness were found between the coastal and Rocky Mountain varieties of *P. menziesii* (Ferrell and Woodard, 1966; Pharis and Ferrell, 1966), reflecting adaptations to broad-scale environmental differences. However, large genetic differences also exist among seed sources. Population variation in drought hardiness traits was associated with environmental gradients in *P. menziesii* (Pharis and Ferrell, 1966; Heiner and Lavender, 1972; White, 1987; Joly et al., 1989; Aitken et al., 1995; Kavanagh et al., 1999) and *P. contorta* (Dykstra, 1974), but less so in *P. ponderosa* (Rehfeldt, 1986b; Zhang and Marshall, 1995; Maherali et al., 2002). There is also some evidence for fine-scale genetic variation in drought resistance that is associated with local environmental differences such as aspect (Ferrell and Woodard, 1966; Campbell, 1979), and genetic variation among trees within populations is readily observed (Feret, 1982; Anekonda et al., 2002; Dalla-Salda et al., 2009, but see White, 1987). The existence of population-level genetic variation and adaptation to local moisture regimes indicates that phenotypic plasticity is insufficient to achieve optimal adaptation across the species range (Morgenstern, 1996; St.Clair and Howe, 2007). Thus, the climatic tolerances of populations, not species, must be considered in process-based modeling approaches designed to understand future species distributions and spatial patterns of forest health and productivity. Furthermore, genetic variation in drought hardiness can be exploited by practicing population-level assisted migration to increase forest adaptability to future climates.

Although drought stress is common in many NW forest ecosystems (Franklin and Dyrness, 1988; Littell et al., 2008), warming will probably increase the frequency, duration, and severity of droughts in the future (Allen et al., 2010), adversely affecting forest growth, survival, and reproduction in many areas. Forest responses will vary because drought tolerance differs by species, population, life stage, and stand structure. Drought-influenced competitive interactions and mortality will change the composition and structure of NW forest ecosystems.

5.5. Changes in natural forest disturbance

Climate change will likely affect forest communities via changes in wildfires, insects and disease. Although climate-induced changes in forest disturbance may be viewed as negative, disturbances also provide opportunities for generation turnover and migration, which should help counteract the increases in genetic maladaptation expected from climate change (St.Clair and Howe, 2007).

5.5.1. Wildfire

Fire regimes in the NW are strongly related to climate (Hessl et al., 2004; Gedalof et al., 2005; Heyerdahl et al., 2008; Taylor et al., 2008; Littell et al., 2009), and before fire suppression, varied widely across the region (Agee, 1993). In arid and semiarid forests such as *P. ponderosa*, frequent low-severity fires resulted in understory mortality, but limited overstory mortality prior to 1900. High-severity fire regimes with infrequent stand-replacing crown fires were typical of subalpine and lower elevation forests with

high precipitation and high biomass (Agee, 1993; McKenzie et al., 2004). Examples of these forest types include coastal *Abies amabilis* and *T. heterophylla*. Mixed-severity fire regimes with widely varying return intervals and elements of surface fires, torching, and crown fires (Lentile et al., 2005) were common in montane forests with intermediate precipitation and moderate fuel accumulations (McKenzie et al., 2004). Mixed-severity regimes occurred in portions of the *P. menziesii* and interior mixed conifer forest types (Morrison and Swanson, 1990; Hessburg et al., 2007).

Fire suppression in the 20th century resulted in less frequent wildfires, increases in stand density, greater fuel quantities, and greater fuel continuity. This has increased the potential for crown fires in forests that historically experienced low-severity fire regimes (Agee, 1998; Peterson et al., 2005) and in some forests that experienced mixed-severity regimes (Taylor and Skinner, 2003). Because of their spatial and temporal variability, however, the effects of fire suppression are unclear in mixed-severity fire regimes. NW forests with high-severity fire regimes and long fire return intervals have not been substantially affected by fire suppression (Keane et al., 2008).

High temperatures and current-year drought are strongly associated with an increase in the number of fires and area burned in a variety of NW forest types (Hessl et al., 2004; Wright and Agee, 2004; Heyerdahl et al., 2008; Taylor et al., 2008). Modern (1970–2003) forest fire records in the western U.S. show that wildfire activity increased substantially in the mid-1980s, including greater numbers of large wildfires, longer fire durations, and longer wildfire seasons. These changes have been associated with warmer temperatures in the spring and summer, which cause earlier snowmelt and lower the moisture contents of soils and fuels (Wotton and Flannigan, 1993; Westerling et al., 2006). Similarly, the annual area burned by western wildfires in the 20th century was greater in years with low precipitation, high drought severity, and high temperatures (Littell et al., 2009). Thus, although fire suppression and other forest management activities can influence fuel and fire regimes, the strong relationships between spring and summer temperatures, drought, wildfire activity, and area burned indicate that climate strongly influences wildfire activity in the western U.S. Consequently, wildfires are expected to increase if climates become warmer and drier in the future, with longer fire seasons and increases in the frequency, extent, and severity of wildfires (Price and Rind, 1994; Gillett et al., 2004; Westerling et al., 2006). For a mean temperature increase of 2 °C, the annual area burned by wildfires is expected to increase by a factor of 1.4–5 for most western states (McKenzie et al., 2004), ultimately leading to greater damage, growth reductions, and mortality in forest ecosystems (Table 1).

Trees have adapted to fire in many ways. Mature trees may resist fire with thick bark or self-pruning, whereas other adaptations allow individuals and populations to persist after fires or other disturbances. These include resprouting, fire-induced flowering, storage of seeds in the soil or canopy (e.g., serotinous cones), and the ability to disperse seeds over long distances (Agee, 1993; Schwilk and Ackerly, 2001; Pausas et al., 2004; Fernandes et al., 2008). Fire regimes exert differential selection pressures on tree populations and cause diverse expression of fire-related traits. In several pine species, for example, variation in the frequency of cone serotiny has been related to fire severity and frequency (Ledig and Fryer, 1972; Muir and Lotan, 1985; Gauthier et al., 1996; Tapias et al., 2004). Therefore, new fire regimes may favor species and populations that resist fires or successfully invade sites after fire (Rowe, 1983; Agee, 1993). The abundance of species that can resprout (fire endurers) or survive in the seed bank (fire evaders) may also increase, although frequent high-severity fires may kill roots and stored seeds (Zedler et al., 1983), limiting the future success of these groups.

Stands of fire-susceptible species, such as *T. heterophylla*, *Abies lasiocarpa*, and *Picea engelmannii*, tend to have higher mortality for a given fire intensity than stands composed of more fire-resistant species, such as mature *P. ponderosa, P. menziesii* and *L. occidentalis*. If fire-susceptible species are not able to re-seed or re-establish themselves into burned areas because of harsh conditions for seedling establishment or competition from other species, these species may be lost from the site. Therefore, increased fire frequency will likely favor more fire-adapted species via direct mortality and lack of regeneration of fire-susceptible species. In addition, expected changes in fire frequency and extent will likely create more opportunities for establishment of invasive species (Joyce et al., 2008).

Increased fire activity may be greater where fires have been limited by climatic conditions, rather than by fuels – that is, in forests with high to moderate precipitation and either high- or mixed-severity fire regimes. This may lead to profound changes in forest structure and composition of these systems (Table 1). However, in the arid and semiarid forests where fires were suppressed, increased fire activity may return these systems to historic conditions.

Large-scale disturbances also influence the spatial mosaic of forest patches and landscape structure (Table 1). Initially, new fire regimes will probably lead to larger burn patches, and greater homogenization of the landscape, particularly in areas characterized by low- and mixed-severity fire regimes. Although young forests with continuous fuels are particularly vulnerable to mortality, all successional stages are susceptible to high-severity fires. Thus, an increase in the frequency and severity of fires may increase the area of early seral forests, decrease the area of old forest patches, and decrease their connectivity (Baker, 1995; McKenzie et al., 2004). Large snags and downed wood may be lost, particularly in fire exclusion areas where crown fire hazards are high. Even if these stands are dominated by fire-adapted species, the greater amount and continuity of fuels will probably lead to greater mortality and likelihood of stand replacement if they burn. It may take several decades before the landscape adjusts to these new fire regimes (Baker, 1995). Eventually, greater fire frequency could lead to a reduction in fuels, resulting in lower intensity fires and a finer-scale patch mosaic.

5.5.2. Epidemics of insects and diseases

Climate and weather are key factors that contribute to epidemics of forest insects and pathogens. Climate change will affect these organisms by directly altering their physiology, development, and reproduction, and by altering the health and vigor of their hosts. Climate change will probably enhance abiotic stress in many areas, and plant stress often precedes pathogen and insect epidemics (Raffa and Berryman, 1983; Raffa et al., 2008; Kliejunas et al., 2009). The general importance of temperature and moisture as predictors of plant disease was emphasized in a recent review (De Wolf and Isard, 2007). Increased climatic stress and changes in the population dynamics of insects and disease has the potential to reduce tree and stand growth, increase damage and mortality, and change the composition and structure of some forest ecosystems (Table 1).

Bark beetles in the subfamily *Scolytidae* (*Coleoptera*: *Curculionidae*: *Scolytinae*), including *Dendroctonus*, *Ips*, and *Scolytus*, are the most important mass mortality agents of conifers in North America. Epidemics are associated with the availability of susceptible hosts, as well as conditions that lower tree vigor and affect beetle population growth (Raffa and Berryman, 1983; Shore et al., 2000; Taylor et al., 2006; Fettig et al., 2007; Raffa et al., 2008). Climate change seems to be partly responsible for epic levels of mountain pine beetle (MPB) (*Dendroctonus ponderosae*) activity and mortality of *P. contorta* across British Columbia and the western U.S. This outbreak, which is greater than any previous MPB epidemic (Kurz

et al., 2008), results from a combination of a large area of susceptible host (older, larger diameter trees resulting from fire suppression) with an expansion of climatically suitable habitat for MPB (Kurz et al., 2008). In areas that were previously unsuitable, warmer temperatures have increased the overwintering survival of MPB, and shortened its generation interval (Logan et al., 2003; Taylor et al., 2006). Although it has been suggested that substantial temperature increases (5 °C) may eventually decrease the area suitable for MPB outbreak (Hicke et al., 2006), it is likely that the western U.S. will experience climate changes favorable to MPB occurrence for a substantial period into the future. Warmer summer temperatures exacerbate drought stress and predispose the trees to insect attack (Breshears et al., 2005, 2009). Stressed, low-vigor trees usually produce fewer and less antagonistic defensive compounds, and are less able to pitch-out the beetles (Barbosa and Wagner, 1989). Inter-tree competition seems to intensify these conditions, and thinning has reduced bark beetle attack in some conifer stands, presumably by increasing the vigor of the residual trees (Mitchell et al., 1983; Waring and Pitman, 1983, 1985; Fettig et al., 2007). If climatic conditions predispose trees to attack and favor increased beetle populations, then individual tree mortality and stand damage is expected to increase in the future (Table 1).

Basidiomycete root decay pathogens (e.g., *Armillaria*, *Heterobasidion*, *Inonotus*, *Ganoderma*) are also important agents of tree damage and mortality (Gilbertson, 1980). Stress predisposes trees to attack from some of these pathogens, particularly *Armillaria* (Shaw and Kile, 1991). In western North America, *Armillaria solidipes* (*A. ostoyae*) is one of the most important root diseases of conifers (Morrison and Mallett, 1996). Habitat type and host vigor influence the fungus' ability to cause mortality. McDonald et al. (1987) found that the incidence of pathogenic *Armillaria* in the northern Rocky Mountains decreased with increasing productivity (site index), and increased with site disturbance (logging). In undisturbed habitats, pathogen activity was greatest in habitat transition zones (i.e., transitions from cold-dry to cold-moist, and from warm-dry to warm-moist habitats). In these transition zones, *P. menziesii* and *Abies grandis* were heavily damaged, possibly indicating that the trees were maladapted to these habitats and predisposed to attack (McDonald et al., 1987). Thus, climatic changes that increase stress will probably put trees at greater risk, particularly at the margins of suitable habitat types (Table 1). For example, the combination of fire suppression and climate change may lead to greater stand densities and shifts in species composition that will increase mortality from *Armillaria* (Kliejunas et al., 2009). Recent modeling suggests that the impact of *Armillaria* root disease on *P. menziesii* will increase because of climate change (Klopfenstein et al., 2009).

