

Capacity of Old Trees to Respond to Environmental Change

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Abstract

Atmospheric carbon dioxide [CO₂] has increased dramatically within the current life spans of long-lived trees and old forests. Consider that a 500-year-old tree in the early twenty-first century has spent 70% of its life growing under pre-industrial levels of [CO₂], which were 30% lower than current levels. Here we address the question of whether old trees have already responded to the rapid rise in [CO₂] occurring over the past 150 years. In spite of limited data, aging trees have been shown to possess a substantial capacity for increased net growth after a period of post-maturity growth decline. Observations of renewed growth and physiological function in old trees have, in some instances, coincided with Industrial Age increases in key environmental resources, including [CO₂], suggesting the potential for continued growth in old trees as a function of continued global climate change.

Key words: carbon dioxide; hydraulic limitation; old growth; stomata; tree rings.

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Over the last two centuries, anthropogenic induced changes in the global environment have altered aspects of the Earth's carbon (C), nitrogen (N), and water cycles, and energy balance (IPCC 2007). Although old trees are the only terrestrial organisms to have lived through the entirety of the Industrial Age, little is known about the effect of these environmental changes on the physiology and growth of old trees (Carey et al. 2001; Chen et al. 2004; Paw et al. 2004; Suchanek et al. 2004). Because of

their unique conservation value and the important role these trees play in the structure and function of old growth forest ecosystems, it is worthwhile to consider the intrinsic capacity of old trees to respond to global environmental change. In this paper, we focus on the potential sensitivity of old growth trees to the major driving force of climate change, which is increasing atmospheric [CO₂].

The few available experimental studies concerning the response of old trees to environmental changes, such as thinning (McDowell et al. 2003; Martínez-Vilalta et al. 2007), reveal that very old trees are capable of dynamic responses to changes in their environment. Evaluating the response of plants to current environmental conditions, when they have developed under pre-industrial conditions, can provide insight into long-term vegetation responses to predicted global environmental change scenarios (Körner 1993; Dippery et al. 1995; Ehleringer and Cerling 1995; Ward and Strain 1997, 1999a; Sage and Cowling 1999). Further, recognition of the unique environmental history experienced by old trees is critical to interpreting contemporary responses of old trees to extreme events such as drought (McDowell et al. 2008).

The dramatic rise in atmospheric [CO₂] and other biogeochemical cycles during the industrial age has occurred during

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the lifetimes of old growth trees, beginning when many of these trees were already old (Figure 1). Because even current levels of $[\text{CO}_2]$ are not sufficient to saturate photosynthesis of C_3 plants, increased $[\text{CO}_2]$ over the last 150 years may have increased photosynthesis and growth of old trees. However, the magnitude of this potential response is unknown (Figure 2). In addition to the difficulty of accessing crowns of large trees, research on old tree growth responses to environmental change may be limited due to a long held view that old trees exhibit little potential

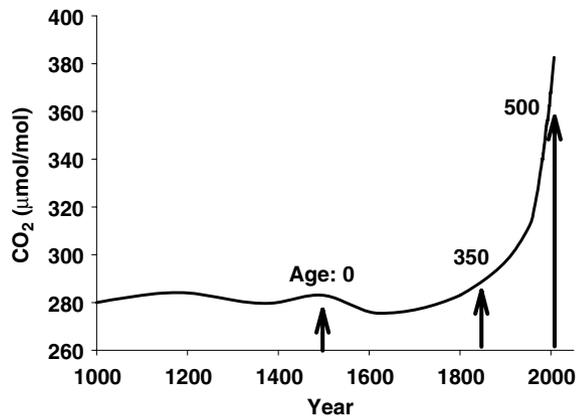


Figure 1. Change in mean global atmospheric carbon dioxide over the last millennium. Arrows indicate the ages of a contemporary 500-year-old tree during this period.

