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Predicting effects of climate change on productivity and persistence of forest trees

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Abstract

Global climate change increases uncertainty in sustained functioning of forest ecosystems. Forest canopies are a key link between terrestrial ecosystems, the atmosphere, and climate. Here, we introduce research presented at the 66th meeting of the Ecological Society of Japan in the symposium “Structure and function of forest canopies under climate change.” Old-growth forest carbon stores are the largest and may be the most vulnerable to climate change as the balance between sequestration and emission could easily be tipped. Detailed structural analysis of individual large, old trees shows they are allocating wood to the trunk and crown in patterns that cannot be deduced from ground, thus can be used to more accurately quantify total forest carbon and sequestration. Slowly migrating species sensitive to novel climatic conditions will have to acclimate at the individual level. Accounting for physiological responses of trees to climate change will improve predictions of future species distributions and subsequent functioning of forest ecosystems. Field experiments manipulating temperature and precipitation show how trees compensate physiologically to mitigate for higher temperatures and drought. However, it is difficult to measure acclimation responses over long timeframes. Intraindividual trait variation is proposed as an indicator of acclimation potential of trees to future conditions and suggests that acclimation potential may vary among regional

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populations within a species. Integrating whole-tree structural data with physiological data offers a promising avenue for understanding how trees will respond to climatic shifts.

KEYWORDS

canopy structure, climate adaptation, physiological acclimation, population dynamics, reproduction

1 | INTRODUCTION

Trees connect the atmosphere to terrestrial ecosystems on ~40% of Earth's land surface (Bastin et al., 2019), comprising biodiverse forests responsible for ~46% of global terrestrial carbon flux (Pan et al., 2011). Biodiversity and carbon storage are linked; more organisms with overlapping functional roles provide functional redundancy. Such redundant systems are more resilient to abiotic perturbation, disease and insect outbreaks (Thompson, Mackey, McNulty, & Mosseler, 2009; Yachi & Loreau, 2007), leading to more stable forest cover and captured carbon through time (Osuri et al., 2019). Global climate change is altering basic physiological processes like photosynthesis and respiration (Kirschbaum, 2004) affecting individual-level integrated processes like growth (Charney et al., 2016), mortality (Carnicer et al., 2011) and phenology (Menzel, Sparks, Estrella, & Roy, 2006). Such alterations will change ecosystem and community structure as well as ability of forests to act as carbon sinks and will likely have cascading effects on geographical-scale species distributions (Iverson & McKenzie, 2013). Therefore, predicting which species persist in an ecosystem and how they maintain productivity will provide insights for the future composition, structure and function of forest ecosystems.

Whether or not a species persists in a forest, either through range-shift or local extinction, is partially dependent on both indirect and direct effects of climate change (Figure 1a). Indirect effects operate through intermediate mechanisms, and as a consequence, are less predictable. Disturbance regime change (Dale et al., 2001) and altered competitive interactions (e.g., Bolte et al., 2010) are two examples of indirect effects. Outcomes of such changes are governed by erratic or heterogeneous processes (e.g., frequency and spatial variability of fires and storms), permit ecological feedbacks (e.g., altered competition with cascading effects), and are probably not stationary through time. Such an assortment of interacting factors makes prediction of species persistence for periods beyond tree lifespans (decades to millennia) highly uncertain.

Some species are likely limited by direct effects of climate. Direct effects result when climatic parameters approach physiological limits and affect tree function. Examples include the ability to photosynthesize at high temperature (Kirschbaum, 2004) or conduct water during drought (Johnson et al., 2018). Physiological and growth responses may be more predictable, especially if species are experiencing climatic extremes because we have sophisticated models of physiological processes based on experimental manipulation (Zimmermann et al., 2009). Physiological response to manipulated temperature, CO_2 concentration and water availability can be elicited and measured during the course of a typical 1–3-year study. Identifying physiological limits of species will help researchers describe their potential to survive and grow under a changing climate. The most vulnerable species will be found in restricted ranges closely tracking a narrow set of climatic variables, such as may be the case with the range of *Picea sitchensis* being largely restricted to coastal environments (Burns & Honkala, 1990).

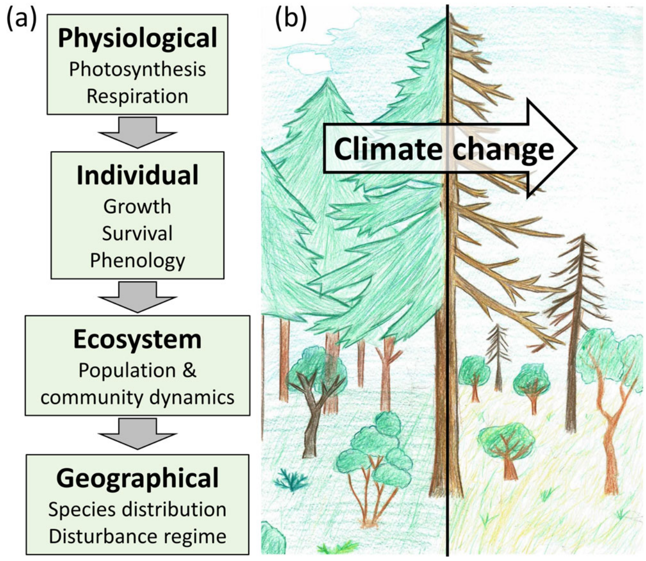

FIGURE 1 Expected cascading effects (direct and indirect) of climate change on forest ecosystems from physiological to geographical processes (a). Being slow-migrating, sessile organisms, extant trees will have to acclimate to climate change *in situ* or, in some extreme cases, face mortality and ultimately local extinction resulting in ecosystem shifts (b, illustration by Hikaru Ishii) [Color figure can be viewed at wileyonlinelibrary.com]

Forest productivity may be fundamentally altered if particularly vulnerable, yet ecologically important species are lost due to physiological stress. To illustrate, *Tsuga heterophylla* from the Pacific Northwest, United States is shallow-rooted and the most sensitive to moisture stress of any co-occurring species (Lassoie, Hinckley, & Grier, 1985; Mathys, Coops, & Waring, 2014). It is numerically dominant, shade-tolerant and accounts for ~21% of leaf area but only ~13% of total mass in moist *Pseudotsuga-Tsuga* forests (Sillett et al., 2018). Due to these attributes, *T. heterophylla* disproportionately contributes to the productive capacity in the mid-canopy and understory. Because higher temperatures increase evapotranspiration, and summers are dry in the Pacific Northwest, *T. heterophylla* is more likely to track poleward movement of temperature than species with wider ecological amplitude like co-occurring *Pseudotsuga menziesii* (Lassoie et al., 1985).

Physiologically vulnerable species whose ranges are receding on one front and constrained on another might need to acclimate to climate change in situ (Figure 1b). Climate warming is progressing at faster rates than any previous climatic transition in Earth's history (Visser, 2008; Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The global mean estimate of the velocity of pole-ward movement of warmer climate zones is 0.42 km/year (Lorie et al., 2009). During past climatic transitions, many plants responded by migrating (Brubaker, 1988; Wing et al., 2005). Currently, however, many species are not migrating as fast as climate zones would imply for reasons discussed above and also because competing species persist in the migration path (Bertrand et al., 2011). Furthermore, contemporary landscapes are highly fragmented, comprising extensive areas of human influence which act as migration barriers (Meier, Lischke, Schmatz, & Zimmermann, 2012).