The occurrence of foliage disease fungi (Ascomycete microfungi) is closely tied to precipitation and temperature. These diseases cause defoliation, leading to growth reductions or tree mortality. Conditions that allow for quick build-up of fungal populations occur when precipitation extends into the spring and summer months, but tree stress is rarely a contributing factor in the development of these diseases. The current Dothistroma needle blight epidemic (caused by *Mycosphaerella pini*) on *P. contorta* in British Columbia has been tied to an increase in summer precipitation during the past 50 years (Woods et al., 2005). In *P. menziesii*, a Swiss needle cast epidemic (caused by *Phaeocryptopus gaeumannii*) is coincident with the mild climate of the Oregon coast. Warmer temperatures, consistently wet springs and summers, and the widespread planting of *P. menziesii* in the coastal hemlock zone are thought to be the primary causes of this epidemic (Rosso and Hansen, 2003; Manter et al., 2005; Black et al., 2010). Overall, changes in foliage diseases will depend heavily on changes in seasonal precipitation, which are still uncertain.

Genetic differences in pest resistance and tolerance exist among tree species and populations in the NW (cf. McDonald, 1979;

Temel et al., 2005; Sniezko, 2006; Yanchuk et al., 2008). For example, the Rocky Mountain variety of *P. menziesii* tends to be less tolerant of Rhabdocline needle cast (caused by *Rhabdocline pseudotsugae*) (Stephan, 1973) and Swiss needle cast disease (Hood, 1982; McDermott and Robinson, 1989) than the coastal variety. Therefore, forest health may decline if climate change causes insects and disease pests to migrate into new populations, leading to changes in landscape structure (Table 1).

Predicting how climate change will affect insect and disease outbreaks is fraught with complications. In the long-term, increases in forest stress suggest that pest problems will increase (Table 1), although impacts will vary. Bark beetles and some fungal diseases are expected to benefit from warmer and drier conditions (Coakley et al., 1999; Harrington et al., 2001; Garrett et al., 2006; Kliejunas et al., 2009); foliage diseases may increase with warmer and wetter conditions; and dwarf mistletoes will likely benefit from climate warming (Kliejunas et al., 2009). Projections are complicated by potential climatic influences on host–pest interactions (e.g., relationships between host resistance and pathogen virulence) (Swedjemark et al., 1999; Burdon, 2001; Sniezko, 2006; Kinloch et al., 2008). Not only are bark beetles, defoliating insects, dwarf mistletoes, and many fungal pathogens host-specific – they may even be specific to certain hosts only under specific environmental conditions. Therefore, knowledge of these interactions could be important for predicting future epidemics (Garrett et al., 2006). Furthermore, the changing dynamics of insect and disease pests, population variation, and interactions with climate should be considered when managers transfer species or seed sources into new habitats.

6. Management implications and research needs

Recent discussions of proactive strategies for helping forests adapt to climate change have outlined several common principles, including assessing risk, acknowledging uncertainty, making use of adaptive learning, and developing novel and flexible approaches that can deal with unforeseen problems (Ledig and Kitzmiller, 1992; Spittlehouse and Stewart, 2003; Ohlson et al., 2005; Spittlehouse, 2005; Millar et al., 2007). Risk, which reflects the probability of an event and its consequences, depends on the desired state of our forests, climate change threats, forest vulnerabilities, and the availability of adaptive management strategies. Above, we described the threats and opportunities expected from climate change, assuming that the current forest condition is close to society's goal. Chief concerns are projected increases in droughts, fires, pest outbreaks, and winter (chilling) temperatures. Long-term studies are needed to help elucidate how climate-related stressors (particularly drought, pests, and fire) will interact to influence forest responses to climate change. We expect that elevated [CO_2] will ameliorate these adverse effects to a small degree, but we need more research in this area. Climate change opportunities include increased growth in areas that are currently cold-limited, and CO_2 fertilization which may have net positive effects, or help ameliorate stresses resulting from climate change. In this section, we discuss forest vulnerabilities and adaptive strategies from a forest management perspective.

Vulnerability, which is the propensity of systems to suffer harm, depends on exposure, sensitivity, and adaptive capacity (Parry et al., 2007), each of which has important spatial and temporal components. Exposure varies across the landscape because current climates and projected climatic changes vary from place to place. Sensitivity varies because of site factors (abiotic and biotic), and genetic differences among species and populations. The capacity to employ adaptive management strategies also varies among land ownerships and management units. To effectively respond to cli-

mate change, land managers need spatially explicit assessments of forest vulnerability that provide combined, integrated assessments of all threats and opportunities. This information could be used to target areas for enhanced monitoring, gene conservation, silvicultural treatments to increase forest resistance or resilience, or priority harvest.

Vulnerability has temporal components because climate change will accumulate over time, and stages of forest development differ in vulnerability to climate change. Managers should seek to lessen vulnerabilities by paying attention to key stages of forest development, and by sustaining or enhancing traits that promote adaptability. Trees are most vulnerable during the regeneration phase (reviewed in van Mantgem et al., 2006; Nitschke and Innes, 2008). In forest trees, we know a great deal about the relationships between winter temperatures, vegetative bud phenology, and frost damage (Howe et al., 2003), but much less about how winter and spring temperatures affect reproductive bud phenology and reproduction. We need more research in this area because fitness may be more affected by climatic effects on reproduction than on vegetative growth. Mortality of seed and seedlings is especially high in naturally regenerated forests, but can be dramatically lessened by planting seedlings. Because of the high mortality of seed and seedlings in naturally regenerated forests, evolutionary adaptation to climate change will be strongest for traits expressed at these stages. Although field-based provenance tests indicate that the long-term effects of climate change will be negative (e.g., Wang et al., 2006), these tests are based on the growth responses on planted seedlings. Therefore, the effects of climate change on the fitness of naturally regenerated stands are probably underestimated, and provenance tests that assess climatic effects on the regeneration phase are sorely needed. Once trees become established, they are generally more resistant to climatic influences. For example, recently germinated seedlings are more susceptible to damage from heat, frost, damping-off fungi, and the drying of the soil surface (Hermann and Chicote, 1965), but may be less susceptible to certain pests (e.g., bark beetles) and competition for limiting resources. We need more research on climate-related stress thresholds that, when crossed, will prevent trees from acclimating, disturb ecosystem resilience, and increase vulnerability. The spatial and temporal variations in vulnerability should be considered when foresters consider the various silvicultural and genetic strategies that are available to help forests adapt to climate change (discussed below). However, the potential effects of climate change on reproduction, recruitment, competition, and succession are particularly unclear, as are the impacts on insects and pathogens.

Although we did not discuss the effects of other stressors that are likely to increase with climate change, this will be important to fully understand the long-term outcome at the ecosystem level. For example, pollutants such as tropospheric ozone and nitrogen deposition, and invasive species will almost certainly modify forest responses to climate change (Bytnerowicz et al., 2007; Hyvonen et al., 2007; Joyce et al., 2008). Because it is difficult to study the interactive and large-scale effects of multiple stressors, it is important to maintain and re-measure long-term research plots (Franklin et al., 1990) and continue integrating information from these sites with results from eddy-flux studies and remote sensing (Xiao et al., 2010). The development of improved forest process models is critical – models that ultimately describe the responses we discussed above (Aber et al., 2001; Hanson et al., 2005; Campbell et al., 2009). Many current models do not incorporate genetic variation in tree responses to changes in climatic and other environmental factors. It is important to continually integrate information from carefully designed physiological and genetic studies into these models to better predict the condition of our future forests.

Various genetic strategies could be used to help forests adapt to climate change, including assisted migration, traditional or molec-

ular breeding, and gene conservation. Existing trees may be able to resist, tolerate, or acclimate to modest changes in climate, but phenotypic plasticity will probably be insufficient in the long-term (Jump and Peñuelas, 2005). Genetic variation among populations can provide adaptability to the more extreme, long-term climatic changes. Knowledge of population-level variation in adaptive traits has been used to develop seed transfer guidelines designed to prevent the use of maladapted seed sources (cf. Campbell, 1974; Rehfeldt, 1987). More recently, field and nursery provenance tests have been used to assess the adaptability of species and populations to new climates (Matyas, 1994; Schmidtling, 1994; Rehfeldt et al., 2001; St.Clair and Howe, 2007). An understanding of among-population genetic variation should be used to guide management decisions at the species and within-species levels, including periodic reconfiguration of seed zones, breeding zones, or general seed transfer guidelines. We should be able to lessen the adverse effects of climate change using within-species assisted migration, which is the purposeful movement of species or populations to areas where they are expected to be better adapted in the future (McLachlan et al., 2007; O'Neill et al., 2008). Despite the promise of this approach, comprehensive studies of adaptive genetic variation are rare in non-commercial and non-threatened tree species, shrubs, and other plant groups.

In contrast to purely genetic approaches, other silvicultural approaches can be used to enhance forest growth and vigor, increase resistance and resilience, and sustain ecosystem services. As part of this strategy, managers should consider potential changes in the type, frequency, and extent of disturbance (Dale et al., 2001; Millar et al., 2007; Joyce et al., 2008, 2009; Peterson et al., in press; Littell et al., in review). Overall, density management should be the most effective approach because of its ability to lessen drought stress, fire risk, and predisposition to insects and disease. In addition to reducing the demand for water and nutrients, thinning can modify stand structures and species assemblages to reduce the risk of fires and insect infestations. Treatments should be applied carefully to avoid physical damage to remaining trees, soil compaction and fuel build-up. Prescribed fires can be used as a thinning tool, or to decrease surface fuels; and if treatments are sufficiently large and strategically arrayed, they can be used to modify disturbance at the landscape level. Furthermore, post-fire reforestation will provide many opportunities to alter species and within-species genetic composition.

7. Conclusions

The climate is expected to change throughout this century. In the NW, the direct positive effects of warmer temperatures and elevated $[CO_2]$ will be realized in only a limited set of environments that do not experience increased droughts, heat stress, or nutrient limitations. Warming-induced decreases in snowpack and increases in evapotranspiration are expected to increase the frequency and intensity of drought stress, with negative consequences for forest growth and health.

Areas that are moisture limited are particularly vulnerable. In the NW, this includes low-elevations in the northern Sierra Nevada, Klamath Mountains, Siskyou Mountains, Blue Mountains, Wallowa Mountains, Steens Mountain; Columbia Highlands, northern Rocky Mountains, and eastern foothills of the Cascade Range (Arno, 1979; Franklin and Dyrness, 1988; West and Young, 2000; Littell et al., 2008). In areas where limitations by soil moisture and temperature are low (e.g., much of the Coast Range, Olympic Mountains, and mid-elevations in the Cascade Range), future water availability is uncertain because it will depend on the net effects of rainfall, snowfall, snowmelt, surface runoff, subsurface flow, and evapotranspiration.

Any forest attribute or management practice that increases stress will also increase forest vulnerability to future climates. Vulnerable stands are those that are comprised of species or seed sources that are maladapted to future conditions, overstocked, or have high levels of competing vegetation. Based on the knowledge of expected impacts of climate change, foresters should employ genetic and silvicultural management options that target the most vulnerable sites, life stages, traits and processes to increase forest adaptability.

Role of the funding source

Acknowledgements

References

Aber, J., Neilson, R.P., McNulty, S., Lenihan, J.M., Bachelet, D., Drapek, R.J., 2001. Forest processes and global environmental change: predicting the effects of individual and multiple stressors. Bioscience 51, 735–751.

Abrams, M.D., 1988. Sources of variation in osmotic potentials with special reference to North American tree species. For. Sci. 34, 1030–1046.

Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiol. 7, 227–238.

Abrams, M.D., 1994. Genotypic and phenotypic variation as stress adaptations in temperate tree species: a review of several case studies. Tree Physiol. 14, 833–842.

Adam, J.C., Hamlet, A.F., Lettenmaier, D.P., 2009. Implications of global climate change for snowmelt hydrology in the twenty-first century. Hydrol. Process. 23, 962–972.

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. USA 106, 7063–7066.

Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC, USA.

Agee, J.K., 1998. The landscape ecology of western forest fire regimes. Northwest Sci. 72, 24–34.

Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol. 165, 351–371.

Ainsworth, E.A., Rogers, A., 2007. The response of photosynthesis and stomatal conductance to rising $[CO_2]$: mechanisms and environmental interactions. Plant Cell Environ. 30, 258–270.

Aitken, S.N., Kavanagh, K.L., Yoder, B.J., 1995. Genetic variation in seedling water-use efficiency as estimated by carbon isotope ratios and its relationship to sapling growth in Douglas-fir. For. Genet. 2, 199–206.

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111.

Alexandersson, E., Fraysse, L., Sjovall-Larsen, S., Gustavsson, S., Fellert, M., Karlsson, M., Johanson, U., Kjellbom, P., 2005. Whole gene family expression and drought stress regulation of aquaporins. Plant Mol. Biol. 59, 469–484.