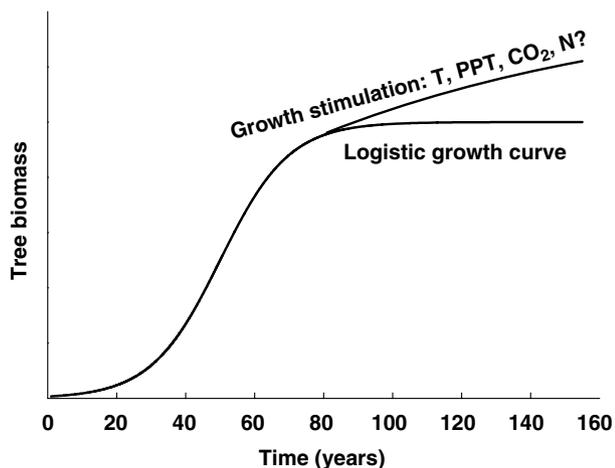


Figure 2. One possible realization of altered tree growth due to changes in environmental variables.

The logistic growth trajectory in this figure is highly idealized and commonly assumed (Weiner and Thomas 2001), and the departure from logistic growth here illustrates the concept that growth of old trees may be affected by environmental change. Resource availability (N, nitrogen availability; PPT, precipitation; T, temperature) increases around approximately year 90 in this illustration.

for growth (e.g., Kozlowski 1962). For example, it is commonly reported that old trees decline in growth rate with age and size (Ryan and Yoder 1997; Carey et al. 2001), and therefore it may seem reasonable to conclude that old trees are not responsive to increased $[\text{CO}_2]$.

On the other hand, because CO_2 is such a central resource to plant function, there are several potential ways in which any plant, including old trees, could be sensitive to elevated $[\text{CO}_2]$. For example, post-industrial age increases in $[\text{CO}_2]$ could alleviate limitations to water supply to the tops of large, old trees (Ryan and Yoder 1997), through increased carbon gain without increased stomatal opening (i.e., increased water use efficiency). In turn, this could promote growth and alter carbon allocation within old trees, which might be detected using tree ring data. However, tree ring analysis for the purpose of climate reconstruction has not produced clear consensus on whether trees show growth stimulation from recent increases in atmospheric $[\text{CO}_2]$ (Jacoby and DiArrigo 1997). Moreover, most tree ring sampling has been conducted in cold climates, such as timberlines, where temperature is expected to most strongly constrain tree growth. In warmer climates, recent data from moist tropical forests (Laurence et al. 2004) and dry temperate woodland (Knapp et al. 2001) suggests that elevated $[\text{CO}_2]$ may be causing dramatic alterations in forest structure and composition.

Our objective here is to challenge a common assumption – that old trees are incapable of increased growth after post-maturity decline in growth (e.g., Kira and Shidei 1967) – which contributes to the widespread view that old trees and forests progressively move toward zero net carbon gain and biomass growth. Here, we address the growth responses of individual trees and not the carbon relations of old growth forests, which are discussed elsewhere (e.g. Carey et al. 2001; Bond and Franklin 2002, and references therein; Pregitzer and Euskirchen 2004; Schuster et al. 2008). Although there is growing recognition that old forests have the capacity for significant carbon gain (e.g. Carey et al. 2001; Zhou et al. 2006), this is often attributed to factors other than the inherent capacity for growth in very old individual trees.

Analysis of the response of old trees to environmental change is necessarily biased toward tree species outside of the humid tropics, mostly conifers from cold, arid environments. This is driven by several factors: (i) Collection and analysis of annual growth rings is much easier in highly seasonal environments; (ii) the longest-lived trees appear to be conifers that occur in seasonally cold and arid environments; and (iii) relatively little research has been conducted on tree age in moist tropical forests (Dean et al. 1996). Therefore it is difficult to generalize how old trees of differing growth form or biogeography, particularly tropical trees, may respond to environmental change. Nevertheless, recent research using sophisticated tree dating methods indicates that trees from the moist tropics can be much longer-lived than previously assumed (Fichtler et al. 2003),

and the continued use of these methods will likely increase knowledge of how old tropical trees respond to environmental change.

In this study, based on our own research in a temperate old growth forest and studies by others in other forests, we suggest that (i) physiological constraints to growth associated with large, old trees may be moderated by the post-industrial age rise in $[\text{CO}_2]$; (ii) old trees may maintain photosynthetic capacity equivalent to young trees, which is a key (if neither necessary nor sufficient) pre-condition for growth in old age; and (iii) old trees may show increased growth after centuries of post-reproductive maturity, which are difficult to interpret other than in light of industrial age environmental change. We focus on trees that were centuries old at the beginning of the industrial age, to avoid the complication of deconvolving growth trends in trees that underwent early development to maturity in concert with the possible influence of Industrial Age environmental change on growth (e.g., Kienast and Luxmoore 1988; Waterhouse et al. 2004; Körner et al. 2005; Schuster et al. 2008).