During the 66th meeting of the Ecological Society of Japan, in a symposium titled "Structure and function of forest canopies under climate change," we explored responses of carbon gain, physiology and trait variability of trees to varying temperature and moisture stress. Here, we summarize and synthesize the findings of these talks with other research. Several questions remain largely unanswered: Can individual trees acclimate physiologically to warmer temperatures and changes in precipitation pattern? How will this affect structure and function of forest ecosystems in the future? Are acclimation potentials of various forest species sufficient to compensate for physiological challenges imposed by climate change? In this review, we explore and propose ways in which forest canopy research can help us better predict future effects of climate on forest composition, structure and function.

2 | ESTIMATING PRODUCTIVITY IN LARGE TREES THROUGH STRUCTURAL ANALYSIS

Old-growth forests store more carbon than younger successional stages because they contain distinguishing features such as large emergent trees, abundant snags and logs and high understory productivity (Spies & Franklin, 1991; Van Pelt, Sillett, Kruse, Freund, & Kramer, 2016). The carbon debt incurred by cutting old forests is so large that it is more beneficial to the global carbon budget (and ecologically) to reserve remaining old-growth forests and accelerate development of mature forest to old-growth conditions rather than harvesting and capturing the carbon off-site in wood products and buildings (Franklin, Johnson, & Johnson, 2018; Law et al., 2018). However, because of their relative inaccessibility, quantifying how much carbon large trees and old forest store is not trivial.

Because large trees are so important for storing carbon and remain an active sink into old age (Bastin et al., 2019; Luyssaert et al., 2008), accurate means of quantifying their size and growth is needed (Sillett, Van Pelt, Carroll, Campbell-Spickler, & Antoine, 2020). The ability to predict contributions of the largest individuals will improve area-based estimates of forest carbon. Although it is socially unacceptable to cut down the largest trees to measure them, including them in allometric equations for predicting biomass and growth is critical to eliminate the danger of extrapolation (Figure 2). Kramer et al. (2018) presented a method called "crown mapping" as an accurate way to quantify biomass and growth of large trees. Crown mapping entails tree climbing, three-dimensional mapping and core sampling large trees at multiple heights (Kramer et al., 2018).

Large and old trees develop irregular basal and crown shapes, therefore typical measurements (i.e., basal diameter and height) are less accurate predictors in biomass and growth equations than equations accounting for old-tree attributes (Ishii, Sillett, & Carroll, 2017). Modified measurements accounting for circumferential air-spaces (functional diameter), inflated diameters due to buttressing (diameter above buttress) and crown volume explain from 97 to 99% of dry biomass variability in even the largest trees (Ishii et al., 2017; Sillett et al., 2020; Sillett, Van Pelt, Carroll, Campbell-Spickler, & Antoine, 2019). Incremental growth can be masked when using repeated basal diameter measurements to infer biomass change because basal irregularities increase measurement error. Additionally, narrow basal ring increments of large trees may imply negligible growth even if the trees are growing rapidly elsewhere. For example, an increasing proportion of diameter growth is allocated to branches and higher along the trunk as trees age (Ishii et al.,

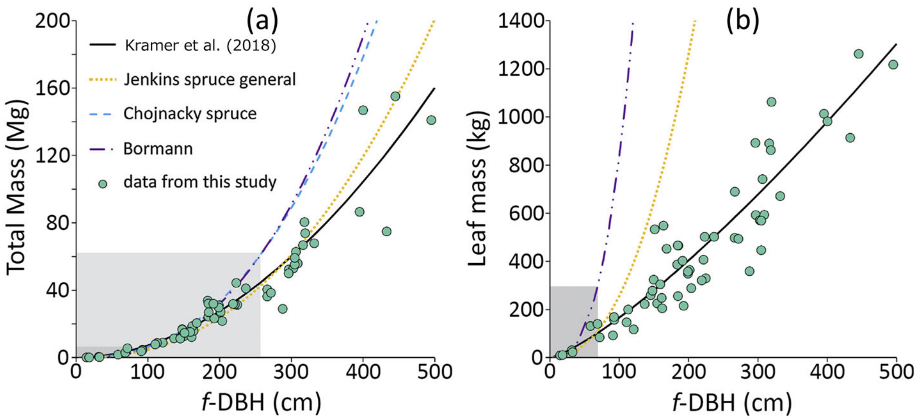

FIGURE 2 Data (green circles) and predictions (solid line) for total dry (a) and leaf mass (b) from *Picea sitchensis* up to ~500-cm diameter plotted with predictions (colored lines) from allometric equations from Jenkins, Chojnacky, Heath, and Birdsey (2004), Chojnacky, Heath, and Jenkins (2014), and Bormann (1990). Diameter is expressed as functional diameter at breast height (*f*-DBH, 1.37 m), which accounts for air spaces of complex tree bases, see Kramer, Sillett, & Van Pelt, 2018. Light and dark gray boxes show range of diameters and predictions reported in Jenkins (≤ 250 cm) and Bormann (≤ 78 cm), respectively. Jenkins leaf mass is calculated from product of the predicted leaf ratio from an equation based on trees ≤ 78-cm diameter and total mass. Chojnacky et al. (2014) predicted leaf mass is the same as Bormann (1990) model and not shown. Figure reprinted from Kramer et al. (2018) with permission from Elsevier [Color figure can be viewed at wileyonlinelibrary.com]

2017; Kramer et al., 2018; Sillett et al., 2010). Despite growth efficiency (defined here as: leaf mass/biomass increment) declines with age, crown mapping shows that individual tree biomass increases with age such that individual redwood trees from ~500 to >2,000 years old can produce an average of ~120 to ~300 kg/year and up to 770 kg/year of dry biomass (Sillett et al., 2015; Sillett et al., 2020). Although rapidly growing fully stocked second-growth forests can produce more biomass per hectare per year than old forests, the greater standing biomass added to substantial growth of large trees in old forests makes them important conservation priorities. For example, plantation redwood can produce ~10 Mg/ha/year more than the heaviest old-growth forest but contain only 227 versus 4,152 Mg/ha of the live biomass, respectively (Sillett et al., 2020).

To prepare forests for climate change, managers are using spatially variable harvests and thinning because these methods are expected to increase ecosystem resistance (ability to resist change) to drought and fire (Restaino et al., 2019), as well as resilience (ability to rebound) after disturbance (Churchill et al., 2013). Trees remaining after such treatments grow and develop with varying numbers of competitors, thus tree and forest carbon gain can be difficult to predict unless equations account for variable tree spatial distribution, crown form, and growth rates. Kramer, Sillett, Van Pelt, and Franklin (2019) presented a chronosequence of tree-crown development in *P. sitchensis* from 100–400 years old and from the full range of natural forest density as an example. For a given diameter, crown volume—crown volume is the best predictor of leaf area and hence reflects growth potential—for trees from 60 to 80 m height can vary 24-fold. After trees reach apex height (~200 years), growth is preferentially allocated to the crown. Crown mass increases as a percent of total mass from ~10 to 20% depending on tree age and how many competitors are nearby. Larger crowns also result in more wood allocation to the tree base than higher along the trunk (Deleuze & Houllier, 2002; Sumida, Miyaura, & Torii, 2013). Therefore, biomass growth is overestimated by equations relying on diameter increments to predict large-crowned trees. Total mass given diameter is actually slightly larger in more dense neighborhoods with small crowns because trunks are more columnar (Kramer et al., 2018). Additionally, branch wood is ~43 to 132% denser than trunk wood (Kramer et al., 2018; Sillett et al., 2018) and trunk wood density changes with height ~18% (Sillett et al., 2018), so wood density needs to be integrated into whole-tree estimates (Wassenberg, Chiu, Guo, & Spiecker, 2015). Thus, detailed mapping of trunk and crown dimensions improve predictions of biomass growth in large trees (Sillett et al., 2020) as well as stand-level consequences of climate-related silvicultural treatments.