Alig, R.J., Krankina, O., Yost, A., Kuzminykh, J., 2006. Forest carbon dynamics in the Pacific Northwest (USA) and the St. Petersburg region of Russia: comparisons and policy implications. Climatic Change 79, 335–360.

Allagulova, C.R., Gimalov, F.R., Shakirova, F.M., Vakhitov, V.A., 2003. The plant dehydrins: structure and putative functions. Biochem. Moscow 68, 945–951.

Allen, A.S., Andrews, J.A., Finzi, A.C., Matamala, R., Richter, D.D., Schlesinger, W.H., 2000. Effects of free-air CO2 enrichment (FACE) on belowground processes in a Pinus taeda forest. Ecol. Appl. 10, 437–448.

Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. USA 95, 14839–14842.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecol. Manag. 259, 660–684.

Anderson, P.D., Houpis, J.L.J., Anschel, D.J., Pushnik, J.C., 2003. Among- and within-provenance variability in *Pinus ponderosa* (Pinaceae) seedling response to long-term elevated CO_2 exposure. Madroño 48, 51–61.

Anderson, P.D., Tomlinson, P.T., 1998. Ontogeny affects response of northern red oak seedlings to elevated CO_2 and water stress – I. Carbon assimilation and biomass production. New Phytol. 140, 477–491.

Anekonda, T.S., Lomas, M.C., Adams, W.T., Kavanagh, K.L., Aitken, S.N., 2002. Genetic variation in drought hardiness of coastal Douglas-fir seedlings from British Columbia. Can. J. For. Res. 32, 1701–1716.

Apple, M.E., Lucash, M.S., Olszyk, D.M., Tingey, D.T., 1998. Morphogenesis of Douglas-fir buds is altered at elevated temperature but not at elevated CO_2. Environ. Exp. Bot. 40, 159–172.

Apple, M.E., Olszyk, D.M., Ormrod, D.P., Lewis, A., Southworth, D., Tingey, D.T., 2000. Morphology and stomatal function of Douglas fir needles exposed to climate chance: elevated CO_2 and temperature. Int. J. Plant Sci. 161, 127–132.

Arno, S.F., 1979. Forest Regions of Montana. USDA Forest Service Intermountain Forest and Range Experiment Station Research Paper INT-218, Ogden, UT, USA.

Asshoff, R., Zotz, G., Körner, C., 2006. Growth and phenology of mature temperate forest trees in elevated CO_2. Glob. Change Biol. 12, 848–861.

Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351.

Badeck, F.W., Bondeau, A., Bottcher, K., Doktor, D., Lucht, W., Schaber, J., Sitch, S., 2004. Responses of spring phenology to climate change. New Phytol. 162, 295–309.

Bader, M., Hiltbrunner, E., Körner, C., 2009. Fine root responses of mature deciduous forest trees to free air carbon dioxide enrichment (FACE). Funct. Ecol. 23, 913–921.

Baker, W.L., 1995. Long-term response of disturbance landscapes to human intervention and global change. Landsc. Ecol. 10, 143–159.

Barbosa, P., Wagner, M.R., 1989. Introduction to Forest and Shade Tree Insects. Adademic Press Inc., San Diego, CA, USA.

Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A.A., Cayan, D.R., Dettinger, M.D., 2008. Human-induced changes in the hydrology of the western United States. Science 319, 1080–1083.

Bates, B.C., Kundzewicz, Z.W., Wu, S., Palutikof, J.P. (Eds.), 2008. Climate Change and Water, Technical Paper of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva.

Beedlow, P.A., Tingey, D.T., Phillips, D.L., Hogsett, W.E., Olszyk, D.M., 2004. Rising atmospheric CO_2 and carbon sequestration in forests. Front. Ecol. Environ. 2, 315–322.

Beerling, D.J., Heath, J., Woodward, F.I., Mansfield, T.A., 1996. Drought-CO_2 interactions in trees: Observations and mechanisms. New Phytol. 134, 235–242.

Beuker, E., 1994. Adaptation to climatic changes of the timing of bud burst in populations of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. Tree Physiol. 14, 961–970.

Black, B.A., Shaw, D.C., Stone, J.K., 2010. Impacts of Swiss needle cast on overstory Douglas-fir forests of the western Oregon Coast Range. For. Ecol. Manag. 259, 1673–1680.

Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants – an economic analogy. Annu. Rev. Ecol. Syst. 16, 363–392.

Bohnert, H.J., Nelson, D.E., Jensen, R.G., 1995. Adaptations to environmental stresses. Plant Cell 7, 1099–1111.

Boisvenue, C., Running, S.W., 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Glob. Change Biol. 12, 862–882.

Bonner, F.T., Karrfalt, R.P. (Eds.), 2008. The Woody Plant Seed Manual, Agriculture Handbook 727. USDA Forest Service.

Bowes, G., 1993. Facing the inevitable: plants and increasing atmospheric CO_2. Annu. Rev. Plant Physiol. Plant Molec. Biol. 44, 309–332.

Boyer, J.S., 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46, 233–235.

Breda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. USA 102, 15144–15148.

Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree die-off in response to global-change type drought: mortality insights from a decade of plant water potential measurements. Fron. Ecol. Environ. 7, 185–189.

Brooks, J.R., Barnard, H.R., Coulombe, R., McDonnell, J.J., 2010. Ecohydrologic separation of water between trees and streams in a mediterranean climate. Nat. Geosci. 3, 100–104.

Burdon, R.D., 2001. Genetic diversity and disease resistance: some considerations for research, breeding, and deployment. Can. J. For. Res. 31, 596–606.

Burns, R.M., Honkala, B.H. (Eds.), 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Bytnerowicz, A., Omasa, K., Paoletti, E., 2007. Integrated effects of air pollution and climate change on forests: a northern hemisphere perspective. Environ. Pollut. 147, 438–445.

Callaway, R.M., Delucia, E.H., Thomas, E.M., Schlesinger, W.H., 1994. Compensatory responses of CO_2 exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO_2 and temperature regimes. Oecologia 98, 159–166.

Campbell, J.L., Rustad, L.E., Boyer, E.W., Christopher, S.F., Driscoll, C.T., Fernandez, I.J., Groffman, P.M., Houle, D., Kiekbusch, J., Magill, A.H., Mitchell, M.J., Ollinger, S.V., 2009. Consequences of climate change for biogeochemical cycling in forests of northeastern North America. Can. J. For. Res. 39, 264–284.

Campbell, R.K., 1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. J. Appl. Ecol. 11, 1069–1080.

Campbell, R.K., 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60, 1036–1050.

Campbell, R.K., Sorensen, F.C., 1973. Cold acclimation in seedling of Douglas-fir related to phenology and provenance. Ecology 54, 1148–1151.

Campbell, R.K., Sugano, A.I., 1979. Genecology of bud-burst phenology in Douglas-fir: response to flushing temperature and chilling. Bot. Gaz. 140, 223–231.

Cannell, M.G.R., Murray, M.B., Sheppard, L.J., 1987. Frost hardiness of red alder (*Alnus rubra*) provenances in Britain. Forestry 60, 57–67.

Cannell, M.G.R., Sheppard, L.J., Smith, R.I., Murray, M.B., 1985. Autumn frost damage on young *Picea sitchensis*, 2. Shoot frost hardening, and the probability of frost damage in Scotland. Forestry 58, 145–166.

Cannell, M.G.R., Smith, R.I., 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. J. Appl. Ecol. 20, 951–963.

Cannell, M.G.R., Smith, R.I., 1986. Climatic warming, spring budburst and frost damage on trees. J. Appl. Ecol. 23, 177–191.

Ceulemans, R., 1997. Direct impacts of CO_2 and temperature of physiological processes in trees. In: Mohren, G.M.J., Kramer, K., Sabate, S. (Eds.), Impacts of Global Change on Tree Physiology and Forest Ecosystems. Kluwer Academic Publishers, The Netherlands, Dordrecht, pp. 3–14.

Ceulemans, R., Mousseau, M., 1994. Effects of elevated atmospheric CO_2 on woody plants. New Phytol. 127, 425–446.

Chaves, M.M., Maroco, J.P., Pereira, J.S., 2003. Understanding plant responses to drought – from genes to the whole plant. Funct. Plant Biol. 30, 239–264.

Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osorio, M.L., Carvalho, I., Faria, T., Pinheiro, C., 2002. How plants cope with water stress in the field, photosynthesis and growth. Ann. Bot. 89, 907–916.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A., Whetton, P., 2007. Regional climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 848–940.

Chuine, I., 2000. A unified model for budburst of trees. J. Theor. Biol. 207, 337–347.

Chuine, I., 2010. Why does phenology drive species distribution? Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 365, 3149–3160.

Chuine, I., Rehfeldt, G.E., Aitken, S.N., 2006. Height growth determinants and adaptation to temperature in pines: a case study of *Pinus contorta* and *Pinus monticola*. Can. J. For. Res. 36, 1059–1066.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533.

Classen, A.T., Norby, R.J., Campany, C.E., Sides, K.E., Weltzin, J.F., 2010. Climate change alters seedling emergence and establishment in an old-field ecosystem. PLoS One 5, e13476, doi:10.1371/journal.pone.0013476.

Cline, M.G., Harrington, C.A., 2007. Apical dominance and apical control in multiple flushing of temperate woody species. Can. J. For. Res. 37, 74–83.

Close, T.J., 1996. Dehydrins: emergence of a biochemical role of a family of plant dehydration proteins. Physiol. Plant 97, 795–803.

Coakley, S.M., Scherm, H., Chakraborty, S., 1999. Climate change and plant disease management. Annu. Rev. Phytopathol. 37, 399–426.

Cochard, H., 1992. Vulnerability of several conifers to air embolism. Tree Physiol. 11, 73–83.

Cochard, H., Breda, N., Granier, A., 1996. Whole tree hydraulic conductance and water loss regulation in Quercus during drought: evidence for stomatal control of embolism? Ann. Sci. For. 53, 197–206.

Comstock, J.P., 2002. Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. J. Exp. Bot. 53, 195–200.

Coops, N.C., Hember, R.A., Waring, R.H., 2010. Assessing the impact of current and projected climates on Douglas-Fir productivity in British Columbia, Canada, using a process-based model (3-PG). Can. J. For. Res. 40, 511–524.

Coops, N.C., Waring, R.H., Brown, S.R., Running, S.W., 2001. Comparisons of predictions of net primary production and seasonal patterns in water use derived with two forest growth models in Southwestern Oregon. Ecol. Model. 142, 61–81.

Coops, N.C., Waring, R.H., Schroeder, T.A., 2009. Combining a generic process-based productivity model and a statistical classification method to predict the presence and absence of tree species in the Pacific Northwest, USA. Ecol. Model. 220, 1787–1796.

Cornic, G., 2000. Drought stress inhibits photosynthesis by decreasing stomatal aperture – not by affecting ATP synthesis. Trends Plant Sci. 5, 187–188.

Cruiziat, P., Cochard, H., Ameglio, T., 2002. Hydraulic architecture of trees: main concepts and results. Ann. For. Sci. 59, 723–752.

Curtis, P.S., Wang, X.Z., 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113, 299–313.

Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M., 2001. Climate change and forest disturbances. Bioscience 51, 723–734.

Dalla-Salda, G., Martinez-Meier, A., Cochard, H., Rozenberg, P., 2009. Variation of wood density and hydraulic properties of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) clones related to a heat and drought wave in France. For. Ecol. Manag. 257, 182–189.

Daly, C., Smith, J.W., Smith, J.I., McKane, R.B., 2007. High-resolution spatial modeling of daily weather elements for a catchment in the Oregon Cascade Mountains, United States. J. Appl. Meteorol. Climatol. 46, 1565–1586.

Darbah, J.N.T., Kubiske, M.E., Nelson, N., Oksanen, E., Vaapavuori, E., Karnosky, D.F., 2007. Impacts of elevated atmospheric CO_2 and O_3 on paper birch (*Betula papyrifera*): reproductive fitness. Sci. World J. 7, 240–246.

De Wolf, E.D., Isard, S.A., 2007. Disease cycle approach to plant disease prediction. Annu. Rev. Phytopathol. 45, 203–220.

Delucia, E.H., Callaway, R.M., Schlesinger, W.H., 1994. Offsetting changes in biomass allocation and photosynthesis in ponderosa pine (*Pinus ponderosa*) in response to climate change. Tree Physiol. 14, 669–677.

DeLucia, E.H., Moore, D.J., Norby, R.J., 2005. Contrasting responses of forest ecosystems to rising atmospheric CO_2: implications for the global C cycle. Glob. Biogeochem. Cycle 19, GB3006.

Dewers, R.S., Moehring, D.M., 1970. Effect of soil water stress on initiation of ovulate primordia in loblolly pine. For. Sci. 16, 219–221.

