

1 **Capacity of old trees to respond to environmental change**

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18 **Abstract**

19 Atmospheric carbon dioxide ($[\text{CO}_2]$) has increased dramatically within the current life
20 spans of long-lived trees and old forests. Consider that a 500-year-old tree in the early
21 21st century has spent 70% of its life growing under pre-industrial levels of $[\text{CO}_2]$, which
22 were 30% lower than current levels. Here we address the question of whether old trees
23 have already responded to the rapid rise in $[\text{CO}_2]$ occurring over the past 150 years. In
24 spite of limited data, aging trees have been shown to possess a substantial capacity for
25 increased net growth after a period of post-maturity growth decline. Observations of
26 renewed growth and physiological function in old trees have, in some instances,
27 coincided with Industrial Age increases in key environmental resources, including $[\text{CO}_2]$,
28 suggesting the potential for continued growth in old trees as a function of continued
29 global climate change.

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31 **Keywords:** carbon dioxide; hydraulic limitation; old growth; stomata; tree rings

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41 **Introduction**

42 Over the last two centuries, anthropogenic induced changes in the global environment
43 have altered aspects of the Earth's carbon (C), nitrogen (N), and water cycles, and energy
44 balance (IPCC, 2007). Although old trees are the only terrestrial organisms to have lived
45 through the entirety of the Industrial Age, little is known about the impact of these
46 environmental changes on the physiology and growth of old trees (Carey *et al.* 2001,
47 Chen *et al.* 2004, Suchanek *et al.* 2004, Paw U *et al.* 2004). Because of their unique
48 conservation value and the important role these trees play in the structure and function of
49 old growth forest ecosystems, it is worthwhile to consider the intrinsic capacity of old
50 trees to respond to global environmental change. In this paper, we focus on the potential
51 sensitivity of old growth trees to the major driving force of climate change, which is
52 increasing atmospheric [CO₂].

53 The few available *experimental* studies concerning the response of old trees to
54 environmental changes, such as thinning (McDowell *et al.* 2003, Martínez-Vilalta,
55 Vanderklein and Mencuccini 2007), reveal that very old trees are capable of dynamic
56 responses to changes in their environment. Evaluating the response of plants to current
57 environmental conditions, when they have developed under pre-industrial conditions, can
58 provide insight into long-term vegetation responses to predicted global environmental
59 change scenarios (Körner 1993, Dippery *et al.* 1995, Ehleringer and Cerling 1995, Ward
60 and Strain 1997, Ward and Strain 1999a, Sage and Cowling 1999, Ehleringer *et al.* 2004).
61 Further, recognition of the unique environmental history experienced by old trees is
62 critical to interpreting contemporary responses of old trees to extreme events such as
63 drought (McDowell *et al.* 2008).

64 The dramatic rise in atmospheric [CO₂] and other biogeochemical cycles during
65 the industrial age has occurred during the lifetimes of old growth trees, beginning when
66 many of these trees were already old (Figure 1). Because even current levels of [CO₂] are
67 not sufficient to saturate photosynthesis of C3 plants, increased [CO₂] over the last 150
68 years may have increased photosynthesis and growth of old trees. However, the
69 magnitude of this potential response is unknown (Figure 2). In addition to the difficulty
70 of accessing crowns of large trees, research on old tree growth responses to
71 environmental change may be limited due to a long held view that old trees exhibit little
72 potential for growth (e.g., Kozlowski 1962). For example, it is commonly reported that
73 old trees decline in growth rate with age and size (reviewed in Ryan and Yoder 1997 and
74 Carey *et al.* 2001), and therefore it may seem reasonable to conclude that old trees are not
75 responsive to increased [CO₂].

76 On the other hand, because CO₂ is such a central resource to plant function, there
77 are several potential ways in which any plant, including old trees, could be sensitive to
78 elevated [CO₂]. For example, post-industrial age increases in [CO₂] could alleviate
79 limitations to water supply to the tops of large, old trees (Ryan and Yoder 1997), through
80 increased carbon gain without increased stomatal opening (i.e., increased water use
81 efficiency). In turn, this could promote growth and alter carbon allocation within old
82 trees, which might be detected using tree ring data. However, tree ring analysis for the
83 purpose of climate reconstruction has not produced clear consensus on whether trees
84 show growth stimulation from recent increases in atmospheric [CO₂] (reviewed in Jacoby
85 and D'Arrigo 1997). Moreover, most tree ring sampling has been conducted in cold
86 climates, such as timberlines, where temperature is expected to most strongly constrain

87 tree growth. In warmer climates, recent data from moist tropical forests (Laurence *et al.*
88 2004) and dry temperate woodland (Knapp *et al.* 2001) suggests that elevated [CO₂] may
89 be causing dramatic alterations in forest structure and composition.