3 | PHYSIOLOGICAL ACCLIMATION TO CHANGES IN TEMPERATURE AND PRECIPITATION

Particular tree species are able to persist in a wide variety of climates because they maintain critical physiological parameters within functional ranges. For example, water content is kept above 0.6–0.75 to maintain leaf turgor pressure (Azuma, Ishii, & Masaki, 2019; Williams, Næsborg & Dawson, 2017). In essence, trees regulate processes like photosynthesis and respiration, or account for inefficiencies in one process by compensating with another. Critical functions affecting the ability of trees to compensate for changes in climatic variables include: maintaining photosynthetic rates, positive carbon balance, hydraulic conductivity and reproduction.

Forests generally absorb more atmospheric CO_2 via photosynthesis than they release via respiration. However, a warming climate has the potential to make forests weaker carbon sinks or even carbon sources (Dusenge, Duarte, & Way, 2019; Luo, 2007). Upper canopies of forests sequester a disproportionate amount of CO_2, relative to whole-forest leaf area (Doughty & Goulden, 2008; Kumagai et al., 2006). The top of the canopy, however, is generally more physiologically stressful, with hotter, windier conditions and higher vapor pressure deficit (e.g., Rey-Sánchez, Slot, Posada, & Kitajima, 2017). Net photosynthesis rates increase with increasing temperature up to a peak, then decline, with the peak rate occurring at the optimum temperature for photosynthesis (T_{opt}, Figure 3). Even though canopy leaves can be quite plastic in response to changing vertical microclimate (e.g., Coble, VanderWall, Mau, & Cavaleri, 2016), recent work has shown that upper canopies in both tropical and temperate forests are experiencing temperatures 3–5°C higher than T_{opt} (Doughty & Goulden, 2008; Mau, Reed, Wood, & Cavaleri, 2018).

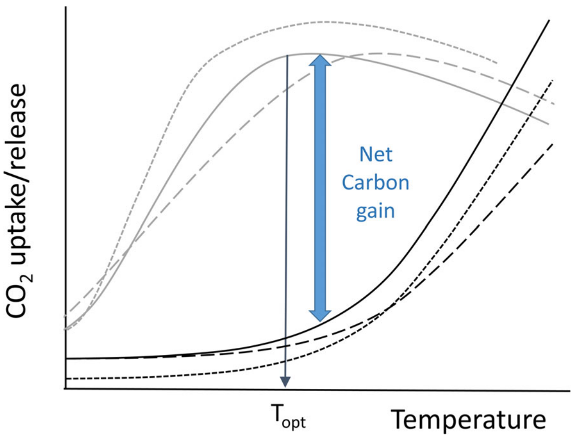

FIGURE 3 Responses of photosynthetic CO_2 uptake (gray lines) and respiratory CO_2 release (black lines) to temperature. T_{opt} is optimal temperature for photosynthesis under normal conditions (solid lines). The difference between uptake and release by photosynthesis and respiration is net carbon gain. Photosynthetic acclimation involves increased rate of CO_2 uptake at higher temperatures, either through a shift in T_{opt} to higher temperature (dashed line) or increasing maximum photosynthetic rate at higher temperature (dotted line). Respiration acclimation involves reduced rate of CO_2 release at a given temperature, either through reduced sensitivity to increasing temperature (dashed line) or reduced basal rates of respiration (dotted line) [Color figure can be viewed at wileyonlinelibrary.com]

Acclimation to warming could be accomplished by either upregulating photosynthesis or downregulating plant respiration (Figure 3). Photosynthetic acclimation involves increased rates of CO_2 uptake at higher temperatures, either through an upward shift of T_{opt} (photosynthesis peaks at higher optimum temperature) or by increasing photosynthetic rates at the optimum temperature (Berry & Bjorkman, 1980; Way & Yamori, 2014). Respiration acclimation, on the other hand, involves reduced rates of CO_2 release at a given temperature, either through reduced sensitivity to increasing temperature (i.e., less steep exponential respiration-temperature response curve) or reduced basal rates of respiration (i.e., lower *y*-intercept of the curve) (Atkin & Tjoelker, 2003). Only a few studies examine physiological responses to leaf-level experimental warming in forest canopies, and they show mixed results. While respiration acclimated (i.e., downregulated) in a tropical forest canopy following several weeks of warming (Slot et al., 2014), photosynthesis did not acclimate (i.e., upregulate) to experimental warming in a temperate forest canopy, and in fact, peak photosynthetic rates at T_{opt} declined (Carter & Cavaleri, 2018). While not specifically measuring acclimation, Doughty (2011) also found decreases in net photosynthetic rates after leaf-level warming in a tropical forest canopy, presumably due to heat-induced biochemical damage.

As a part of the tropical responses to altered climate experiment in Puerto Rico (Kimball et al., 2018) the first canopy warming experiment was initiated to measure both photosynthetic and respiratory acclimation along the canopy height gradient (Figure 4, using methods described in Carter & Cavaleri, 2018). After 1 month, leaf respiration acclimated through a downregulation of temperature sensitivity across the canopy height gradient, where respiration rates did not increase as steeply with measurement temperature in the experimentally warmed leaves compared to control leaves (K. Carter, unpublished). Net photosynthesis did not acclimate (i.e., upregulate with warming) at any height, and the rate of photosynthetic electron transport upregulated only in the understory. The lack of photosynthetic acclimation of upper canopy leaves following canopy warming suggests that the most productive portion of canopy trees are operating near their acclimation limit, and further increases in temperature may push some tropical tree species beyond their physiological optima, potentially resulting in reduced overall forest carbon uptake.

Trees can also compensate for reduced photosynthesis by distributing net carbon gain over whole seasons.

Because trees integrate photosynthesis and respiration over time, measurements of responses over a few months may not provide a complete picture of whole-plant or whole-forest carbon balance. This is an especially important consideration because, although photosynthesis may upregulate in hotter temperatures, it does not increase exponentially like respiration often does (Ryan, Linder, Vose, & Hubbard, 1994). If photosynthesis adjusts to optimize at a higher temperature, such acclimation could be canceled by increasing respiration rates, and could lead to less CO_2 sequestration by forest canopies under global warming. Respiration rates, however, can be highly variable with season. Araki, Gyokusen, and Kajimoto (2017) show that temperature acclimation of leaf respiration could mitigate negative effects of higher temperatures on canopy carbon exchange. They show that in a young *Chamaecyparis obtusa* plantation, leaf respiration is less sensitive to the short-term temperature change in summer than in winter, suggesting that leaf respiration can acclimate to ambient (growth) temperatures. When incorporated into predictions of monthly canopy respiration, acclimation of leaf respiration contributed to decreasing canopy respiration under future warming scenarios (Figure 5). Thus, incorporating temperature acclimation of leaf respiration into carbon cycle models could reduce predictions of increased CO_2 release from forests in response to warming.