Dixon, M., Lethiec, D., Garrec, J.P., 1995. The growth and gas exchange response of soil-planted Norway spruce [*Picea abies* (L.) Karst.] and red oak (*Quercus rubra* L.) exposed to elevated CO_2 and to naturally occurring drought. New Phytol. 129, 265–273.

Dodd, I.C., 2003. Hormonal interactions and stomatal responses. J. Plant Growth Regul. 22, 32–46.

Dohrenbusch, A., Jaehne, S., Bredemeier, M., Lamersdorf, N., 2002. Growth and fructification of a Norway spruce (*Picea abies* L, Karst) forest ecosystem under changed nutrient and water input. Ann. For. Sci. 59, 359–368.

Downs, R.J., Bevington, J.M., 1981. Effect of temperature and photoperiod on growth and dormancy of *Betula papyrifera*. Am. J. Bot. 68, 795–800.

Drake, B.G., Azcon-Bieto, J., Berry, J., Bunce, J., Dijkstra, P., Farrar, J., Gifford, R.M., Gonzalez-Meler, M.A., Koch, G., Lambers, H., Siedow, J., Wullschleger, S., 1999. Does elevated atmospheric CO_2 concentration inhibit mitochondrial respiration in green plants? Plant Cell Environ. 22, 649–657.

Drake, B.G., GonzalezMeler, M.A., Long, S.P., 1997. More efficient plants: a consequence of rising atmospheric CO_2? Annu. Rev. Plant Physiol. Plant Molec. Biol. 48, 609–639.

Dreyer, E., Colinbelgrand, M., Biron, P., 1991. Photosynthesis and shoot water status of seedlings from different oak species submitted to waterlogging. Ann. Sci. For. 48, 205–214.

Duffy, P.B., Arritt, R.W., Coquard, J., Gutowski, W., Han, J., Iorio, J., Kim, J., Leung, L.R., Roads, J., Zeledon, E., 2006. Simulations of present and future climates in the western United States with four nested regional climate models. J. Clim. 19, 873–895.

Dykstra, G.F., 1974. Drought resistance of lodgepole pine seedlings in relation to provenance and tree water potential. Research Note 62. British Columbia Forest Service, Victoria, BC, Canada.

Eamus, D., Jarvis, P.G., 1989. The direct effects of increase in the global atmospheric CO_2 concentration on natural and commercial temperate trees and forests. Adv. Ecol. Res. 19, 1–55.

Easterling, W., Apps, M., 2005. Assessing the consequences of climate change for food and forest resources: a view from the IPCC. Clim. Change 70, 165–189.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697.

Ellsworth, D.S., 1999. CO_2 enrichment in a maturing pine forest: are CO_2 exchange and water status in the canopy affected? Plant Cell Environ. 22, 461–472.

Elsner, M.M., Cuo, L., Voisin, N., Deems, J.S., Hamlet, A.F., Vano, J.A., Mickelson, K.E.B., Lee, S.-Y., Lettenmaier, D.P., 2009. Implications of 21st century climate change for the hydrology of Washington state. In: McGuire Elsner, M., Littell, J., Binder, L.W. (Eds.), The Washington Climate Change Impacts Assessment. A Report by The Climate Impacts Group, University of Washington. Center for Science in the Earth System, Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Seattle, WA, pp. 69–106.

Falk, M., Wharton, S., Schroeder, M., Ustin, S.U.K.T.P., 2008. Flux partitioning in an old-growth forest: seasonal and interannual dynamics. Tree Physiol. 28, 509–520.

Farmer Jr., R.E., 1997. Seed Ecophysiology of Temperate and Boreal Zone Forest Trees. St. Lucie Press, Delray Beach, FL, USA.

Farquhar, G.D., von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Physiological Plant Ecology II. Water Relations and Carbon Assimilation. Springer–Verlag, Berlin, Heidelberg, pp. 549–587.

Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe, D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O., 2003. Nitrogen

emissions, deposition, and monitoring in the western United States. Bioscience 53, 391–403.

Fenn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNulty, S.G., Ryan, D.E., Stottlemyer, R., 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. Ecol. Appl. 8, 706–733.

Feret, P.P., 1982. Effect of moisture stress on the growth of *Pinus ponderosa* Dougl. ex. Laws seedlings in relation to their field performance. Plant Soil 69, 177–186.

Fernandes, P.M., Vega, J.A., Jimenez, E., Rigolot, E., 2008. Fire resistance of European pines. For. Ecol. Manag. 256, 246–255.

Ferrell, W.K., Woodard, E.S., 1966. Effect of seed origin on drought resistance of Douglas-fir (*Pseudotsuga menziesii*) (Mirb.) Franco. Ecology 47, 499–503.

Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negron, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manag. 238, 24–53.

Finch-Savage, W.E., Leubner-Metzger, G., 2006. Seed dormancy and the control of germination. New Phytol. 171, 501–523.

Finzi, A.C., Allen, A.S., DeLucia, E.H., Ellsworth, D.S., Schlesinger, W.H., 2001. Forest litter production, chemistry, and decomposition following two years of free-air CO_2 enrichment. Ecology 82, 470–484.

Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.-S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., Schlesinger, W.H., 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO_2 in a warm-temperate forest. Ecology 87, 15–25.

Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO_2. Proc. Natl. Acad. Sci. USA 104, 14014–14019.

Flexas, J., Bota, J., Galmes, J., Medrano, H., Ribas-Carbo, M., 2006. Keeping a positive carbon balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiol. Plant. 127, 343–352.

Flexas, J., Bota, J., Loreto, F., Cornic, G., Sharkey, T.D., 2004. Diffusive and metabolic limitations to photosynthesis under drought and salinity in C-3 plants. Plant Biol. 6, 269–279.

Forster, P., Ramaswamy, V., Artaxo, P., Berntsen, T., Betts, R., Fahey, D.W., Haywood, J., Lean, J., Lowe, D.C., Myhre, G., Nganga, J., Prinn, R., Raga, G., Schulz, M., Van Dorland, R., 2007. Changes in atmospheric constituents and in radiative forcing. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 129–234.

Franklin, J.F., Bledsoe, C.S., Callahan, J.T., 1990. Contributions of the long-term ecological research program. Bioscience 40, 509–523.

Franklin, J.F., Dyrness, C.T., 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR, USA.

Franklin, J.F., Halpern, C.B., 2000. Pacific northwest forests. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, New York, NY, USA, pp. 123–159.

Fritts, H.C., 1966. Growth-rings of trees: their correlation with climate. Science 154, 973–979.

Gardiner, E.S., Hodges, J.D., 1996. Physiological, morphological and growth responses to rhizosphere hypoxia by seedlings of North American bottomland oaks. Ann. Sci. For. 53, 303–316.

Garrett, K.A., Dendy, S.P., Frank, E.E., Rouse, M.N., Travers, S.E., 2006. Climate change effects on plant disease: genomes to ecosystems. Annu. Rev. Phytopathol. 44, 489–509.

Gauthier, S., Bergeron, Y., Simon, J.P., 1996. Effects of fire regime on the serotiny level of jack pine. J. Ecol. 84, 539–548.

Gebre, G.M., Kuhns, M.R., Brandle, J.R., 1994. Organic solute accumulation and dehydration tolerance in three water-stressed *Populus deltoides* clones. Tree Physiol. 14, 575–587.

Gedalof, Z., Peterson, D.L., Mantua, N.J., 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. Ecol. Appl. 15, 154–174.

Gessler, A., Keitel, C., Nahm, M., Rennenberg, H., 2004. Water shortage affects the water and nitrogen balance in central European beech forests. Plant Biol. 6, 289–298.

Gilbertson, R.L., 1980. Wood-rotting fungi of North America. Mycologia 72, 1–49.

Gillett, N.P., Weaver, A.J., Zwiers, F.W., Flannigan, M.D., 2004. Detecting the effect of climate change on Canadian forest fires. Geophys. Res. Lett. 31, L18211.

Glenz, C., Schlaepfer, R., Iorgulescu, I., Kienast, F., 2006. Flooding tolerance of Central European tree and shrub species. For. Ecol. Manag. 235, 1–13.

Gower, S.T., 2003. Patterns and mechanisms of the forest carbon cycle. Annu. Rev. Env. Resour. 28, 169–204.

Gu, L., Hanson, P.J., Mac Post, W., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G., Meyers, T., 2008. The 2007 eastern US spring freezes: Increased cold damage in a warming world? Bioscience 58, 253–262.

Guak, S., Olsyzk, D.M., Fuchigami, L.H., Tingey, D.T., 1998. Effects of elevated CO_2 and temperature on cold hardiness and spring bud burst and growth in Douglas-fir (*Pseudotsuga menziesii*). Tree Physiol. 18, 671–679.

Guehl, J.M., Picon, C., Aussenac, G., Gross, P., 1994. Interactive effects of elevated CO_2 and soil drought on growth and transpiration efficiency and its determinants in two European forest tree species. Tree Physiol. 14, 707–724.

Gugger, P.F., Sugita, S., Cavender-Bares, J., 2010. Phylogeography of Douglas-fir based on mitochondrial and chloroplast DNA sequences: testing hypotheses from the fossil record. Mol. Ecol. 19, 1877–1897.

Gunderson, C.A., Norby, R.J., Wullschleger, S.D., 2000. Acclimation of photosynthesis and respiration to simulated climatic warming in northern and southern populations of *Acer saccharum*: laboratory and field evidence. Tree Physiol. 20, 87–96.

Hamilton, J.G., DeLucia, E.H., George, K., Naidu, S.L., Finzi, A.C., Schlesinger, W.H., 2002. Forest carbon balance under elevated CO_2. Oecologia 131, 250–260.

Hamilton, J.G., Thomas, R.B., Delucia, E.H., 2001. Direct and indirect effects of elevated CO_2 on leaf respiration in a forest ecosystem. Plant Cell Environ. 24, 975–982.

Hamlet, A.F., Lettenmaier, D.P., 2007. Effects of 20th century warming and climate variability on flood risk in the western U.S. Water Resour. Res. 43, W06427.

Hamlet, A.F., Mote, P.W., Clark, M.P., Lettenmaier, D.P., 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. J. Clim. 18, 4545–4561.

Hannerz, M., Ekberg, I., Norell, L., 2003. Variation in chilling requirements for completing bud rest between provenances of Norway spruce. Silvae Genet. 52, 161–168.

Hänninen, H., 1991. Does climatic warming increase the risk of frost damage in northern trees. Plant Cell Environ. 14, 449–454.

Hänninen, H., 2006. Climate warming and the risk of frost damage to boreal forest trees: identification of critical ecophysiological traits. Tree Physiol. 26, 889–898.

Hänninen, H., Beuker, E., Johnsen, Ø., Leinonen, I., Murray, M., Sheppard, L., Skrøppa, T., 2001. Impacts of climate change on cold hardiness of conifers. In: Bigras, F.J., Colombo, S.J. (Eds.), Conifer Cold Hardiness. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 305–333.

Hänninen, H., Kramer, K., 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. Silva. Fenn. 41, 167–205.

Hansen, A.J., Neilson, R.R., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R., Bartlein, P.J., 2001. Global change in forests: responses of species, communities, and biomes. Bioscience 51, 765–779.

Hanson, P.J., Todd, D.E., Amthor, J.S., 2001. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. Tree Physiol. 21, 345–358.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262, 205–220.

Hanson, P.J., Wullschleger, S.D., Norby, R.J., Tschaplinski, T.J., Gunderson, C.A., 2005. Importance of changing CO_2, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. Glob. Change Biol. 11, 1402–1423.

Harrington, C.A., Gould, P.J., St Clair, J.B., 2010. Modeling the effects of winter environment on dormancy release of Douglas-fir. For. Ecol. Manag. 259, 798–808.

Harrington, R., Fleming, R.A., Woiwod, I.P., 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agric. For. Entomol. 3, 233–240.

Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecol. Lett. 12, 1040–1049.

Hattenschwiler, S., Miglietta, F., Raschi, A., Körner, C., 1997. Morphological adjustments of mature *Quercus ilex* trees to elevated CO_2. Acta Oecol. Int. J. Ecol. 18, 361–365.

Heath, J., 1998. Stomata of trees growing in CO_2-enriched air show reduced sensitivity to vapour pressure deficit and drought. Plant Cell Environ. 21, 1077–1088.

Hegerl, G.C., Zwiers, F.W., Braconnot, P., Gillett, N.P., Luo, Y., Marengo Orsini, J.A., Nicholls, N., Penner, J.E., Stott, P.A., 2007. Understanding and attributing climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 663–745.

Heide, O.M., 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiol. 23, 931–936.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog. Phys. Geogr. 30, 751–777.