Environmental Modification of Hydraulic Limitation?

Research over the past decade (e.g., Yoder et al. 1994; Ryan and Yoder 1997; McDowell et al. 2002; Phillips et al. 2002, 2003; Woodruff et al. 2004; Ryan et al. 2006) provides a compelling indication that the response of tall, old trees to resource variation may potentially differ from that in younger trees. In particular, to the extent that physiological constraints in tall, old trees result in carbon limitation, it is plausible to expect these trees to show greater potential sensitivity to $[\text{CO}_2]$ variation than younger trees in comparable environments. This hypothesis is consistent with the general hypothesis that $[\text{CO}_2]$ responses of vegetation should increase with water supply limitations (Strain and Bazzaz 1983; Nowak et al. 2004), coupled with the fact that hydraulic constraints in tall trees constitute a fundamental form of water limitation; indeed, one that is indistinguishable from soil water limitations (Koch et al. 2004; Woodruff et al. 2004). Furthermore, recent research indicates that tree size and its hydraulic correlates, rather than age *per se*, controls carbon gain in old trees (Mencuccini et al. 2005). This suggests that factors that alleviate internal or external resource constraints on old trees could improve physiological function and ultimately growth.

There are two key mechanisms by which tall trees are hydraulically constrained in their ability to grow, and may be partially relieved of this limitation by increased atmospheric $[\text{CO}_2]$. Both are caused by the increasingly negative water potentials that leaves atop tall trees must maintain to drive water flow against both the large gravitational head and the long hydraulic path length with its increased resistance (Yoder et al. 1994; Ryan and Yoder 1997). First, large negative water potential in

tall trees may reduce photosynthesis, and thus carbon supply for growth, either by reducing stomatal apertures (Yoder et al. 1994; McDowell et al. 2002) or by affecting mesophyll function (Friend 1993; Tezara et al. 1999). Post-industrial age increases in $[\text{CO}_2]$ could offset either of these effects, thereby alleviating hydraulic constraints on carbon supply for growth.

Second, growth in tall trees is fundamentally constrained by reduced leaf water status and its effects on cell turgor, which drives expansion of newly formed tissues including leaves (Woodruff et al. 2004). The effect on leaf expansion in particular may initiate a feedback, wherein carbon gain becomes progressively more limited by leaf area. Industrial increases in $[\text{CO}_2]$ could ameliorate these constraints in two ways: (i) by increasing photosynthetic carbon gain (as discussed above) in the leaf area that is successfully produced; or (ii) by directly reducing stomatal conductance (Darwin 1898) and thus water loss, thereby increasing water potential and turgor. We note that these two outcomes cannot both be fully realized; rather, they are limiting cases in a continuum of feasible responses. For example, if trees grow more leaves in response to elevated $[\text{CO}_2]$, this would increase transpiration and reduce benefits for turgor (Woodward 1990).

Notwithstanding the potential complexity of long-term responses of forests to elevated $[\text{CO}_2]$ (Norby and Luo 2004), the above considerations suggest a fundamental potential for old growth trees to show greater photosynthesis and growth under industrial age increases in $[\text{CO}_2]$ than they would under constant, pre-industrial $[\text{CO}_2]$ levels. Simulations of $[\text{CO}_2]$ responses in hydraulically constrained tall trees demonstrate that these effects of industrial age $[\text{CO}_2]$ on growth are theoretically possible (figures 1, 3 in Buckley 2008); clearly, plausibility as described above does not indicate probability. Yet, at the very least, there are clear mechanisms by which hydraulic limitations to growth in old trees could be modified by environmental change. To date no experiments on hydraulic limitation to growth in trees have acknowledged this possibility (Ryan et al. 2006, and papers cited therein).