FIGURE 4 Examples of leaf heaters in the upper canopy of *Ocotea sintensii*, part of the Tropical Responses to Altered Climate Experiment (TRACE) in the Luquillo Experimental Forest in Puerto Rico (photo credit M. Cavaleri) [Color figure can be viewed at wileyonlinelibrary.com]

Many forests will also need to contend with drought as the distribution of precipitation over space and time changes (Allen et al., 2010). Two contrasting responses of trees to drought include avoidance and tolerance (McDowell et al., 2008). Drought avoidance involves stomatal control to maintain leaf water potential and conserve water at the cost of reduced CO_2 uptake (photosynthetic production), but could lead to carbon starvation under prolonged drought. In contrast, drought tolerance involves maintaining leaf gas exchange and decreased water potential, risking loss of hydraulic conductivity. The latter mechanism appears to dominate as the leading cause of mortality under drought because, in a study of 26 tree species, 100% of dead trees showed > 60% loss of conductivity, whereas only 62% had low carbohydrate reserves following drought (Adams et al., 2017; Johnson et al., 2018). Therefore, mechanisms for acclimating to water stress will likely be reflected in traits that increase a tree's ability to maintain leaf gas exchange.

As with carbon gain and temperature, leaf hydraulic properties are maintained despite increasing water stress. A throughfall exclusion experiment was conducted in a

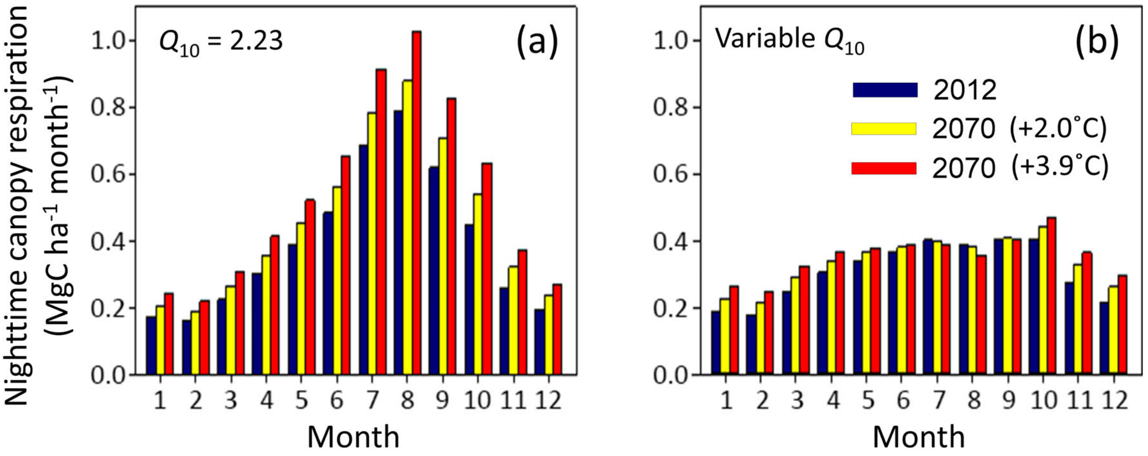

FIGURE 5 Monthly estimates of canopy respiration with no temperature acclimation of leaf respiration rate (a, static Q_{10}) and those with temperature acclimation (b, variable Q_{10}). Q_{10} is the change in respiration rate per 10°C change in temperature. Bars represent empirical data for 2012 and two warming scenarios for 2070 (+2.0 and +3.9°C) [Color figure can be viewed at wileyonlinelibrary.com]

40-year-old *Cryptomeria japonica* plantation to investigate response of the most prominent plantation species in Japan to drought (Y. Inoue, unpublished). Barriers were built around the base of the trees to exclude throughfall completely, reducing soil water potential to a range of −0.1 to −0.5 MPa. Results from the first growing season indicate no effect of drought on leaf water status, stomatal sensitivity, or morphology, suggesting that this species may be less sensitive to drought, at least in the short term. Long-term effects of drought on hydraulic acclimation of *C. japonica* are still being tested, and results could have important implications for the future of Japanese plantation forests.

Responses to drought may also vary with tree age. Azuma et al. (2019) compared mature (~100 years) and old trees (~300 years) of *Pinus densiflora* with similar height, growing next to each other in a natural experiment to test effects of tree age on leaves' ability to maintain homeostasis along the hydrostatic gradient associated with tree height. Leaves of mature trees have higher capacitance but less resistance to lower water potential than old trees. These traits, in combination with large amounts of water that can release from leaves prior to turgor loss (Azuma et al., 2019; Williams et al., 2017), may mean younger trees can compensate for water stress in the short term. In contrast, we might expect old trees to be more vulnerable to loss of hydraulic conductivity because of their lower capacitance and elasticity (Azuma et al., 2019). Older trees also have more energetic demands due to increased defense against higher pathogen loads (e.g., Shigo, 1984; Taylor, Gartner, & Morrell, 2002). Lower nitrogen (N) content in upper crown leaves and reduced photosynthesis of old *P. densiflora* (Azuma et al., 2019) may be because of the N needed by adenosine tri-phosphate to form energy-rich defensive compounds. If old trees are more carbon limited, they would adopt a drought-tolerant rather than drought-avoidant strategy to conserve carbohydrates. For older *P. densiflora* trees with higher leaf mass to area ratio (LMA), less photosynthetic mesophyll and lower N, there may be a tradeoff between anatomical acclimation to water stress, photosynthesis and energetic demand. Testing this hypothesis would necessitate integration across whole trees.

4 | PREDICTING ACCLIMATION POTENTIAL OF INDIVIDUALS AND ITS EFFECTS ON SPECIES PERSISTENCE

Because most studies only last a few years, limited data exist to quantify acclimation responses of trees over long periods, suggesting the need for surrogate indices of acclimation potential. The acclimation potential of individual organisms depends on their phenotypic plasticity and the ability of a given genotype to express different phenotypes in response to variable environmental conditions (Schlichting, 1986; Sultan, 1987). Phenotypic plasticity is especially important for sessile organisms like trees to cope with environmental perturbation and changes in growing condition during their long lives (Nicotra et al., 2010; Valladares, Gianoli, & Gómez, 2007). Thus, phenotypic plasticity will likely be a key mechanism for acclimation of trees to climate change (Chambel, Climent, Alia, & Fernando, 2005; Grulke, 2010).

Trait variation present in populations represents combined effects of physiological acclimation, phenotypic plasticity and genotypic variation in response to environmental conditions (Kreyling et al., 2014; Stojnic et al., 2015). Because individual trees must survive long-term climatic shifts, they have evolved to retain high phenotypic plasticity (Duptie, Rutschmann, Ronce, & Chuine, 2015; Petit & Hampe, 2006). In trees, phenotypic plasticity can be observed as trait variation within individuals, for example, by morphological or physiological variation from sun to shade leaves within a crown. Intraindividual trait variation represents phenotypic plasticity and the acclimation potential of individuals to gradients in environmental conditions, thus gives insight to the breadth of environmental conditions individuals can endure and could be used as a surrogate measure of acclimation potential to future climate change.

Ishii, Horikawa, Noguchi, and Azuma (2018) show that intra-canopy leaf trait variation varies among regional populations of *Fagus crenata*, suggesting that individual-level phenotypic plasticity may also vary (Figure 6). Populations near the northern and altitudinal distribution limits, where *F. crenata* is expanding its distribution range, had high intra-canopy trait variation, whereas trait variation was low for southern populations. *F. crenata* populations in southwestern Japan are isolated at high elevations, thus their low trait variability may imply low acclimation potential of individuals to climate change. Current models predicting future distribution of tree species do not take into account physiological acclimation (Smith & Dukes, 2013). If individual trees are able to acclimate, they could survive longer than predicted, while those that do not acclimate may disappear sooner.