Heiner, T.C., Lavender, D.P., 1972. Early growth and drought avoidance in Douglas-fir seedlings. Research Paper 14. Forest Research Laboratory, School of Forestry, Oregon State University, Corvallis, OR.

Helgerson, O.T., 1990. Heat damage in tree seedlings and its prevention. New For. 3, 333–358.

Hermann, R.K., Chicote, W.W., 1965. Effects of seedbeds on germination and survival of Douglas-fir. Res. Pap. 4. Forest Research Laboratory, Oregon State University, Corvallis, OR.

Hessburg, P.F., Salter, R.B., James, K.M., 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. Landsc. Ecol. 22, 5–24.

Hessl, A.E., McKenzie, D., Schellhaas, R., 2004. Drought and pacific decadal oscillation linked to fire occurrence in the inland Pacific Northwest. Ecol. Appl. 14, 425–442.

Heyerdahl, E.K., McKenzie, D., Daniels, L.D., Hessl, A.E., Littell, J.S., Mantua, N.J., 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). Int. J. Wildland Fire 17, 40–49.

Hicke, J.A., Logan, J.A., Powell, J., Ojima, D.S., 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. J. Geophys. Res. Biogeosci. 111, G02019.

Hinckley, T.M., Dougherty, P.M., Lassoie, J.P., Roberts, J.E., Teskey, R.O., 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. Am. Midl. Nat. 102, 307–316.

Hobbins, M.T., Ramirez, J.A., Brown, T.C., 2004. Trends in pan evaporation and actual evapotranspiration across the conterminous US: Paradoxical or complementary? Geophys. Res. Lett. 31, L13503.

Hoekstra, F.A., Golovina, E.A., Buitink, J., 2001. Mechanisms of plant desiccation tolerance. Trends Plant Sci. 6, 431–438.

Hogg, E.H., Brandt, J.P., Michaellian, M., 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Can. J. For. Res. 38, 1373–1384.

Holbrook, N.M., Ahrens, E.T., Burns, M.J., Zwieniecki, M.A., 2001. In vivo observation of cavitation and embolism repair using magnetic resonance imaging. Plant Physiol. 126, 27–31.

Hood, I.A., 1982. *Phaeocryptopus gaeumannii* on Pseudotsuga menziesii in southern British Columbia. N Z J. For. Sci. 12, 415–424.

Houpis, J.L.J., Anderson, P.D., Pushnik, J.C., Anschel, D.J., 1999. Among-provenance variability of gas exchange and growth in response to long-term elevated CO_2 exposure. Water Air Soil Pollut. 116, 403–412.

Houpis, J.L.J., Surano, K.A., Cowles, S., Shinn, J.H., 1988. Chlorophyll and carotenoid concentrations in two varieties of Pinus ponderosa seedlings subjected to long-term elevated carbo dioxide. Tree Physiol. 4, 187–193.

Howe, G.T., Aitken, S.N., Neale, D.B., Jermstad, K.D., Wheeler, N.C., Chen, T.H.H., 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. Can. J. Bot. 81, 1247–1266.

Hsiao, T.C., Acevedo, E., Fereres, E., Henderson, D.W., 1976. Stress metabolism – water stress, growth, and osmotic adjustment. Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci. 273, 479–500.

Hungate, B.A., Reichstein, M., Dijkstra, P., Johnson, D., Hymus, G., Tenhunen, J.D., Hinkle, C.R., Drake, B.G., 2002. Evapotranspiration and soil water content in a scrub-oak woodland under carbon dioxide enrichment. Glob. Change Biol. 8, 289–298.

Hussain, M., Kubiske, M.E., Connor, K.F., 2001. Germination of CO_2-enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO_2 enrichment. Funct. Ecol. 15, 344–350.

Hyvonen, R., Agren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomaki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, K., Ryan, M.G., Sigurdsson, B.D., Stromgren, M., van Oijen, M., Wallin, G., 2007. The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. New Phytol. 173, 463–480.

IPCC, 2000. In: Nakicenovic, N., Swarts, R. (Eds.), Special Report on Emissions Scenarios. Cambridge University Press, Cambridge, UK.

IPCC, 2001. Climate Change 2001: Synthesis Report. Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA.

IPCC, 2007. Summary for Policymakers. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1–18.

Irland, L.C., Adams, D., Alig, R., Betz, C.J., Chen, C.C., Hutchins, M., McCarl, B.A., Skog, K., Sohngen, B.L., 2001. Assessing socioeconomic impacts of climate change on US forests, wood-product markets, and forest recreation. Bioscience 51, 753–764.

Jablonski, L.M., Wang, X.Z., Curtis, P.S., 2002. Plant reproduction under elevated CO_2 conditions: a meta-analysis of reports on 79 crop and wild species. New Phytol. 156, 9–26.

Jackson, M.B., 2002. Long-distance signalling from roots to shoots assessed: the flooding story. J. Exp. Bot. 53, 175–181.

Jansen, E., Overpeck, J., Briffa, K.R., Duplessy, J.-C., Joos, F., Masson-Delmotte, V., Olago, D., Otto-Bliesner, B., Peltier, W.R., Rahmstorf, S., Ramesh, R., Raynaud, D., Rind, D., Solomina, O., Villalba, R., Zhang, D., 2007. Paleoclimate. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 433–497.

Jarvis, A.J., Davies, W.J., 1998. The coupled response of stomatal conductance to photosynthesis and transpiration. J. Exp. Bot. 49, 399–406.

Jarvis, A.J., Mansfield, T.A., Davies, W.J., 1999. Stomatal behaviour, photosynthesis and transpiration under rising CO_2. Plant Cell Environ. 22, 639–648.

Johnson, M.G., Rygiewicz, P.T., Tingey, D.T., Phillips, D.L., 2006. Elevated CO_2 and elevated temperature have no effect on Douglas-fir fine-root dynamics in nitrogen-poor soil. New Phytol. 170, 345–356.

Joly, R.J., Adams, W.T., Stafford, S.G., 1989. Phenological and morphological responses of mesic and dry site sources of coastal Douglas-fir to water deficit. For. Sci. 35, 987–1005.

Jones, H.G., Sutherland, R.A., 1991. Stomatal control of xylem embolism. Plant Cell Environ. 14, 607–612.

Jönsson, A.M., Linderson, M.L., Stjernquist, I., Schlyter, P., Bärring, L., 2004. Climate change and the effect of temperature backlashes causing frost damage in *Picea abies*. Glob. Planet. Change 44, 195–207.

Joslin, J.D., Wolfe, M.H., Hanson, P.J., 2000. Effects of altered water regimes on forest root systems. New Phytol. 147, 117–129.

Joyce, L.A., Blate, G.M., Littell, J.S., McNulty, S.G., Millar, C.I., Moser, S.C., Neilson, R.P., O'Halloran, K., Peterson, D.L., 2008. National forests. In: Julius, S.H., West, J.M. (Eds.), Preliminary Review of Adaptation Options for Climate-Sensitive Ecosystems and Resources. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. U.S. Environmental Protection Agency, Washington, D.C., USA, pp. 3-1–3-127.

Joyce, L.A., Blate, G.M., Littell, J.S., McNulty, S.G., Millar, C.I., Moser, S.C., Neilson, R.P., Peterson, D.L., 2009. Managing for multiple resources under climate change: national forests. Environ. Manag. 44, 1022–1032.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020.

Junttila, O., 1980. Effect of photoperiod and temperature on apical growth cessation in two ecotypes of Salix and Betula. Physiol. Plant. 48, 347–352.

Junttila, O., Nilsen, J., Igeland, B., 2003. Effect of temperature on the induction of bud dormancy in ecotypes of *Betula pubescens* and *Betula pendula*. Scand. J. For. Res. 18, 208–217.

Kaldenhoff, R., Ribas-Carbo, M., Flexas, J., Lovisolo, C., Heckwolf, M., Uehlein, N., 2008. Aquaporins and plant water balance. Plant Cell Environ. 31, 658–666.

Kavanagh, K.L., Bond, B.J., Aitken, S.N., Gartner, B.L., Knowe, S., 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. Tree Physiol. 19, 31–37.

Keane, R.E., Agee, J.K., Fule, P., Keeley, J.E., Key, C., Kitchen, S.G., Miller, R., Schulte, L.A., 2008. Ecological effects of large fires on US landscapes: benefit or catastrophe? Int. J. Wildland Fire 17, 696–712.

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. 12, 334–350.

Keenan, T., Sierra, J.M., Lloret, F., Ninyerola, M., Sabate, S., 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: CO_2 matters! Glob. Change Biol. 17, 565–579.

Kinloch, B.B., Davis, D.A., Burton, D., 2008. Resistance and virulence interactions between two white pine species and blister rust in a 30-year field trial. Tree Genet. Genomes 4, 65–74.

Kliejunas, J.T., Geils, B.W., Glaeser, J.M., Goheen, E.M., Hennon, P., Kim, M.-S., Kope, H., Stone, J., Sturrock, R., Frankel, S.J., 2009. Review of literature on climate change and forest diseases of western North America. General Technical Report, PSW-GTR-225. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA, USA.

Klopfenstein, N.B., Kim, M.-S., Hanna, J.W., Richardson, B.A., Lundquist, J., 2009. Approaches to predicting potential impacts of climate change on forest disease: an example with *Armillaria* root disease. Research Paper, RMRS-RP-76. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA.

Koenig, W.D., Knops, J.M.H., 2005. The mystery of masting in trees. Am. Sci. 93, 340–347.

Körner, C., 2000. Biosphere responses to CO_2 enrichment. Ecol. Appl. 10, 1590–1619.

Körner, C., Asshoff, R., Bignucolo, O., Hattenschwiler, S., Keel, S.G., Pelaez-Riedl, S., Pepin, S., Siegwolf, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309, 1360–1362.

Körner, C., Basler, D., 2010. Phenology under global warming. Science 327, 1461–1462.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. Monogr. No. 1 (http://heronpublishing.com/tp/monograph/kozlowski.pdf).

Kozlowski, T.T., Pallardy, S.G., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68, 270–334.

Kramer, K., Friend, A., Leinonen, I., 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. Clim. Res. 7, 31–41.

Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. Int. J. Biometeorol. 44, 67–75.

Kramer, P.J., Boyer, J.S., 1995. Water Relations of Plants and Soils. Academic Press, Inc., San Diego, California.

Krankina, O.N., Harmon, M.E., 2006. Forest management strategies for carbon storage. In: Forests, Carbon and Climate Change – Summary of Science Findings. Oregon Forest Resources Institute, pp. 79–92.

Kreuzwieser, J., Furniss, S., Rennenberg, H., 2002. Impact of waterlogging on the N-metabolism of flood tolerant and non-tolerant tree species. Plant Cell Environ. 25, 1039–1049.

Kreuzwieser, J., Papadopoulou, E., Rennenberg, H., 2004. Interaction of flooding with carbon metabolism of forest trees. Plant Biol. 6, 299–306.

Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452, 987–990.

Kuser, J.E., Ching, K.K., 1980. Provenance variation in phenology and cold hardiness of western hemlock seedlings. For. Sci. 26, 463–470.

LaDeau, S.L., Clark, J.S., 2001. Rising CO_2 levels and the fecundity of forest trees. Science 292, 95–98.

LaDeau, S.L., Clark, J.S., 2006a. Elevated CO_2 and tree fecundity: the role of tree size, interannual variability, and population heterogeneity. Glob. Change Biol. 12, 822–833.

LaDeau, S.L., Clark, J.S., 2006b. Pollen production by *Pinus taeda* growing in elevated atmospheric CO_2. Funct. Ecol. 20, 541–547.

Lambers, H., Chapin, F.S., Pons, T.L., 2008. Plant Physiological Ecology. Springer Science + Business Media, LLC, New York.

Lasch, P., Badeck, F.W., Suckow, F., Lindner, M., Mohr, P., 2005. Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). For. Ecol. Manag. 207, 59–74.

Lawlor, D.W., Cornic, G., 2002. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. Plant Cell Environ. 25, 275–294.

Ledig, F.T., Fryer, J.H., 1972. Pocket of variability in *Pinus rigida*. Evolution 26, 259–266.

Ledig, F.T., Kitzmiller, J.H., 1992. Genetic strategies for reforestation in the face of global climate change. For. Ecol. Manag. 50, 153–169.

Leinonen, I., 1996. Dependence of dormancy release on temperature in different origins of *Pinus sylvestris* and *Betula pendula* seedlings. Scand. J. For. Res. 11, 122–128.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768–1771.

Lentile, L.B., Smith, F.W., Shepperd, W.D., 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Can. J. For. Res. 35, 2875–2885.