Observations on the Physiology of Old Growth Trees

The premise of the preceding discussion is that growth in old trees is limited by changes in resource supply, not by intrinsic suppression of photosynthetic function. Our work and that of others (e.g., Yoder et al. 1994; McDowell et al. 2002; Winner et al. 2004; Delzon et al. 2005) demonstrates that, at least in some old trees, photosynthetic capacity (i.e., defined here as maximum photosynthetic rate under non-limiting light and CO_2) may be unaltered by age and size of tree, even if net photosynthesis under ambient growth conditions may become limited by stomatal closure. At the leaf level, 500- and 20-year-old Douglas-fir trees both show high sensitivity of

photosynthesis to atmospheric $[\text{CO}_2]$ (Figure 3). Consideration of the photosynthetic saturation response of a wide range of plant types to $[\text{CO}_2]$ supply indicates that the greatest sensitivity of photosynthesis to $[\text{CO}_2]$ may occur at lower ranges of $[\text{CO}_2]$ (e.g., Baker et al. 1990; Polley et al. 1992, 1993; Sage and Reid 1992; Johnson et al. 1993; Tissue et al. 1995; Ziska 2003), including the transition between pre-industrial levels and today. Figure 3 indicates that under optimal conditions there exists the potential for an approximately 30% increase in photosynthetic rate with an increase in $[\text{CO}_2]$ from pre-industrial to current levels in old trees.

Leaf level photosynthetic data (see Figure 3) cannot generally be scaled directly to long-term growth (Lloyd and Farquhar 1996; Drake et al. 1997; Morison and Lawlor 1999; Norby and Luo 2004). Therefore, photosynthetic data demonstrates only that the primary step in overall carbon gain by trees (photosynthesis) may be affected by changes in atmospheric $[\text{CO}_2]$. To the extent that old trees – in fact, trees that were already old and in a presumably stable, minimal growth phase when large scale anthropogenic environmental change commenced – are physiologically sensitive to altered $[\text{CO}_2]$ levels, we suggest that much of the terrestrial vegetation currently growing on earth may already be functioning differently than it would have before the industrial revolution (Sage and Cowling 1999). Consequently, we may need to re-evaluate the response of vegetation to “elevated” $[\text{CO}_2]$ relative to “ambient” $[\text{CO}_2]$ in our experimental manipulations (e.g., Free-Air CO_2 Enrichment (FACE)), given that the ambient $[\text{CO}_2]$ conditions has changed from 280 to 385 parts per million (ppm) in the last 150 years, and is increasing at approximately 2 ppm per year (IPCC 2007). This shifting

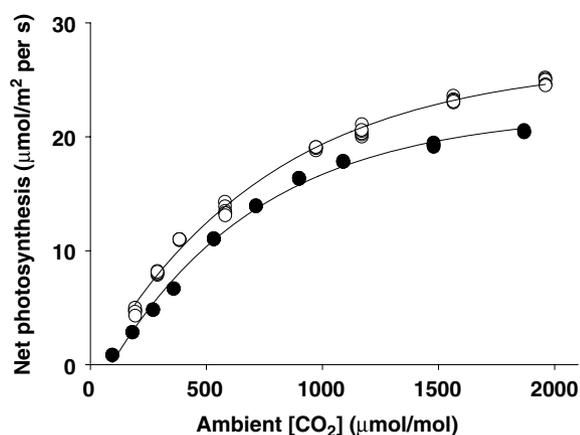


Figure 3. Typical responses of leaf net photosynthesis (measured as net CO_2 uptake) to ambient $[\text{CO}_2]$ in the crowns of (●) 500- and (○) 20-year-old Douglas-fir trees.

Data from Wind River, Washington, June 22, 1999, during conditions of saturating light. Site and sampling details are described in McDowell et al. 2002.

ambient $[\text{CO}_2]$ “baseline” is well recognized (Polley et al. 1993; Dippert et al. 1995; Tissue et al. 1995; Cowling and Sage 1998; Ward et al. 1999b; Ward et al. 2000; Ward 2005), but it nevertheless presents complications in interpretations of global change biology experiments.