90 Our objective here is to challenge a common assumption - that old trees are
91 incapable of increased growth after post-maturity decline in growth (e.g., Kira and Shidei
92 1967) - which contributes to the widespread view that old trees and forests progressively
93 move toward zero net carbon gain and biomass growth. Here, we address the growth
94 responses of individual trees and not the carbon relations of old growth forests, which are
95 discussed elsewhere (e.g. Carey *et al.* 2001; Bond and Franklin 2002, and references
96 therein; Pregitzer and Euskirchen 2004; Schuster *et al.* 2008). Although there is growing
97 recognition that old forests have the capacity for significant carbon gain (e.g. Carey *et al.*
98 2001, Zhou *et al.* 2006), this is often attributed to factors other than the inherent capacity
99 for growth in very old individual trees.

100 Analysis of the response of old trees to environmental change is necessarily
101 biased toward tree species outside of the humid tropics, mostly conifers from cold, arid
102 environments. This is driven by several factors: (1) Collection and analysis of annual
103 growth rings is much easier in highly seasonal environments; (2) the longest-lived trees
104 appear to be conifers that occur in seasonally cold and arid environments; and (3)
105 relatively little research has been conducted on tree age in moist tropical forests (Dean *et*
106 *al.* 1996). Therefore it is difficult to generalize how old trees of differing growth form or
107 biogeography, particularly tropical trees, may respond to environmental change.
108 Nevertheless, recent research using sophisticated tree dating methods indicates that trees
109 from the moist tropics can be much longer-lived than previously assumed (Fichtler *et al.*

110 2003), and the continued use of these methods will likely increase knowledge of how old
111 tropical trees respond to environmental change.

112 In this study, based on our own research in a temperate old growth forest and
113 studies by others in other forests, we suggest that (1) physiological constraints to growth
114 associated with large, old trees may be moderated by the post-industrial age rise in [CO₂];
115 (2) old trees may maintain photosynthetic capacity equivalent to young trees, which is a
116 key (if neither necessary nor sufficient) pre-condition for growth in old age; and (3) old
117 trees may show increased growth after centuries of post-reproductive maturity, which are
118 difficult to interpret other than in light of industrial age environmental change. We focus
119 on trees which were centuries old at the beginning of the industrial age, to avoid the
120 complication of deconvolving growth trends in trees that underwent early development to
121 maturity in concert with the possible influence of Industrial Age environmental change
122 on growth (*e.g.* Waterhouse *et al.* 2004; Kienast and Luxmoore 1988, Körner *et al.* 2005;
123 Schuster *et al.* 2008).

124

125 **Environmental Modification of Hydraulic Limitation?**

126 Research over the past decade (*e.g.*, Yoder *et al.* 1994, Ryan and Yoder 1997, Phillips *et*
127 *al.* 2002, McDowell *et al.* 2002, Phillips *et al.* 2003, Woodruff *et al.* 2004, Ryan, Phillips,
128 and Bond 2006) provides compelling indication that the response of tall, old trees to
129 resource variation may potentially differ from that in younger trees. In particular, to the
130 extent that physiological constraints in tall, old trees result in carbon limitation, it is
131 plausible to expect these trees to show greater potential sensitivity to [CO₂] variation than
132 younger trees in comparable environments. This hypothesis is consistent with the general
133 hypothesis that [CO₂] responses of vegetation should increase with water supply

134 limitations (Strain and Bazzaz 1983, Nowak *et al.* 2004), coupled with the fact that
135 hydraulic constraints in tall trees constitute a fundamental form of water limitation;
136 indeed, one that is indistinguishable from soil water limitations (Koch *et al.* 2004,
137 Woodruff *et al.* 2004). Furthermore, recent research indicates that tree size and its
138 hydraulic correlates, rather than age *per se*, controls carbon gain in old trees (Mencuccini
139 *et al.* 2005). This suggests that factors that alleviate internal or external resource
140 constraints on old trees could improve physiological function and ultimately growth.

141 There are two key mechanisms by which tall trees are hydraulically constrained in
142 their ability to grow, and may be partially relieved of this limitation by increased
143 atmospheric [CO₂]. Both are caused by the increasingly negative water potentials that
144 leaves atop tall trees must maintain to drive water flow against both the large
145 gravitational head and the long hydraulic path length with its increased resistance (Yoder
146 *et al.* 1994, Ryan and Yoder 1997). First, large negative water potential in tall trees may
147 reduce photosynthesis, and thus carbon supply for growth -- either by reducing stomatal
148 apertures (Yoder *et al.* 1994, McDowell *et al.* 2002) or by impacting mesophyll function
149 (Friend 1993, Tezara *et al.* 1999). Post-industrial age increases in [CO₂] could offset
150 either of these effects, thereby alleviating hydraulic constraints on carbon supply for
151 growth.