Persistence of local populations also depends on reproductive output of individual trees. Reproduction dynamics are affected by climate change, and, through its effects on seed production, germination and seedling survival/growth, could lead to population and community structure shifts (Figure 7). Producing large quantities of

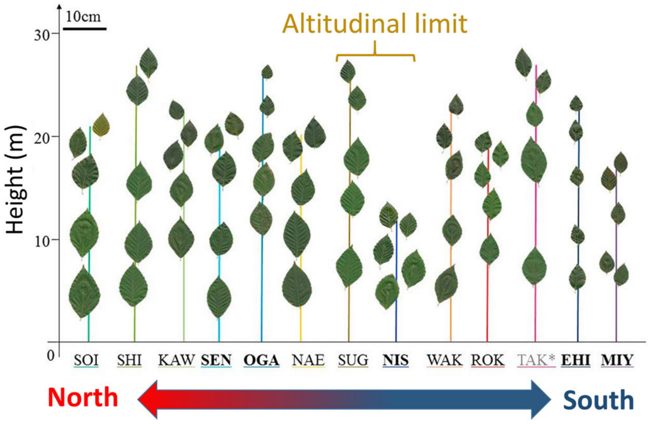

FIGURE 6 Leaf trait variation among *Fagus crenata* populations in Japan. Three-letter-acronyms stand for different regional populations including the northern distribution limit, Soibetsu Forest (SOI, 42°41′N), in Hokkaido Pref., altitudinal limits Sugadaira Field Station (SUG, 1315 m asl) and Nishikoma Research Forest (NIS, 1600 m asl) in Nagano Pref. and near the southern limit, Shiiba Research Forest (MIY, 32°13′N) in Miyazaki Pref. Other sites are: Shirakami Mts. (SHI, Aomori Pref.), Kawatabi Field Station (KAW, Miyagi Pref.), Tohoku Univ. Botanical Garden in Sendai (SEN, Miyagi Pref.), Ogawa Forest Reserve (OGA, Ibaraki Pref.), Naeba Mts. (NAE, Niigata Pref.), Wakasugi Forest Reserve (WAK, Okayama Pref.), Mt. Rokko (ROK, Hyogo Pref.), Mt. Takanosu (TAK, Hiroshima Pref.) and Komenono Research Forest (EHI, Ehime Pref.). Figure reprinted form Ishii et al. (2018) with permission from Elsevier [Color figure can be viewed at wileyonlinelibrary.com]

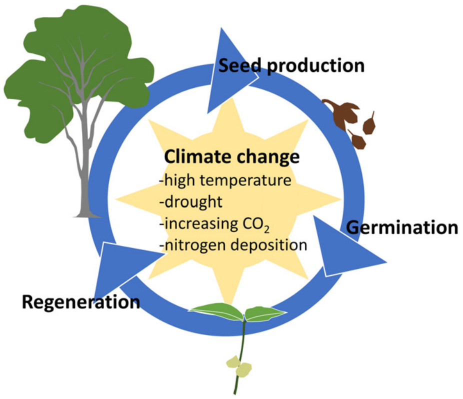

FIGURE 7 Climate-related changes in temperature, rainfall and nitrogen deposition can affect tree seed production, germination and seedling survival/growth. Ultimately affecting population and community structure of forests [Color figure can be viewed at wileyonlinelibrary.com]

flowers and seeds consumes substantial photosynthate (Ichie et al., 2013; Y. Miyazaki, Hiura, Kato, & Funada, 2002) and mineral nutrients (Han, Kabeya, & Inagaki, 2017; Sala, Hopping, McIntire, Delzon, & Crone, 2012). In particular, physiological mechanisms of intermittent and synchronous reproduction by perennial plants, called masting (Kelly, 1994), are responsive to temperature as well as resource availability (Bogdziewicz et al., 2020). Some synchronizing climatic reproduction cues, such as temperature and precipitation, may be mediated via changes in soil nutrient availability (Smaill, Clinton, Allen, & Davis, 2011). For example, in a masting species *F. crenata* flowering is induced in response to nitrogen levels in current-year shoots (Miyazaki et al., 2014). Prior studies suggest masting intensity will change in response to climate change (Monks, Monks, & Tanentzap, 2016), while masting will be unaffected by increasing mean temperatures (Kelly et al., 2013). This uncertainty may arise from different masting mechanisms among taxa. More studies designed to test physiological hypotheses of masting are needed to better predict direct and indirect effects of changing climate on plant reproductive patterns and global vegetation dynamics (Bogdziewicz et al., 2020).

In a population of *F. crenata* from a cool-temperate forest in western Japan (Akaji, Miyazaki, Hirobe, Makimoto, & Sakamoto, 2016; Ariya et al., 2016), masting intensity of mature trees affects demography via seed availability and seedling survival with time lags of up to 5 years (Y. Miyazaki, unpublished). Here, reproduction had occurred every other year for more than 14 years. Biennial seed production negatively affected shoot elongation in the canopy but not annual ring growth. The amount of viable seeds produced in a single reproductive event was small (0–64 sound seeds per m/year, mean value of 15 seed traps in a 0.5-ha plot), but mortality of seedlings during the first growing season was very low (27.6%: during the first year after germination), although it is generally higher for *F. crenata* in other forests (ca. 80%, Akashi, 1997; Masaki, Osumi, Takahashi, & Hozshizaki, 2005). As a result, masting was reflected in the age structure of the seedling population for up to 5 years. This study suggested that, if climate change affects the periodicity and intensity of reproductive output of a masting species, it may have long-term effects on the population dynamics and species persistence with several years' time lag, which must be accounted for in future demographic study designs.

5 | CONCLUSIONS AND SYNTHESIS

Mysteries of how climate will change in the future are still unveiling themselves, and responses of forests to this change are even less certain. In this review, we explore ways forest canopy research can provide insights for answering questions such as how climate change will affect productivity of forest ecosystems and whether species will be able to persist without migrating. During the 66th annual Ecological Society of Japan symposium "Structure and Function of Forest Canopies under Climate Change," topics explored how biomass, growth, metabolism, hydraulic function, reproduction and trait variation are expressed in trees under different conditions. In general, effects of increased temperature and drought were either compensated for or dampened when expressed in tree processes and traits, a scenario that suggests a lagged response to changing climate. A portion of this compensation is due to the amount of trait variability in species. How do we integrate what we have learned from these findings into a consistent strategy for determining how forests will respond to climate change? Below we outline a two-step approach that recognizes limitations of physiological studies by first limiting investigative scope, and second, posits that integrating whole-tree structure data with measurements of trait and physiological variability will allow us to predict more accurately how trees will respond.

Uncertainty is very high for how climatic stressors will affect tree survival; therefore, we first need to focus investigations to a limited set of tree species to reduce confounding variables. Despite assumptions that species must migrate poleward or up in elevation to avoid rising temperatures (e.g., Iverson & McKenzie, 2013), many move counterintuitively or not at all due to unforeseen or indirect effects of climate interactions (Zhu, Woodall, & Clark, 2012). For example, shade-intolerant *Pinus heldreichii*, is moving down in elevation as well as up, likely because stressed *Fagus sylvatica* forests along the low-elevation boundary are less competitive (Piovesan, 2019; Piovesan, Biondi, Di Filipo, & Maugeri, 2008). In such cases, ranges are constrained by factors other than climate. Climate envelopes based on species' ranges contain incomplete information about where trees can survive and no information about where they cannot, thus represent realized rather than actual niches. In reality, tree range is limited by factors such as seasonality (Bolte et al., 2010), competition (Meier et al., 2012) and disturbance regime (Johnstone et al., 2016; Serra-Diaz, Scheller, Syphard, & Franklin, 2015) at least as much as they are by mean temperature and rainfall. Many species are therefore adapted to a wider range of climate than where we currently find them. If what limits their range is not obvious or involves nonstationary complex processes, predicting their future ranges centuries or even decades ahead will not be successful.