For example, in a recent study, Körner et al. (2005) observed the responses of approximately 100-year-old temperate trees to $[\text{CO}_2]$ of 530 ppm and found that elevated $[\text{CO}_2]$ stimulated carbon uptake by crowns of mature trees but did not increase tree growth or litter production. However, the study by Körner et al. (2005) was not designed to investigate, whether (i) trees have already shown a ‘treatment effect’ in response to the 30% increase in $[\text{CO}_2]$ that has occurred over the past 150 years; and (ii) whether 100-year-old trees developing in concert with the Industrial Revolution might show a different ‘treatment effect’ than trees that were already reproductively mature when the Industrial Revolution began. Indeed, even untreated reference trees in the study by Körner et al. (2005) were in a vigorous growth phase. To properly address this question would require a pre-industrial $[\text{CO}_2]$ treatment, along with a current-day ‘ambient’ control treatment, imposed from early development through maturity. This is impracticable for several reasons, which make it necessary to rely instead on observational data like that provided by tree rings and modeling.

Tree Ring Increases in the Twentieth Century

Contrary to the view that old trees approach zero growth, these trees in the late twentieth century have the potential to exhibit similar increases in girth as those observed in their early growth years (Figure 4). Indeed, the doubling of ring width (from ca 1750 to ca 1950) as trees grow larger implies a more-than doubling

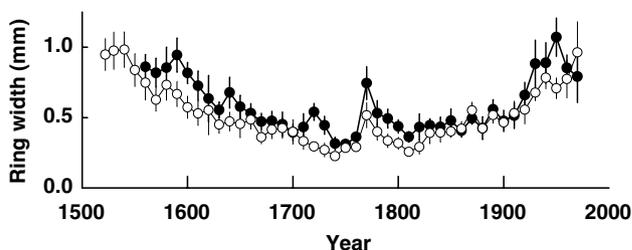


Figure 4. Ring width chronology from an approximately 500-year-old dominant Douglas-fir tree at Lava Beds, Washington, approximately 10 km from where the leaf level data were taken in Figure 3.

Each symbol is a decadal average, with standard deviations from 10-year averages. Symbols correspond to two tree cores from different sides of the tree. Data obtained from the National Oceanic and Atmospheric Administration paleoclimate web page (originally collected by L. Brubaker).

of area increment (Figure 4). At this site (Lava Beds, WA, USA), at least half of 14 trees that were ca 600 years old displayed mid-to-late twentieth century increases in ring width. For trees at this site that did not exhibit such strong growth responses, there are many reasons, including biotic competition (e.g., light), disease and disturbance. Whether the rate of increase in tree girth at this site is due to elevated $[\text{CO}_2]$ or other environmental variables, and whether or not wood density decreased in the newest growth rings, it is clear that, contrary to idealized growth curves, old trees have the capacity to exhibit sustained diameter growth in old age.

The phenomenon of twentieth century ring width increase has been noted by other studies (e.g. La Marche et al. 1984; Jacoby 1986; Graybill 1987; Kienast and Luxmoore 1988; Graumlich 1991; Knapp et al. 2001; Bunn et al. 2005; Soulé and Knapp 2006). A particularly notable study was that of La Marche et al. (1984), that found latter twentieth century increases in ring widths in many-centuries-old bristlecone pine trees (Figure 5). Subsequent work has even further strengthened the evidence for twentieth century growth increases in old trees at high

elevation (Bunn et al. 2005). The results from La Marche et al. (1984) could not be explained by temperature or precipitation variation over this time period, but were consistent with, and attributed to the rise in atmospheric $[\text{CO}_2]$. Although these data appear to represent compelling circumstantial evidence for carbon fertilization of old growth trees, this possibility has been discounted and climate change has instead been implicated for the observed responses in subsequent research (Bunn et al. 2005). Moreover, recent work has shown that pan evaporation, the geometry of solar radiation, and forest carbon gain have varied in concert over the last several decades (Gu et al. 2003; Roderick and Farquhar 2005) and must also be considered as potential drivers of these responses.