Leung, L.R., Qian, Y., Bian, X.D., Washington, W.M., Han, J.G., Roads, J.O., 2004. Mid-century ensemble regional climate change scenarios for the western United States. Clim. Change 62, 75–113.

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O., Runge, M., 2001. Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. For. Ecol. Manag. 149, 33–46.

Leuzinger, S., Bigler, C., Wolf, A., Korner, C., 2009. Poor methodology for predicting large-scale tree die-off. Proc. Natl. Acad. Sci. USA 106, E106.

Leuzinger, S., Körner, C., 2007. Water savings in mature deciduous forest trees under elevated CO_2. Glob. Change Biol. 13, 2498–2508.

Leuzinger, S., Zotz, G., Asshoff, R., Körner, C., 2005. Responses of deciduous forest trees to severe drought in Central Europe. Tree Physiol. 25, 641–650.

Levitt, J., 1980. Responses of Plants to Environmental Stresses, vol. I. Chilling, Freezing, and High Temperature Stresses, 2nd ed. Academic Press, Inc, Orlando, FL, USA.

Lewis, J.D., Lucash, M., Olszyk, D., Tingey, D.T., 2001. Seasonal patterns of photosynthesis in Douglas fir seedlings during the third and fourth year of exposure to elevated CO_2 and temperature. Plant Cell Environ. 24, 539–548.

Lewis, J.D., Lucash, M., Olszyk, D.M., Tingey, D.T., 2002. Stomatal responses of Douglas-fir seedlings to elevated carbon dioxide and temperature during the third and fourth years of exposure. Plant Cell Environ. 25, 1411–1421.

Lewis, J.D., Olszyk, D., Tingey, D.T., 1999. Seasonal patterns of photosynthetic light response in Douglas-fir seedlings subjected to elevated atmospheric CO_2 and temperature. Tree Physiol. 19, 243–252.

Lewis, J.D., Tissue, D.T., Strain, B.R., 1996. Seasonal response of photosynthesis to elevated CO2 in loblolly pine (*Pinus taeda* L) over two growing seasons. Global Change Biol. 2, 103–114.

Linkosalo, T., Carter, T.R., Hakkinen, R., Hari, P., 2000. Predicting spring phenology and frost damage risk of Betula spp. under climatic warming: a comparison of two models. Tree Physiol. 20, 1175–1182.

Linkosalo, T., Hakkinen, R., Hanninen, H., 2006. Models of the spring phenology of boreal and temperate trees: is there something missing? Tree Physiol. 26, 1165–1172.

Linkosalo, T., Hakkinen, R., Terhivuo, J., Tuomenvirta, H., Hari, P., 2009. The time series of flowering and leaf bud burst of boreal trees (1846–2005) support the direct temperature observations of climatic warming. Agric. For. Meteorol. 149, 453–461.

Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021.

Littell, J.S., Peterson, D.L., Millar, C.I., O'Halloran, K. U.S. National Forests adapt to climate change through science-management partnerships. Climatic Change, in review.

Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecol. Monogr. 78, 349–368.

Logan, J.A., Regniere, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1, 130–137.

Long, S.P., 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: has its importance been underestimated? Plant. Cell Environ. 14, 729–739.

Loreto, F., Centritto, M., 2008. Leaf carbon assimilation in a water-limited world. Plant Biosyst. 142, 154–161.

Lovisolo, C., Perrone, I., Carra, A., Ferrandino, A., Flexas, J., Medrano, H., Schubert, A., 2010. Drought-induced changes in development and function of grapevine (Vitis spp.) organs and in their hydraulic and non-hydraulic interactions at the whole-plant level: a physiological and molecular update. Funct. Plant Biol. 37, 98–116.

Luce, C.H., Holden, Z.A., 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948–2006. Geophys. Res. Lett. 36, L16401.

Lukac, M., Calfapietra, C., Godbold, D.L., 2003. Production, turnover and mycorrhizal colonization of root systems of three Populus species grown under elevated CO_2 (POPFACE). Global Change Biol. 9, 838–848.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R., Field, C.B., 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54, 731–739.

Luu, D.T., Maurel, C., 2005. Aquaporins in a challenging environment: molecular gears for adjusting plant water status. Plant Cell Environ. 28, 85–96.

Maherali, H., Pockman, W.T., Jackson, R.B., 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85, 2184–2199.

Maherali, H., Williams, B.L., Paige, K.N., Delucia, E.H., 2002. Hydraulic differentiation of Ponderosa pine populations along a climate gradient is not associated with ecotypic divergence. Funct. Ecol. 16, 510–521.

Malhi, Y., Baldocchi, D.D., Jarvis, P.G., 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22, 715–740.

Malhi, Y., Meir, P., Brown, S., 2002. Forests, carbon and global climate. Philos. Trans. R. Soc. Lond. Ser. A-Math. Phys. Eng. Sci. 360, 1567–1591.

Man, R.Z., Kayahara, G.J., Dang, Q.L., Rice, J.A., 2009. A case of severe frost damage prior to budbreak in young conifers in Northeastern Ontario: consequence of climate change? For. Chron 85, 453–462.

Manter, D.K., Reeser, P.W., Stone, J.K., 2005. A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon Coast Range. Phytopathology 95, 1256–1265.

Martínez-Vilalta, J., Piñol, J., Beven, K., 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. Ecol. Model. 155, 127–147.

Martinez-Vilalta, J., Sala, A., Pinol, J., 2004. The hydraulic architecture of Pinaceae – a review. Plant Ecol. 171, 3–13.

Matyas, C., 1994. Modeling climate change effects with provenance test data. Tree Physiol. 14, 797–804.

Maurel, C., Verdoucq, L., Luu, D.T., Santoni, V., 2008. Plant aquaporins: membrane channels with multiple integrated functions. Annu. Rev. Plant Biol. 59, 595–624.

McCarthy, H.R., Oren, R., Johnsen, K.H., Gallet-Budynek, A., Pritchard, S.G., Cook, C.W., LaDeau, S.L., Jackson, R.B., Finzi, A.C., 2010. Re-assessment of plant carbon dynamics at the Duke free-air CO_2 enrichment site: interactions of atmospheric [CO_2] with nitrogen and water availability over stand development. New Phytol. 185, 514–528.

McCulloh, K., Sperry, J.S., Lachenbruch, B., Meinzer, F.C., Reich, P.B., Voelker, S., 2010. Moving water well: comparing hydraulic efficiency in twigs and trunks of coniferous, ring-porous, and diffuse-porous saplings from temperate and tropical forests. New Phytol. 186, 439–450.

McDermott, J.M., Robinson, R.A., 1989. Provenance variation for disease resistance in Pseudotsuga menziesii to the Swiss needle cast pathogen, *Phaeocryptopus gaeumannii*. Can. J. For. Res. 19, 244–246.

McDonald, G.I., 1979. Resistance of Douglas-Fir to Western Spruce Budworm: Results of a Preliminary Progeny Test. Research Note INT-264. USDA Forest Service, Intermountain Forest and Range Experimental Station, Ogden, UT.

McDonald, G.I., Martin, N.E., Harvey, A.E., 1987. *Armillaria* in the Northern Rockies: Pathogenicity and Host Susceptibility on Pristine and Disturbed Sites. Research Note, INT-371. USDA Forest Service, Intermountain Southwest.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–739.

McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conserv. Biol. 18, 890–902.

McLachlan, J.S., Clark, J.S., Manos, P.S., 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology 86, 2088–2098.

McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conserv. Biol. 21, 297–302.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 747–845.

Meinzer, F.C., Bond, B.J., Karanian, J.A., 2008. Biophysical constraints on leaf expansion in a tall conifer. Tree Physiol. 28, 197–206.

Meinzer, F.C., Clearwater, M.J., Goldstein, G., 2001. Water transport in trees: current perspectives, new insights and some controversies. Environ. Exp. Bot. 45, 239–262.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, A., Defila, C., Donnelly, A., Filella, Y., Jatcza, K., Mage, F., Mestre, A., Nordli, O., Peñuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969–1976.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Mitchell, R.G., Waring, R.H., Pitman, G.B., 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. For. Sci. 29, 204–211.

Mohan, J.E., Clark, J.S., Schlesinger, W.H., 2007. Long-term CO_2 enrichment of a forest ecosystem: implications for forest regeneration and succession. Ecol. Appl. 17, 1198–1212.

Mohan, J.E., Cox, R.M., Iverson, L.R., 2009. Composition and carbon dynamics of forests in northeastern North America in a future, warmer world. Can. J. For. Res. 39, 213–230.

Moore, D.J.P., Aref, S., Ho, R.M., Pippen, J.S., Hamilton, J.G., De Lucia, E.H., 2006. Annual basal area increment and growth duration of Pinus taeda in response to eight years of free-air carbon dioxide enrichment. Glob. Change Biol. 12, 1367–1377.

Morgenstern, E.K., 1996. Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. UBC Press, Vancouver, BC, Canada.

Morin, X., Lechowicz, M.J., Augspurger, C., O' Keefe, J., Viner, D., Chuine, I., 2009. Leaf phenology in 22 North American tree species during the 21st century. Glob. Change Biol. 15, 961–975.

Morison, J.I.L., Baker, N.R., Mullineaux, P.M., Davies, W.J., 2008. Improving water use in crop production. Philos. Trans. R. Soc. B-Biol. Sci. 363, 639–658.

Morrison, D., Mallett, K., 1996. Silvicultural management of Armillaria root disease in western Canadian forests. Can. J. Plant Pathol. 18, 194–199.

Morrison, P.H., Swanson, F.J., 1990. Fire History and Pattern in a Cascade Range Landscape. USDA Forest Service General Technical Report PNW-GTR-254, Portland, OR, USA, p. 77.

Mote, P., Salathé, E., Dulière, V., Jump, E., 2008. Scenarios of future climate for the Pacific Northwest. Climate Impacts Group. University of Washington, Seattle, WA, p. 14.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093.

Muir, P.S., Lotan, J.E., 1985. Disturbance history and serotiny of Pinus contorta in western Montana. Ecology 66, 1658–1668.

Murray, M.B., Cannell, M.G.R., Smith, R.I., 1989. Date of budburst of fifteen tree species in Britain following climatic warming. J. Appl. Ecol. 26, 693–700.

Murray, M.B., Smith, R.I., Leith, I.D., Fowler, D., Lee, H.S.J., Friend, A.D., Jarvis, P.G., 1994. Effects of elevated CO_2, nutrition and climatic warming on bud phenology in Sitka spruce (Picea sitchensis) and their impact on the risk of frost damage. Tree Physiol. 14, 691–706.

Nilsen, E.T., Orcutt, D.M., 1996. The Physiology of Plants Under Stress. John Wiley & Sons, Inc., New York, NY, USA.

Nitschke, C.R., Innes, J.L., 2008. A tree and climate assessment tool for modelling ecosystem response to climate change. Ecol. Model. 210, 263–277.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc. Natl. Acad. Sci. USA 102, 18052–18056.

Norby, R.J., Hartz-Rubin, J.S., Verbrugge, M.J., 2003a. Phenological responses in maple to experimental atmospheric warming and CO_2 enrichment. Glob. Change Biol. 9, 1792–1801.

Norby, R.J., Ledford, J., Reilly, C.D., Miller, N.E., O'Neill, E.G., 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO_2 enrichment. Proc. Natl. Acad. Sci. USA 101, 9689–9693.

Norby, R.J., Luo, Y.Q., 2004. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytol. 162, 281–293.

Norby, R.J., Ogle, K., Curtis, P.S., Badeck, F.W., Huth, A., Hurtt, G.C., Kohyama, T., Penuelas, J., 2001. Aboveground growth and competition in forest gap models: an analysis for studies of climatic change. Clim. Change 51, 415–447.

Norby, R.J., Sholtis, J.D., Gunderson, C.A., Jawdy, S.S., 2003b. Leaf dynamics of a deciduous forest canopy: no response to elevated CO_2. Oecologia 136, 574–584.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO_2 enhancement of forest productivity constrained by limited nitrogen availability. Proc. Natl. Acad. Sci. USA 107, 19368–19373.

Norby, R.J., Wullschleger, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO_2 in field experiments: implications for the future forest. Plant Cell Environ. 22, 683–714.

Nowak, R.S., Ellsworth, D.S., Smith, S.D., 2004. Functional responses of plants to elevated atmospheric CO_2 – do photosynthetic and productivity data from FACE experiments support early predictions? New Phytol. 162, 253–280.