Projections of the global distribution of forest ecosystems and their rates of carbon sequestration are made using correlational bio-climate envelope models (see Discussion by Hampe & Petit, 2005). These models tend to overestimate species losses and productivity decline because key biological aspects such as physiological acclimation and phenotypic plasticity and are not considered (Thuiller et al., 2008). Models also do not consider species interactions affecting community dynamics, such as trait-mediated interactions arising from trait plasticity (Callaway, Pennings, & Richards, 2003; Werner & Peacor, 2003). Thus, quantification of physiological acclimation and phenotypic plasticity can improve prediction of species responses to climate change and of future forest distribution.

For the second step of our approach, we suggest whole-tree integration of physiological and morphological characteristics. Trees integrate processes throughout their crowns as well as over time, therefore isolated measurements will miss emergent properties of whole trees. An example of this from the structural analysis above is that basal increment growth of a large tree can over- or underestimate whole-tree growth because it ignores the crown. Similarly, measurements during one season or in one location ignore the ability of trees to concentrate or distribute photosynthetic gain across seasons or in various parts of the crown as the sun changes position. Because trees are large and long-lived, accurately documenting and integrating spatial/temporal variation is important for understanding their physiological function. For example, tissue-based respiration is a function of tissue volume including cambium, sapwood and heartwood, which all increase with size (West, 2020). Integrating chamber-style measurements of physiology with whole-tree structure and function could explain apparently paradoxical observations. One seeming paradox is that upper leaves in the tallest angiosperm (*Eucalyptus regnans*) are more costly to make and less efficient because they have higher LMA (England & Attiwill, 2006) and lower stomatal conductance (Koch, Sillett, Antoine, & Williams, 2015), however most wood is produced by leaves in the upper crown even though these leaves are more hydraulically stressed. At the whole-tree level, it is apparently more beneficial to have more inefficient leaves in full sun than fewer efficient ones in partial shade.

Scaling from individual trees to forest ecosystems represents an even greater challenge than from isolated measurements to whole trees. Ecologists must meet this challenge because forest ecosystems represent approximately half of total global terrestrial carbon sequestration (Beer et al., 2010), and thus, are highly influential to the carbon cycle. We must gain a better understanding of the effects of climate change on forest canopy physiology, including responses to warmer temperatures and more variable rainfall, using both observations of natural variation and long-term manipulative experiments. Large-scale experimental manipulations and long term monitoring are essential for demonstrating forest-climate responses, yet such monitoring is the first to lose funding when budgets contract. If forest ecologists and physiologists are able to coalesce around a few long-term experiments such as TRACE, then we are more likely to discover consistent forest responses to climate change.

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REFERENCES

Adams, H. D., Zeppel, M. J. B., Anderegg, W. R. L., Hartmann, H., Landhäusser, S. M., Tissue, D. T., … McDowell, N. G. (2017). A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution*, *1*(9), 1285–1291. https://doi.org/10.1038/s41559-017-0248-x

Akaji, Y., Miyazaki, Y., Hirobe, M., Makimoto, T., & Sakamoto, K. (2016). The relationship between seedling survival rates and their genetic relatedness to neighboring conspecific adults. *Plant Ecology*, *217*(4), 465–470. https://doi.org/10.1007/s11258-016-0591-z

Akashi, N. (1997). Dispersion pattern and mortality of seeds and seedlings of *Fagus crenata* Blume in a cool temperate forest in western Japan. *Ecological Research*, *12*(2), 159–165. https://doi.org/10.1007/BF02523781

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., … Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, *259*(4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001

Araki, M. G., Gyokusen, K., & Kajimoto, T. (2017). Vertical and seasonal variations in temperature responses of leaf respiration in a *Chamaecyparis obtusa* canopy. *Tree Physiology*, *37*(10), 1269–1284.

Ariya, U., Hamano, K.-Y., Makimoto, T., Kinoshita, S., Akaji, Y., Miyazaki, Y., & Sakamoto, K. (2016). Temporal and spatial dynamics of an old-growth beech forest in western Japan. *Journal of Forest Research*, *21*(2), 73–83. https://doi.org/10.1007/s10310-015-0514-1

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, *8*, 343–351.

Azuma, W., Ishii, H. R., & Masaki, T. (2019). Height-related variations of leaf traits reflect strategies for maintaining photosynthetic and hydraulic homeostasis in mature and old *Pinus densiflora* trees. *Oecologia*, *189*, 317–328.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., … Crowther, T. W. (2019). The global tree restoration potential. *Science*, *365*(6448), 76–79. https://doi.org/10.1126/science.aax0848

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., … Bonan, G. B. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, *329*, 834–838.

Berry, J., & Bjorkman, O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, *31*, 491–543.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrio-Dillon, G., de Ruffray, P., Vidal, C., … Gegout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*, 517–520.

Bogdziewicz, M., Ascoli, D., Hacket-Pain, A., Koenig, W. D., Pearse, I., Pesendorfer, M., … Tanentzap, A. (2020). From theory to experiments for testing the proximate mechanisms of mast seeding: An agenda for an experimental ecology. *Ecology Letters*, *23*, 210–220.

Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J., & Roloff, A. (2010). Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. *European Journal of Forest Research*, *129*(3), 261–276. https://doi.org/10.1007/s10342-009-0323-1

Bormann, B. T. (1990). Diameter-based biomass regression models ignore large sapwood-related variation in Sitka spruce. *Canadian Journal of Forest Research*, *20*, 1098–1104.

Brubaker, L. B. (1988). Vegetation history and anticipating future vegetation change. In J. K. Agee & D. R. Johnson (Eds.), *Ecosystem management for parks and wilderness* (pp. 41–61). Seattle: University of Washington Press.

Burns, R. M., & Honkala, B. H. (1990). *Silvics of North America. Vol. 1: Conifers* (pp. 260–267). Washington, DC: U.S. Department of Agriculture, Forest Service.

Callaway, R. M., Pennings, A. C., & Richards, C. L. (2003). Phenotypic plasticity and interactions among plants. *Ecology and Evolution*, *84*, 1115–1128.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., & Peñuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 1474–1478.

Carter, K. R., & Cavaleri, M. A. (2018). Within-canopy experimental leaf warming induces photosynthetic decline instead of acclimation in two northern hardwood species. *Frontiers in Forests and Global Change*, *1*, 11.

Chambel, M. R., Climent, J., Alia, R., & Fernando, V. (2005). Phenotypic plasticity: A useful framework for understanding adaptation in forest species. *Investigación Agraria. Sistemas y Recursos Forestales*, *14*, 334–344.

Charney, N. D., Babst, F., Poulter, B., Record, S., Trouet, V. M., Frank, D., … Evans, M. E. K. (2016). Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecology Letters*, *19*(9), 1119–1128. https://doi.org/10.1111/ele.12650

Chojnacky, D. C., Heath, L. S., & Jenkins, J. C. (2014). Updated generalized biomass equations for north American tree species. *Forestry*, *87*, 129–151.

Churchill, D. J., Larson, A. J., Dahlgreen, M. C., Franklin, J. F., Hessburg, P. F., & Lutz, J. A. (2013). Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management*, *291*, 442–457. https://doi.org/10.1016/j.foreco.2012.11.007

Coble, A. P., VanderWall, B., Mau, A. C., & Cavaleri, M. A. (2016). How vertical patterns in leaf traits shift seasonally and the implications for modeling canopy photosynthesis in a temperate deciduous forest. *Tree Physiology*, *36*, 1077–1091.