The capacity of old trees to respond to environmental change has a key applied consequence: interpretation of annual rings to detect climate change. A key initial step in tree ring analysis is the detrending of biological growth curves, which are of secondary interest (e.g., Esper et al. 2002). A continuing, central challenge in tree ring-based climate analysis is to assess whether changes occur in the growth curves themselves, due to

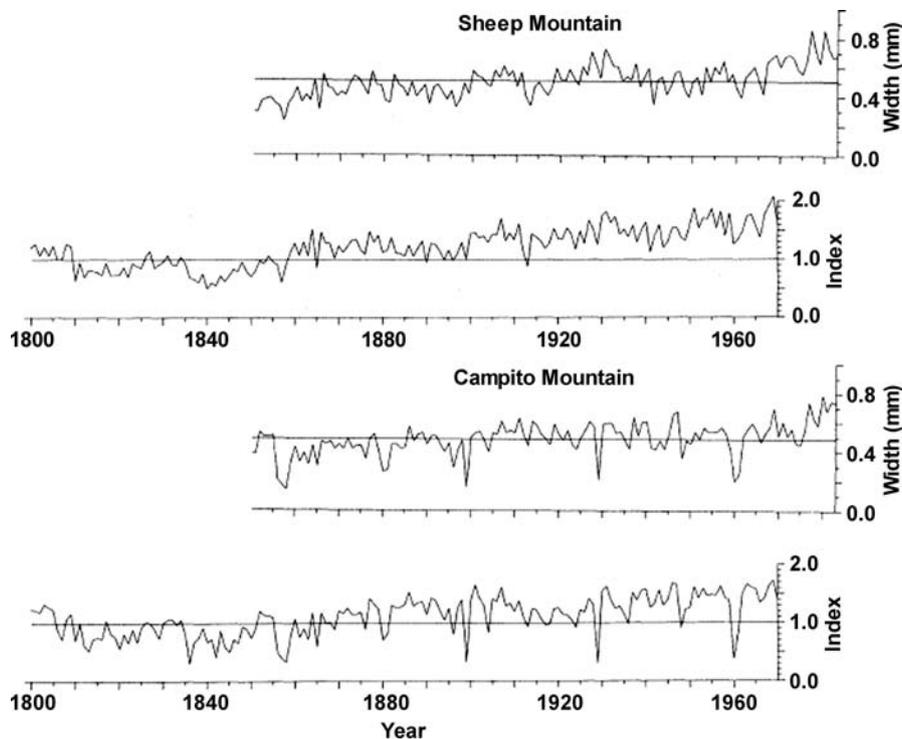


Figure 5. Ring width time series in bristlecone pine trees from two sites in California, showing increases in the latter part of the twentieth century that were uncorrelated with climate variation (temperature and precipitation data not shown).

Data represent averages of 13–15 trees in each site. In each of two sites above, the upper time series in the upper panel supplements the longer time series in the lower panel of each site (which was obtained for a previous study), and shows ring widths (mm) instead of a standardized ring width index (dimensionless; see www.ncdc.noaa.gov/paleo/treeinfo.html), because standardization procedures can confound environmental variation from biological growth. From LaMarche VC et al. (1984), *Science* **225**, 1019–1021. Reprinted with permission from American Association for the Advancement of Science.

[CO₂] or to other environmental changes. Several approaches have been developed to meet this analytical challenge (Graumlich 1991; Briffa et al. 1992; Knapp et al. 2001; Monserud and Marshall 2001; Esper et al. 2002). Notwithstanding their value in separating climate change signals from biological growth in old trees, these techniques face a fundamental challenge in attempting to separate (i) low frequency climate variation from (ii) a “low frequency”, often sigmoidal, tree growth curve, especially as they may interact.

Rings versus Leaders: Girth versus Height Growth

The universally-observed cessation of height growth in long-lived trees may promote a simplistic inference that growth in general ceases in old trees. However, girth growth is common in old trees and may even increase after centuries of stable or decreasing girth growth. Regarding height, observations of the annual leader on old trees with apical dominance show that they do approach zero (Phillips, pers. obs. on 500 year old Douglas-fir, Western hemlock, and Western red cedar trees, 1998, 1999, 2000), but the vertical position of the leader can fluctuate inter-annually in response to inter-annual variation in soil or atmospheric moisture (e.g., Koch et al. 2004). The cessation of height but not girth growth is a provocative clue that height growth cessation in old trees may be due to hydraulic (e.g. cell turgor, expansion, and gravity; Koch et al. 2004; Woodruff et al. 2004) or biomechanical limitations that do not constrain girth growth. This phenomenon also raises interesting questions. Could increased atmospheric [CO₂] have caused a gradual, albeit small increase in tree height over what would have been obtained in the absence of the industrial age rise in [CO₂]? More fundamentally, is continued girth growth of functional benefit in old trees? At least two features of girth growth argue for potential functional benefit: increased biomechanical support, and provision of new vascular tissue to replace permanently dysfunctional vascular tissue (Thomas 1996).