O'Neill, G.A., Ukrainetz, N.K., Carlson, M.R., Cartwright, C.V., Jaquish, B.C., King, J.N., Krakowski, J., Russell, J.H., Stoehr, M.U., Xie, C., Yanchuk, A.D., 2008. Assisted migration to address climate change in British Columbia: recommendations for interim seed transfer standards. Technical Report 048. B.C. Ministry of Forests and Range, Research Branch, Victoria, B.C. Canada.

Obeso, J.R., 2002. The costs of reproduction in plants. New Phytol. 155, 321–348.

Ohlson, D.W., McKinnon, G.A., Hirsch, K.G., 2005. A structured decision-making approach to climate change adaptation in the forest sector. For. Chron 81, 97–103.

Oliver, M.J., 1996. Desiccation tolerance in vegetative plant cells. Physiol. Plant 97, 779–787.

Olszyk, D., Wise, C., VanEss, E., Apple, M., Tingey, D., 1998a. Phenology and growth of shoots, needles, and buds of Douglas-fir seedlings with elevated CO_2 and (or) temperature. Can. J. Bot. 76, 1991–2001.

Olszyk, D., Wise, C., VanEss, E., Tingey, D., 1998b. Elevated temperature but not elevated CO_2 affects long-term patterns of stem diameter and height of Douglas-fir seedlings. Can. J. For. Res. 28, 1046–1054.

Olszyk, D.M., Johnson, M.G., Tingey, D.T., Rygiewicz, P.T., Wise, C., VanEss, E., Benson, A., Storm, M.J., King, R., 2003. Whole-seedling biomass allocation, leaf area, and

tissue chemistry for Douglas-fir exposed to elevated CO_2 and temperature for 4 years. Can. J. For. Res. 33, 269–278.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schafer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., Katul, G.G., 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411, 469–472.

Pallardy, S.G., 1981. Closely related woody plants. In: Kozlowski, T.T. (Ed.), Water Deficits and Plant Growth, vol. 6, Woody Plant Communities. Academic Press, Inc., New York, pp. 511–548.

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob. Change Biol. 13, 1860–1872.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), 2007. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Partanen, J., 2004. Dependence of photoperiodic response of growth cessation on the stage of development in Picea abies and Betula pendula seedlings. For. Ecol. Manag. 188, 137–148.

Pausas, J.G., Bradstock, R.A., Keith, D.A., Keeley, J.E., 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085–1100.

Peet, R.K., 2000. Forests and meadows of the Rocky Mountains. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, New York, NY, USA, pp. 75–121.

Perry, T.O., Wu, W.C., 1960. Genetic variation in the winter chilling requirement for date of dormancy break for Acer rubrum. Ecology 41, 790–794.

Peters, R.L., 1990. Effects of global warming on forests. For. Ecol. Manag. 35, 13–33.

Peterson, D.J., Halofsky, J.E., Johnson, M.C. Managing and adapting to changing fire regimes in a warmer climate. In: McKenzie, D., Miller, C., Falk, D. (Eds.), The Landscape Ecology of Fire. Springer Verlag, New York, NY, USA, doi:10.1007/978-94-007-0301-8, in press.

Peterson, D.W., Johnson, M.C., Agee, J.K., Jain, T.B., McKenzie, D., Reinhardt, E.R., 2005. Forest Structure and Fire Hazard in Dry Forests of the Western United States. USDA Forest Service General Technical Report PNW-GTR-628, Portland, OR, USA, p. 30.

Peterson, D.W., Peterson, D.L., 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. Ecology 82, 3330–3345.

Pezeshki, S.R., Pardue, J.H., DeLaune, R.D., 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. Tree Physiol. 16, 453–458.

Pharis, R.P., Ferrell, W.K., 1966. Differences in drought resistance between coastal and inland sources of Douglas fir. Can. J. Bot. 44, 1651–1659.

Pharis, R.P., Webber, J.E., Ross, S.D., 1987. The promotion of flowering in forest trees by gibberellin A4/7 and cultural treatments: a review of the possible mechanisms. For. Ecol. Manag. 19, 65–84.

Piovesan, G., Adams, J.M., 2001. Masting behaviour in beech: linking reproduction and climatic variation. Can. J. Bot. 79, 1039–1047.

Pockman, W.T., Sperry, J.S., 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. Am. J. Bot. 87, 1287–1299.

Pregitzer, K.S., Burton, A.J., Zak, D.R., Talhelm, A.F., 2008. Simulated chronic nitrogen deposition increases carbon storage in Northern Temperate forests. Glob. Change Biol. 14, 142–153.

Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quéré, C., Scholes, R.J., Wallace, D.W.R., 2001. The carbon cycle and atmospheric carbon dioxide. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 183–237.

Prescott, C.E., 2005. Decomposition and mineralization of nutrients from litter and humus. In: BassiriRad, H. (Ed.), Ecological Studies. Springer–Verlag, Berlin Heidelberg, pp. 15–41.

Price, C., Rind, D., 1994. The impact of a $2 \times CO_2$ climate on lightning-caused fires. J. Clim. 7, 1484–1494.

Pritchard, S.G., Strand, A.E., McCormack, M.L., Davis, M.A., Finz, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., Oren, R., 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO_2-enrichment: a six-year-minirhizotron study. Glob. Change Biol. 14, 588–602.

Pushnik, J.C., Demaree, R.S., Houpis, J.L.J., Flory, W.B., Bauer, S.M., Anderson, P.D., 1995. The effect of elevated carbon dioxide on a Sierra-Nevadan dominant species: Pinus ponderosa. J. Biogeogr. 22, 249–254.

Pushnik, J.C., Garcia-Ibilcieta, D., Bauer, S., Anderson, P.D., Bell, J., Houpis, J.L.J., 1999. Biochemical responses and altered genetic expression patterns in ponderosa pine (Pinus ponderosa Doug ex P, Laws) grown under elevated CO_2. Water Air Soil Pollut. 116, 413–422.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.

Raffa, K.F., Berryman, A.A., 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol. Monogr. 53, 27–49.

Rehfeldt, G.E., 1978. Genetic differentiation of Douglas-fir populations from the northern Rocky Mountains. Ecology 59, 1264–1270.

Rehfeldt, G.E., 1979. Ecotypic differentiation in populations of *Pinus monticola* in north Idaho – myth or reality? Am. Nat. 114, 627–636.

Rehfeldt, G.E., 1982. Differentiation of *Larix occidentalis* populations from the northern Rocky Mountains. Silvae Genet. 31, 13–19.

Rehfeldt, G.E., 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. Silvae Genet. 32, 9–14.

Rehfeldt, G.E., 1986a. Adaptive variation in *Pinus ponderosa* from intermountain regions, I. Snake and Salmon River Basins. For. Sci. 32, 79–92.

Rehfeldt, G.E., 1986. Adaptive variation in *Pinus ponderosa* from intermountain regions. II. Middle Columbia River system. Research Paper INT-737. USDA Forest Service, Intermountain Research Station.

Rehfeldt, G.E., 1987. Adaptive variation and seed transfer for ponderosa pine in central Idaho. Research Note INT-373. USDA Forest Service, Intermountain Research Station.

Rehfeldt, G.E., 1988. Ecological genetics of *Pinus contorta* from the Rocky Mountains (USA): a synthesis. Silvae Genet. 37, 131–135.

Rehfeldt, G.E., Hoff, R.J., Steinhoff, R.J., 1984. Geographic patterns of genetic variation in *Pinus monticola*. Bot. Gazette 145, 229–239.

Rehfeldt, G.E., Wykoff, W.R., Ying, C.C., 2001. Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. Clim. Change 50, 355–376.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S., Gessler, A., 2006. Physiological responses of forest trees to heat and drought. Plant Biol. 8, 556–571.

Repo, T., Hanninen, H., Kellomaki, S., 1996. The effects of long-term elevation of air temperature and CO_2 on the frost hardiness of Scots pine. Plant Cell Environ. 19, 209–216.

Robinson, D.C.E., Beukema, S.J., Greig, L.A., 2008. Vegetation models and climate change: workshop results. In: Prepared by ESSA Technologies Ltd., for Western Wildlands Environmental Threat Assessment Center, Prineville, OR, p. 50.

Rogers, H.H., Runion, G.B., Krupa, S.V., 1994. Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. Environ. Pollut. 83, 155–189.

Ross, S.D., 1991. Promotion of flowering in potted white spruce grafts by root pruning: its relationship to drought and shoot elongation. Can. J. For. Res. 21, 680–685.

Ross, S.D., Webber, J.E., Pharis, R.P., Owens, J.N., 1985. Interaction between gibberellin A4/7 and root-pruning on the reproductive and vegetative process in Douglas-fir. I. Effects on flowering. Can. J. For. Res. 15, 341–347.

Rosso, P.H., Hansen, E.M., 2003. Predicting Swiss needle cast disease distribution and severity in young Douglas-fir plantations in coastal Oregon. Phytopathology 93, 790–798.

Rowe, J.S., 1993. Concepts of fire effects on plant individuals and species. In: Wein, R.W., Maclean, D.A. (Eds.), The Role of Fire in Northern Circumpolar Ecosystems. John Wiley & Sons, Ltd., New York, NY, USA.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126, 543–562.

Sage, R.F., Sharkey, T.D., Seemann, J.R., 1989. Acclimation of photosynthesis to elevated CO_2 in five C3 species. Plant Physiol. 89, 590–596.

Saito, T., Terashima, I., 2004. Reversible decreases in the bulk elastic modulus of mature leaves of deciduous *Quercus* species subjected to two drought treatments. Plant Cell Environ. 27, 863–875.

Sala, A., 2009. Lack of direct evidence for the carbon-starvation hypothesis to explain drought-induced mortality in trees. Proc. Natl. Acad. Sci. USA 106, E68.

Sala, A., Piper, F., Hoch, G., 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. New Phytol. 186, 274–281.

Salathé Jr., E.P., Leung, L.R., Qian, Y., Zhang, Y., 2009. Regional climate models: regional climate model projections for the state of Washington. In: McGuire Elsner, M., Littell, J., Binder, L.W. (Eds.), Implications of 21st Century Climate Change for the Hydrology of Washington State. Center for Science in the Earth System, Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Seattle, WA, pp. 45–67.

Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G., Vourlitis, G., 2001. Tree and forest functioning in response to global warming. New Phytol. 149, 369–399.

Saxe, H., Ellsworth, D.S., Heath, J., 1998. Tree and forest functioning in an enriched CO_2 atmosphere. New Phytol. 139, 395–436.

Schmidtling, R.C., 1994. Use of provenance tests to predict response to climatic change: loblolly pine and Norway spruce. Tree Physiol. 14, 805–817.

Schoffl, F., Prandl, R., Reindl, A., 1998. Regulation of the heat-shock response. Plant Physiol. 117, 1135–1141.

Schwilk, D.W., Ackerly, D.D., 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94, 326–336.

Seidel, K.W., 1986. Tolerance of seedlings of ponderosa pine, Douglas-fir, grand fir, and Engelmann spruce for high temperatures. Northwest Sci. 60, 1–7.

Selas, V., Piovesan, G., Adams, J.M., Bernabei, M., 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. Can. J. For. Res. 32, 217–225.

Seymour, V.A., Hinckley, T.M., Morikawa, Y., Franklin, J.F., 1983. Foliage damage in coniferous trees following volcanic ashfall from Mt St. Helens. Oecologia 59, 339–343.

Shaw III, C.G., Kile, G.A., 1991. *Armillaria* Root Disease Agricultural Handbook No. 691. U.S. Department of Agriculture, Washington D.C., USA.

Shore, T.L., Safranyik, L., Lemieux, J.P., 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Can. J. For. Res. 30, 44–49.

Silen, R.R., 1963. Effects of altitude on factors of pollen contamination of Douglas-fir seed orchards. J. For. 61, 281–283.

Slaney, M., Wallin, G., Medhurst, J., Linder, S., 2007. Impact of elevated carbon dioxide concentration and temperature on bud burst and shoot growth of boreal Norway spruce. Tree Physiol. 27, 301–312.

Slavov, G.T., Howe, G.T., Adams, W.T., 2005. Pollen contamination and mating patterns in a Douglas-fir seed orchard as measured by simple sequence repeat markers. Can. J. For. Res. 35, 1592–1603.

Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Glob. Ecol. Biogeogr. 10, 621–637.

Smith, S.A., Beaulieu, J.M., 2009. Life history influences rates of climatic niche evolution in flowering plants. Proc. R. Soc. B-Biol. Sci. 276, 4345–4352.

Sniezko, R.A., 2006. Resistance breeding against nonnative pathogens in forest Trees-current successes in North America. Can. J. Plant Pathol. 28, S270–S279.

Søgaard, G., Johnsen, Ø., Nilsen, J., Junttila, O., 2008. Climatic control of bud burst in young seedlings of nine provenances of Norway spruce. Tree Physiol. 28, 311–320.