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., … Wotton, B. M. (2001). Climate change and forest disturbances: Climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *Bioscience*, *51*(9), 723–734. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

Deleuze, C., & Houllier, F. (2002). A flexible radial increment taper equation derived from a process-based carbon partitioning model. *Annals of Forest Science*, *59*, 141–154.

Doughty, C. E. (2011). An in situ leaf and branch warming experiment in the Amazon. *Biotropica*, *43*, 658–665.

Doughty, C. E., & Goulden, M. L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences*, *221*, 32–49.

Duptie, A., Rutschmann, A., Ronce, O., & Chuine, I. (2015). Phenological plasticity will not help all species adapt to climate change. *Global Change Biology*, *21*, 3062–3073.

Dusenge, M. E., Duarte, A. G., & Way, D. A. (2019). Plant carbon metabolism and climate change: Elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist*, *221*, 32–49.

England, J. R., & Attiwill, P. M. (2006). Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. *Trees*, *20*, 79–90.

Franklin, J. F., Johnson, N. K., & Johnson, D. L. (2018). Climate change, carbon, and forests. In *Ecological forests management* (pp. 404–437). Long Grove, IL: Waveland Press.

Grulke, N. E. (2010). Plasticity in physiological traits in conifers: Implications for response to climate change in the western U.S. *Environmental Pollution*, *158*, 2032–2042.

Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, *8*, 461–467.

Han, Q., Kabeya, D., & Inagaki, Y. (2017). Influence of reproduction on nitrogen uptake and allocation to new organs in *Fagus crenata*. *Tree Physiology*, *36*(10), 1436–1443.

Ichie, T., Igarashi, S., Yoshida, S., Kenzo, T., Masaki, T., & Tayasu, I. (2013). Are stored carbohydrates necessary for seed production in temperate deciduous trees? *Journal of Ecology*, *101*(2), 525–531. https://doi.org/10.1111/1365-2745.12038

Ishii, H., Sillett, S. C., & Carroll, A. L. (2017). Crown dynamics and wood production of Douglas-fir trees in an old-growth forest. *Forest Ecology and Management*, *384*, 157–168.

Ishii, H. R., Horikawa, S., Noguchi, Y., & Azuma, W. (2018). Variation of intra-crown leaf plasticity of *Fagus crenata* across its geographical range in Japan. *Forest Ecology and Management*, *429*, 437–448.

Iverson, L. R., & McKenzie, D. (2013). Tree-species range shifts in a changing climate: Detecting, modeling, assisting. *Landscape Ecology*, *28*, 879–889.

Jenkins, J. C., Chojnacky, D. C., Heath, L. S., & Birdsey, R. A. (2004). Comprehensive database of diameter-based biomass regression for North American tree species. *USDA Forest Service General Technical Report* (Vol. NE-319).

Johnson, D. M., Domec, J.-C., Carter Berry, Z., Schwantes, A. M., McCulloh, K. A., Woodruff, D. R., … Jackson, R. B. (2018). Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. *Plant, Cell & Environment*, *41*(3), 576–588. https://doi.org/10.1111/pce.13121

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., … Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*(7), 369–378. https://doi.org/10.1002/fee.1311

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, *9*(12), 465–470. https://doi.org/10.1016/0169-5347(94)90310-7

Kelly, D., Geldenhuis, A., James, A., Penelope Holland, E., Plank, M. J., Brockie, R. E., … Byrom, A. E. (2013). Of mast and mean: Differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters*, *16*(1), 90–98. https://doi.org/10.1111/ele.12020

Kimball, B. A., Alonso-Rodriguez, A., Cavaleri, M. A., Reed, S. C., Gonzalez, G., & Wood, T. E. (2018). Infrared heater system for warming tropical forest understory plants and soils. *Ecology and Evolution*, *8*, 1932–1944.

Kirschbaum, M. U. F. (2004). Direct and indirect climate change effects on photosynthesis and transpiration. *Plant Biology*, *6*, 242–253.

Koch, G. W., Sillett, S. C., Antoine, M. E., & Williams, C. B. (2015). Growth maximization trumps maintenance of leaf conductance in the tallest angiosperm. *Oecologia*, *177*, 321–331.

Kramer, R. D., Sillett, S. C., & Van Pelt, R. (2018). Quantifying aboveground components of *Picea sitchensis* for allometric comparisons among tall conifers in North American rainforests. *Forest Ecology and Management*, *430*, 59–77.

Kramer, R. D., Sillett, S. C., Van Pelt, R., & Franklin, J. F. (2019). Neighborhood competition mediates crown development of *Picea sitchensis* in Olympic rainforests: Implications for restoration management. *Forest Ecology and Management*, *441*, 127–143. https://doi.org/10.1016/j.foreco.2019.03.027

Kreyling, J., Buhk, C., Backhaus, S., Hallinger, M., Huber, G., Huber, L., … Beierkuhnlein, C. (2014). Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. *Ecology and Evolution*, *4*(5), 594–605.

Kumagai, T., Ichie, T., Yoshimura, M., Yamashita, M., Kenzo, T., Saitoh, T. M., … Komatsu, H. (2006). Modelling CO_2 exchange over a Bornean tropical rain forest using measured vertical and horizontal variations in leaf-level physiological parameters and leaf area densities. *Journal of Geophysical Research Atmospheres*, *111*, 1–16.

Lassoie, J., Hinckley, T. M., & Grier, C. C. (1985). Ecophysiology of the forests of the pacific northwest. In B. F. CHabot & H. A. Mooney (Eds.), *Physiological ecology in North American plant communities*. London, England: Chapman and Hall.

Law, B. E., Hudiburg, T. W., Berner, L. T., Kent, J. J., Buotte, P. C., & Harmon, M. E. (2018). Land use strategies to mitigate climate change in carbon dense temperate forests. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 3663–3668.

Lorie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*, 1052–1055.

Luo, T. (2007). Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 683–712.

Luyssaert, S., Schulze, E.-D., Borner, A., Knohl, A., Hessenmoller, D., Law, B. E., … Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, *455*, 213–215.

Masaki, T., Osumi, K., Takahashi, K., & Hozshizaki, K. (2005). Seedling dynamics of Acer mono and *Fagus crenata*: An environmental filter limiting their adult distributions. *Plant Ecology*, *177*(2), 189–199. https://doi.org/10.1007/s11258-005-2177-z

Mathys, A., Coops, N. C., & Waring, R. H. (2014). Soil water availability effect on the distribution of 20 tree species in western North America. *Forest Ecology and Management*, *313*, 144–152.

Mau, A., Reed, S., Wood, T., & Cavaleri, M. (2018). Temperate and tropical forest canopies are already functioning beyond their thermal thresholds for photosynthesis. *Forests*, *9*, 47.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., … Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739.

Meier, E. S., Lischke, H., Schmatz, D. R., & Zimmermann, N. E. (2012). Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, *21*(2), 164–178.

Menzel, A., Sparks, T. H., Estrella, N., & Roy, D. B. (2006). Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography*, *15*(5), 498–504.

Miyazaki, Y., Hiura, T., Kato, E., & Funada, R. (2002). Allocation of resources to reproduction in *Styrax obassia* in a masting year. *Annals of Botany*, *89*, 767–772.