Simulating Old Tree Response to Environmental Change

Tree growth modeling may be used to assess changes in carbon uptake, growth, and allocation in old growth trees due to alteration of [CO₂], but validation of growth simulations in old trees presents special challenges. First, there are no old growth trees that can serve as “controls” (i.e., 500-year-old trees having grown under pre-industrial [CO₂] levels for their entire lives). Second, directly determining above- and below-ground allocation in old growth trees of large size would require the harvesting of protected old trees and would be extremely costly. Therefore, models are the only appropriate approach to address these issues.

We used the DESPOT model (Buckley and Roberts 2006) to evaluate differences in tree physiology and growth for a generalized conifer growing in an even-aged stand over 400 years, comparing steady pre-industrial [CO₂] (280 μmol/mol) versus monotonically increasing [CO₂] (280–370 μmol/mol). Key attributes of this model that made it appropriate for use here are that it: (i) simulates long term (centuries) tree growth and carbon allocation; and (ii) does not impose pre-determined constraints on carbon gain or allocation. Instead, physiological constraints (e.g., hydraulic, nutritional, and metabolic) emerge and are modified as a result of optimal carbon allocation to maximize net carbon gain (discounted by probability of mechanical failure). It allows for stand level feedbacks; specifically, changes in stem density and canopy leaf area that may feedback to influence individual tree growth and allocation.

Our model simulation predicts substantial changes in tree structure – increased height, diameter, leaf area, and sapwood area – and reduced stand density over 400 years, comparing trees growing through the Industrial Revolution with those growing through a constant pre-industrial [CO₂] environment (Table 1). This model predicts instantaneous water use efficiency (i.e., photosynthesis per unit transpiration) is higher today than in a low [CO₂] world, and this drives changes in tree carbon allocation and stand structure. It also suggests an explanation for confounding results such as those of Körner et al. (2005): namely, that the responses of leaf area production, stem growth and height growth differ widely under different assumptions about stomatal physiology (Buckley 2008) because those assumptions greatly affect the adaptive landscape on which alternative strategies for investing the extra CO₂ are parsed. These non-intuitive predictions, and similarly non-intuitive results from enrichment experiments, suggest that an understanding of tree response to climate change may require a more integrative and dynamical conceptual perspective than currently used by physiologists.

Table 1. Simulated differences in tree properties after 400 years, comparing constant 280 μmol/mol [CO₂] with monotonically rising [CO₂] from 280–370 μmol/mol (rate step = 0.23 μmol/mol per year).

Variable	Percent change with [CO ₂] rise
Tree height	+9
Tree diameter	+9
Tree sapwood area	+36
Tree leaf area	+43
Stem density	–12

Input parameters used for this simulation are for a generalized conifer tree, under unchanging climate conditions. Positive values of percent change correspond to fertilizing effects of elevated [CO₂]. The simulations assume no effect of [CO₂] on photosynthetic capacity or foliar or wood respiration rates (see text for discussion of those assumptions).

Even these results are based on an extreme simplification of reality (e.g., constant environment except for $[\text{CO}_2]$). A more sophisticated approach, but outside of the scope of this study, would be to obtain species and site-specific parameters for use in this model, and use historical climate data instead of assuming steady climate and edaphic (soil moisture, nutrition) conditions. This would allow an evaluation of the sensitivity of the simulations to multiple environmental variables, including temperature, precipitation, nitrogen deposition, and atmospheric $[\text{CO}_2]$.

Future Research Opportunities

The topic of the capacity of old trees to respond to environmental change is necessarily speculative because almost no data from controlled experiments exists to address this question. However, future studies on this topic will benefit from continuing improvements in research technologies that more directly allow evaluation of old tree responses to environmental change. We conclude here with a number of general recommendations for future studies designed to evaluate responses of old trees to environmental change.