Sparks, J.P., Walker, J., Turnipseed, A., Guenther, A., 2008. Dry nitrogen deposition estimates over a forest experiencing free air CO_2 enrichment. Glob. Change Biol. 14, 768–781.

Sperry, J.S., Tyree, M.T., 1988. Mechanism of water stress-induced xylem embolism. Plant Physiol. 88, 581–587.

Sperry, J.S., Tyree, M.T., 1990. Water-stress-induced xylem embolism in three species of conifers. Plant Cell Environ. 13, 427–436.

Spittlehouse, D.L., 2005. Integrating climate change adaptation into forest management. For. Chron 81, 691–695.

Spittlehouse, D.L., Stewart, R.B., 2003. Adaptation to climate change in forest management. BC J. Ecosyst. Manag. 4, 1–11.

St.Clair, J.B., Howe, G.T., 2007. Genetic maladaptation of coastal Douglas-fir seedlings to future climates. Glob. Change Biol. 13, 1441–1454.

St.Clair, J.B., Mandel, N.L., Vance-Boland, K.W., 2005. Genecology of Douglas fir in western Oregon and Washington. Ann. Bot. 96, 1199–1214.

Stephan, B.R., 1973. Über Anfälligkeit und Resistenz von Douglasien-Herkünften gegenüber *Rhabdocline pseudotsugae*. Silvae Genet. 22, 149–153.

Stitt, M., 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. Plant Cell Environ. 14, 741–762.

Surano, K.A., Daley, P.F., Houpis, J.L.J., Shinn, J.H., Helms, J.A., Palassou, R.J., Costella, M.P., 1986. Growth and physiological responses of *Pinus ponderosa* Dougl ex P. Laws. to long-term elevated CO_2 concentrations. Tree Physiol. 2, 243–259.

Swedjemark, G., Johannesson, H., Stenlid, J., 1999. Intraspecific variation in *Heterobasidion annosum* for growth in sapwood of *Picea abies* and *Pinus sylvestris*. Eur. J. For. Pathol. 29, 249–258.

Tague, C., Grant, G., Farrell, M., Choate, J., Jefferson, A., 2008. Deep groundwater mediates streamflow response to climate warming in the Oregon Cascades. Clim. Change 86, 189–210.

Tague, C., Grant, G.E., 2009. Groundwater dynamics mediate low-flow response to global warming in snow-dominated alpine regions. Water Resour. Res. 45, W07421.

Tapias, R., Climent, J., Pardos, J.A., Gil, L., 2004. Life histories of Mediterranean pines. Plant Ecol. 171, 53–68.

Tardieu, F., Davies, W.J., 1993. Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. Plant Cell Environ. 16, 341–349.

Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecol. Appl. 13, 704–719.

Taylor, A.H., Trouet, V., Skinner, C.N., 2008. Climatic influences on fire regimes in montane forests of the southern Cascades, California USA. Int. J. Wildland Fire 17, 60–71.

Taylor, S.W., Carroll, A.L., Alfaro, R.I., Safranyik, L., 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. In: Safranyik, L., Willson, B. (Eds.), The Mountain Pine Beetle. A Synthesis of Biology, Management, and Impacts on Lodgepole Pine. Natural Resources Canada. Canadian Forest Service, Victoria, BC, Canada.

Temel, F., Johnson, G., Adams, W., 2005. Early genetic testing of coastal Douglas-fir for Swiss needle cast tolerance. Can. J. For. Res. 35, 521–529.

Teskey, R.O., Grier, C.C., Hinckley, T.M., 1984. Change in photosynthesis and water relations with age and season in *Abies amabilis*. Can. J. For. Res. 14, 77–84.

Teskey, R.O., Will, R.E., 1999. Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. Tree Physiol. 19, 519–525.

Tezara, W., Mitchell, V.J., Driscoll, S.D., Lawlor, D.W., 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature 401, 914–917.

Timmis, R., Flewelling, J., Talbert, C., 1994. Frost injury prediction model for Douglas-fir seedlings in the Pacific Northwest. Tree Physiol. 14, 855–869.

Tingey, D.T., Lee, E.H., Phillips, D.L., Rygiewicz, P.T., Waschmann, R.S., Johnson, M.G., Olszyk, D.M., 2007. Elevated CO_2 and temperature alter net ecosystem C exchange in a young Douglas fir mesocosm experiment. Plant Cell Environ. 30, 1400–1410.

Tingey, D.T., Phillips, D.L., Johnson, M.G., 2000. Elevated CO_2 and conifer roots: effects on growth, life span and turnover. New Phytol. 147, 87–103.

Tissue, D.T., Griffin, K.L., Ball, J.T., 1999. Photosynthetic adjustment in field-grown ponderosa pine trees after six years of exposure to elevated CO_2. Tree Physiol. 19, 221–228.

Tjoelker, M.G., Oleksyn, J., Reich, P.B., 1998. Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature. Tree Physiol. 18, 715–726.

Tjoelker, M.G., Oleksyn, J., Reich, P.B., 1999. Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. Glob. Change Biol. 5, 679–691.

Tognetti, R., Longobucco, A., Miglietta, F., Raschi, A., 1999. Water relations, stomatal response and transpiration of Quercus pubescens trees during summer in a Mediterranean carbon dioxide spring. Tree Physiol. 19, 261–270.

Tolley, L.C., Strain, B.R., 1984. Effects of CO_2 enrichment and water stress on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings. Can. J. Bot. 62, 2135–2139.

Trenberth, K.E., Jones, P.D., Ambenje, P., Bojariu, R., Easterling, D., Klein Tank, A., Parker, D., Rahimzadeh, F., Renwick, J.A., Rusticucci, M., Soden, B., Zhai, P., 2007. Observations: surface and atmospheric climate change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 235–336.

Tschaplinski, T.J., Stewart, D.B., Hanson, P.J., Norby, R.J., 1995. Interactions between drought and elevated CO_2 on growth and gas exchange of seedlings of three deciduous tree species. New Phytol. 129, 63–71.

Turner, D.P., Ritts, W.D., Law, B.E., Cohen, W.B., Yang, Z., Hudiburg, T., Campbell, J.L., Duane, M., 2007. Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. Biogeosciences 4, 597–612.

Tyree, M.T., Cochard, H., Cruiziat, P., Sinclair, B., Ameglio, T., 1993. Drought induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant Cell Environ. 16, 879–882.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. New Phytol. 119, 345–360.

Tyree, M.T., Salleo, S., Nardini, A., Lo Gullo, M.A., Mosca, R., 1999. Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? Plant Physiol. 120, 11–21.

Tyree, M.T., Sperry, J.S., 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. Plant Physiol. 88, 574–580.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.

van Mantgem, P.J., Stephenson, N.L., Keeley, J.E., 2006. Forest reproduction along a climatic gradient in the Sierra Nevada, California. For. Ecol. Manag. 225, 391–399.

Wang, T., Hamann, A., Yanchuk, A., O'Neill, G.A., Aitken, S.N., 2006. Use of response functions in selecting lodgepole pine populations for future climates. Glob. Change Biol. 12, 2404–2416.

Wang, W.X., Vinocur, B., Altman, A., 2003. Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218, 1–14.

Wang, Y.P., Jarvis, P.G., 1990. Description and validation on an array model – MAESTRO. Agric. For. Meteorol. 51, 257–280.

Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204, 1380–1386.

Waring, R.H., Pitman, G.B., 1983. Physiological stress in lodgepole pine as a precursor for mountain pine beetle attack. Z Angew Entomol. 96, 265–270.

Waring, R.H., Pitman, G.B., 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. Ecology 66, 889–897.

Way, D.A., Sage, R.F., 2008. Elevated growth temperatures reduce the carbon gain of black spruce [*Picea mariana* (Mill.) BSP]. Glob. Change Biol. 14, 624–636.

Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Johnson, G.P., 2010. A hybrid model for intensively managed Douglas-fir plantations in the Pacific Northwest, USA. Eur. J. For. Res. 129, 325–338.

West, N.E., Young, J.A., 2000. Intermountain valleys and lower mountain slopes. In: Barbour, M.G., Billings, W.D. (Eds.), North American Terrestrial Vegetation. Cambridge University Press, New York, NY, USA, pp. 255–284.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943.

White, T.L., 1987. Drought tolerance of southwestern Oregon Douglas-fir. For. Sci. 33, 283–293.

Wilkinson, S., Davies, W.J., 2002. ABA-based chemical signalling: the co-ordination of responses to stress in plants. Plant Cell Environ. 25, 195–210.

Winnett, S.M., 1998. Potential effects of climate change on US forests: a review. Clim. Res. 11, 39–49.

Woodruff, D.R., Bond, B.J., Meinzer, F.C., 2004. Does turgor limit growth in tall trees? Plant Cell Environ. 27, 229–236.

Woodruff, D.R., Meinzer, F.C., Lachenbruch, B., 2008. Height-related trends in leaf xylem anatomy and shoot hydraulic characteristics in a tall conifer: safety versus efficiency in water transport. New Phytol. 180, 90–99.

Woods, A., Coates, K.D., Hamann, A., 2005. Is an unprecedented dothistroma needle blight epidemic related to climate change? Bioscience 55, 761–769.

Worrall, J., 1983. Temperature – bud-burst relationships in amabilis and subalpine fir provenance tests replicated at different elevations. Silvae Genet. 32, 203–209.

Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. For. Ecol. Manag. 255, 686–696.

Wotton, B.M., Flannigan, M.D., 1993. Length of the fire season in a changing climate. For. Chron 69, 187–192.

Wright, C.S., Agee, J.K., 2004. Fire and vegetation history in the eastern Cascade Mountains Washington. Ecol. Appl. 14, 443–459.

Wullschleger, S.D., Gunderson, C.A., Hanson, P.J., Wilson, K.B., Norby, R.J., 2002a. Sensitivity of stomatal and canopy conductance to elevated CO_2 concentration – interacting variables and perspectives of scale. New Phytol. 153, 485–496.

Wullschleger, S.D., Jackson, R.B., Currie, W.S., Friend, A.D., Luo, Y., Mouillot, F., Pan, Y., Shao, G.F., 2001. Below-ground processes in gap models for simulating forest response to global change. Clim. Change 51, 449–473.

Wullschleger, S.D., Tschaplinski, T.J., Norby, R.J., 2002b. Plant water relations at elevated CO_2 – implications for water-limited environments. Plant Cell Environ. 25, 319–331.

Xiao, J.F., Zhuang, Q.L., Law, B.E., Chen, J.Q., Baldocchi, D.D., Cook, D.R., Oren, R., Richardson, A.D., Wharton, S., Ma, S.Y., Martini, T.A., Verma, S.B., Suyker, A.E., Scott, R.L., Monson, R.K., Litvak, M., Hollinger, D.Y., Sun, G., Davis, K.J., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Fischer, M.L., Foster, D.R., Gu, L.H., Hadley, J.L., Katul, G.G., Roser, Y., McNulty, S., Meyers, T.P., Munger, J.W., Noormets, A., Oechel, W.C., Paw, K.T., Schmid, H.P., Starr, G., Torn, M.S., Wofsy, S.C., 2010. A continuous measure of gross primary production for the conterminous United States derived from MODIS and AmeriFlux data. Remote Sens. Environ. 114, 576–591.

Yanchuk, A.D., Murphy, J.C., Wallin, K.F., 2008. Evaluation of genetic variation of attack and resistance in lodgepole pine in the early stages of a mountain pine beetle outbreak. Tree Genet. Genomes 4, 171–180.

Yordanov, I., Velikova, V., Tsonev, T., 2000. Plant responses to drought, acclimation, and stress tolerance. Photosynthetica 38, 171–186.

Zak, D.R., Holmes, W.E., Finzi, A.C., Norby, R.J., Schlesinger, W.H., 2003. Soil nitrogen cycling under elevated CO_2: a synthesis of forest FACE experiments. Ecol. Appl. 13, 1508–1514.

Zedler, P.H., Gautier, C.R., McMaster, G.S., 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64, 809–818.

Zhang, J.W., Marshall, J.D., 1995. Variation in carbon isotope discrimination and photosynthetic gas exchange among populations of *Pseudotsuga menziesii* and *Pinus ponderosa* in different environments. Funct. Ecol. 9, 402–412.

Zobel, D.B., 1974. Local variation in intergrading *Abies grandis* – A. concolor populations in central Oregon Cascades II. Stomatal reaction to moisture stress. Bot. Gaz. 135, 200–210.

Zwieniecki, M.A., Holbrook, N.M., 2009. Confronting Maxwell's demon: biophysics of xylem embolism repair. Trends Plant Sci. 14, 530–534.