Miyazaki, Y., Maruyama, Y., Chiba, Y., Kobayashi, M. J., Joseph, B., Shimizu, K. K., … Satake, A. (2014). Nitrogen as a key regulator of flowering in *Fagus crenata*: Understanding the physiological mechanism of masting by gene expression analysis. *Ecology Letters*, *17*(10), 1299–1309. https://doi.org/10.1111/ele.12338

Monks, A., Monks, J. M., & Tanentzap, A. J. (2016). Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist*, *210*, 419–430.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., … van Kleunen, M. (2010). Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, *15*, 684–692.

Osuri, A. M., Gopal, A., Raman, T. S., DeFries, R., Cook-Patton, S. C., & Naeem, S. (2019). Greater stability of carbon capture in species-rich natural forests compared to species-poor plantations. *Environmental Research Letters*, *15*(3), 034011. https://doi.org/10.1088/1748-9326/ab5f75.

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Petit, R. J., & Hampe, A. (2006). Some evolutionary consequences of being a tree. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 187–214.

Piovesan, G. (2019). A light-demanding pine spreads into a closed forest. *Frontiers in Ecology and the Environment*, *17*, 454–454.

Piovesan, G., Biondi, F., Di Filipo, A., & Maugeri, M. (2008). Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology*, *14*, 1265–1281.

Restaino, C., Young, D. J. N., Estes, B., Gross, S., Wuenschel, A., Meyer, M., & Safford, H. (2019). Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecological Applications*, *29*, 1–14.

Rey-Sánchez, A. C., Slot, M., Posada, J. M., & Kitajima, K. (2017). Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. *Climate Research*, *71*, 75–89.

Ryan, M. G., Linder, S., Vose, J. M., & Hubbard, R. M. (1994). Dark respiration in pines. *Ecological Bulletins*, *43*, 50–63.

Sala, A., Hopping, K., McIntire, E. J. B., Delzon, S., & Crone, E. E. (2012). Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*, *196*(1), 189–199. https://doi.org/10.1111/j.1469-8137.2012.04257.x

Schlichting, C. D. (1986). The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics*, *17*, 667–693.

Serra-Diaz, J. M., Scheller, R. M., Syphard, A. D., & Franklin, J. (2015). Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landscape Ecology*, *30*, 1039–1053.

Shigo, A. L. (1984). Compartmentalization: A conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology*, *22*, 189–214.

Sillett, S. C., Van Pelt, R., Carroll, A. L., Campbell-Spickler, J., & Antoine, M. E. (2019). Structure and dynamics of forests dominated by *Sequoiadendron giganteum*. *Forest Ecology and Management*, *448*, 218–239.

Sillett, S. C., Van Pelt, R., Carroll, A. L., Campbell-Spickler, J., & Antoine, M. E. (2020). Aboveground biomass dynamics and growth efficiency of *Sequoia sempervirens* forests. *Forest Ecology and Management*, *458*, 117740.

Sillett, S. C., Van Pelt, R., Carroll, A. L., Kramer, R. D., Ambrose, A. R., & D'Arcy, T. (2015). How do tree structure and old age affect growth potential in California redwoods? *Ecological Monographs*, *85*, 181–212.

Sillett, S. C., Van Pelt, R., Freund, J. A., Campbell-Spickler, J., Carroll, A. L., & Kramer, R. D. (2018). Development and dominance of Douglas-fir in North American rainforests. *Forest Ecology and Management*, *429*, 93–114.

Sillett, S. C., Van Pelt, R., Koch, G. W., Ambrose, A. R., Carroll, A. L., Antoine, M. E., & Mifsud, B. M. (2010). Increasing wood production through old age in tall trees. *Forest Ecology and Management*, *259*(5), 976–994.

Slot, M., Rey-Sánchez, C., Gerber, S., Lichstein, J. W., Winter, K., & Kitajima, K. (2014). Thermal acclimation of leaf respiration of tropical trees and lianas: Response to experimental canopy warming, and consequences for tropical forest carbon balance. *Global Change Biology*, *20*, 2915–2926.

Smaill, S. J., Clinton, P. W., Allen, R. B., & Davis, M. R. (2011). Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, *99*(3), 870–877. https://doi.org/10.1111/j.1365-2745.2011.01803.x

Smith, N. G., & Dukes, J. S. (2013). Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO_2. *Global Change Biology*, *19*, 45–63.

Spies, T. A., & Franklin, J. F. (1991). The structure of natural young, mature and old-growth Douglas-fir forests in Oregon and Washington. In L. F. Ruggiero, Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), *Wildlife and vegetation of unmanaged Douglas-fir forests* (Vol. USDA Forest Service General Technical Report PNW-285, pp. 91–109). Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

Stojnic, S., Orlovic, S., Miljkovic, D., Galic, Z., Kebert, M., & von Wuehlisch, G. (2015). Provenance plasticity of European beech leaf traits under differing environmental conditions at two Serbian common garden sites. *European Journal of Forest Research*, *134*(6), 1109–1125.

Sultan, S. E. (1987). Evolutionary implications of phenotypic plasticity in plants. In M. K. Hecht, B. Wallace, & G. T. Prance (Eds.), *Evolutionary biology* (pp. 127–178). New York, NY: Plenum Press.

Sumida, A., Miyaura, T., & Torii, H. (2013). Relationships of tree height and diameter at breast height revisited: Analyses of stem growth using 20-year data of an even-aged *Chamaecyparis obtusa* stand. *Tree Physiology*, *33*, 106–118.

Taylor, A. M., Gartner, B. L., & Morrell, J. J. (2002). Heartwood formation and natural durability – A review. *Wood Fiber Science*, *34*, 587–611.

Thompson, I., Mackey, B., McNulty, S., & Mosseler, A. (2009). *Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems.* Technical Series no. 43. *Secretariat of the Convention on Biological Diversity* (p. 67).

Thuiller, W., Albert, C. H., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, G., … Zimmermann, N. E. (2008). Predicting global change impacts on plant species distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Sytematics*, *9*, 137–152.

Valladares, F., Gianoli, E., & Gómez, J. M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist*, *176*(4), 749–763.

Van Pelt, R., Sillett, S. C., Kruse, W. A., Freund, J. A., & Kramer, R. D. (2016). Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. *Forest Ecology and Management*, *375*, 279–308.

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 49–659.

Wassenberg, M., Chiu, H.-S., Guo, W., & Spiecker, H. (2015). Analysis of wood density profiles of tree stems: Incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. *Trees*, *29*, 551–561.

Way, D. A., & Yamori, W. (2014). Thermal acclimation of photosynthesis: On the importance of adjusting our definitions and accounting for thermal acclimation of respiration. *Photosynthesis Research*, *119*, 89–100.

Werner, E. E., & Peacor, S. D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology and Evolution*, *84*, 1083–1100.

West, P. W. (2020). Do increasing respiratory costs explain the decline with age of forest growth rate? *Journal of Forestry Research*, **31**, 693–712. https://doi.org/10.1007/s11676-019-01020-w

Williams, C. B., Næsborg, R. R., & Dawson, T. E. (2017). Coping with gravity: The foliar water relations of giant sequoia. *Tree Physiology*, *37*(10), 1312–1326.

Wing, S. L., Harrington, G. J., Smith, F. A., Bloch, J. I., Boyer, D. M., & Freeman, K. H. (2005). Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science*, *310*, 993–996.

Yachi, S., & Loreau, M. (2007). Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecology Letters*, *10*, 54–62.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, *292*, 686–693.

Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, *18*, 1042–1052.

Zimmermann, N. E., Yoccoz, N. G., Edwards, T. C., Meier, E. S., Thuiller, W., Guisan, A., … Pearman, P. B. (2009). Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19723–19728.

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