Evaluating effects of multiple environmental variables on old tree function

Variation in water, nutrient availability, pollutants, $[\text{CO}_2]$ and/or temperature may independently and interactively affect plant function (Luo et al. 1999; Oren et al. 2001), including in old trees. To make progress in deconvolving and synthesizing old tree response to multiple environmental changes, judicious choices of old trees for study can be critical. For example, old growth coniferous forests of the Pacific Northwest often experience low soil nutrient status, particularly N. Moreover, N deposition in montane forests of the Pacific Northwest has remained near pre-industrial levels (Holland et al. 1999). Trees from such a condition, possibly compared with trees closer to anthropogenic sources of N, but otherwise exposed to similar environments, could be used to evaluate the influence of environmental changes in N as part of a suite of environmental changes including $[\text{CO}_2]$. Similarly, old trees that differed throughout their lives in access to soil water or in seasonal temperature variation could be compared and contrasted in their response to the industrial rise in $[\text{CO}_2]$. In particular, trees that experience moderate temperatures year round (e.g., old growth forests of the Pacific Northwest, or tropical regions) may be expected to show greater response to post-industrial age $[\text{CO}_2]$ than trees that are severely temperature limited.

Finally, selection of tree species for these studies is crucial, especially regarding life history traits. In particular, trees that remain canopy dominants throughout their lifetimes (e.g., Douglas-fir in the Pacific Northwest United States), or are other-

wise naturally open-grown (e.g., palm species like *Washingtonia robusta* H. Wendl.) may be especially tractable study subjects. This trait simplifies environmental history through maintenance of a similar light environment during the same time that atmospheric $[\text{CO}_2]$ has risen.

Old questions applied in a new context

Several topics of current research interest in global change biology have yet to be examined specifically in old trees, and have direct relevance to the questions addressed in this paper. For example, there are no studies to our knowledge that have examined how tree foliar and reproductive phenology varies with both age and environmental change, although phenology has been shown to vary with tree age (e.g., Lugo and Battle 1987; Augsburger 2004) and climate (e.g., Myneni et al. 1997) and $[\text{CO}_2]$ (Springer and Ward 2007 and references therein). However, the interactive effects of phenology, ontogeny, and environmental change remains unexplored.

A second unexplored research area concerns whether tall, old trees differ from young trees in nocturnal hydraulic limitation and gas exchange (e.g., Ryan et al. 2006; Phillips et al. 2007), what implications this holds for old tree function (e.g., cell turgor and leaf expansion at night; Woodruff et al. 2004), and how nocturnal climate change (as distinct from diurnal climate change) may differentially affect physiology and growth of old compared with young trees.

New technologies

Over the last several decades, environmental treatment and measurement techniques have been developed that provide new insights into old tree response to environmental change. Canopy access to the tops of large, old trees (e.g., Shaw et al. 2004) has opened up new research opportunities. Moving canopy science from observation to environmental manipulation is likely the wave of the future. For example, the webface technology (Körner et al. 2005) could be implemented on very old trees, including those showing post-maturity growth declines. This technology could also supply pre-industrial levels of $[\text{CO}_2]$ to crowns of old trees as a way to 'set the clock back' on the environment that old trees experienced for most of their life, thereby allowing examination of the 'normal' baseline environmental condition and physiological response of ancient trees, and consequently providing knowledge of whether these trees have likely already experienced an Industrial Age "treatment effect". Whole tree chamber technology (e.g., as described in Phillips et al. 2004) or desert FACE technology (Jordan et al. 1999) could feasibly be placed over very old, but relatively small trees like millennium-aged bristlecone pines (or even in bonsai trees), to vary $[\text{CO}_2]$ from pre-industrial to present, and future levels.

After nearly two centuries of industrialization, there is now a confluence of factors – rapidly depleting stocks of old trees,

exponential global environmental change, and technological advances in canopy access and monitoring – that make the study of old tree growth and physiology increasingly compelling and timely. We have shown here that old trees have the capacity to grow well past a post-maturity growth decline. Yet the understanding of old tree responses to the environment remains necessarily speculative, because (i) there is ultimately no substitute for time in experiments on centuries-old organisms; and (ii) canopy access to tall, old trees remains a formidable challenge. For these reasons, modeling and observational studies will continue to prove essential to our assessments of the capacity of old trees to respond to environmental change.

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