152 Second, growth in tall trees is fundamentally constrained by reduced leaf water
153 status and its effects on cell turgor, which drives expansion of newly formed tissues
154 including leaves (Woodruff 2004). The effect on leaf expansion in particular may initiate
155 a feedback, wherein carbon gain becomes progressively more limited by leaf area.
156 Industrial increases in [CO₂] could ameliorate these constraints in two ways: (1) by

157 increasing photosynthetic carbon gain (as discussed above) in the leaf area that is
158 successfully produced, or (2) by directly reducing stomatal conductance (Darwin 1898)
159 and thus water loss, thereby increasing water potential and turgor. We note that these two
160 outcomes cannot both be fully realized; rather, they are limiting cases in a continuum of
161 feasible responses. For example, if trees grow more leaves in response to elevated [CO₂],
162 this would increase transpiration and reduce benefits for turgor (Woodward 1990).

163 Notwithstanding the potential complexity of long-term responses of forests to
164 elevated [CO₂] (Norby and Luo 2004), the above considerations suggest a fundamental
165 potential for old growth trees to show greater photosynthesis and growth under industrial
166 age increases in [CO₂] than they would under constant, pre-industrial [CO₂] levels.
167 Simulations of [CO₂] responses in hydraulically constrained tall trees demonstrate that
168 these effects of industrial age [CO₂] on growth are theoretically possible (Figures 1 and 3
169 in Buckley 2008); clearly, plausibility as described above does not indicate probability.
170 Yet, at the very least, there are clear mechanisms by which hydraulic limitations to
171 growth in old trees could be modified by environmental change. To date no experiments
172 on hydraulic limitation to growth in trees have acknowledged this possibility (Ryan,
173 Phillips and Bond 2006, and papers cited therein).

174

175 **Observations on the Physiology of Old Growth Trees**

176 The premise of the preceding discussion is that growth in old trees is limited by changes
177 in resource supply, not by intrinsic suppression of photosynthetic function. Our work and
178 that of others (*e.g.* Yoder *et al.* 1994, McDowell *et al.* 2002; Winner *et al.* 2004, Delzon
179 *et al.* 2005) demonstrates that, at least in some old trees, photosynthetic capacity (*i.e.*,

180 defined here as maximum photosynthetic rate under non-limiting light and CO₂) may be
181 unaltered by age and size of tree, even if net photosynthesis under ambient growth
182 conditions may become limited by stomatal closure. At the leaf level, data from 500
183 year-old Douglas-fir trees shows high sensitivity of photosynthesis to atmospheric [CO₂]
184 (Figure 3), and the response to either ambient or inter-cellular [CO₂] was not different
185 compared with 20 year old individuals of the same species in a nearby stand (data not
186 shown). Consideration of the photosynthetic saturation response of a wide range of plant
187 types to [CO₂] supply indicates that the greatest sensitivity of photosynthesis to [CO₂]
188 may occur at lower ranges of [CO₂] (*e.g.*, Baker *et al.* 1990, Polley *et al.* 1992, 1993,
189 Sage and Reid 1992, Johnson *et al.* 1993, Tissue *et al.* 1995, Ziska 2003), including the
190 transition between pre-industrial levels and today. Under optimal conditions there exists
191 the potential for a 30% increase in photosynthetic rate with an increase in [CO₂] from
192 pre-industrial to current levels (Figure 3).

193 Leaf level photosynthetic data (see Figure 3) cannot generally be scaled directly
194 to long-term growth (Lloyd and Farquhar 1996, Drake *et al.* 1997, Morison and Lawlor
195 1999, Norby and Luo 2004). Therefore, photosynthetic data demonstrates only that the
196 primary step in overall carbon gain by trees (photosynthesis) *may* be affected by changes
197 in atmospheric [CO₂]. To the extent that old trees - in fact, trees that were already old
198 and in a presumably stable, minimal growth phase when large scale anthropogenic
199 environmental change commenced - *are* physiologically sensitive to altered [CO₂] levels,
200 we suggest that much of the terrestrial vegetation currently growing on earth may already
201 be functioning differently than it would have before the industrial revolution (Sage and
202 Cowling 1999). Consequently, we may need to re-evaluate the response of vegetation to

203 “elevated” [CO₂] relative to “ambient” [CO₂] in our experimental manipulations (*e.g.*,
204 FACE), given that the ambient [CO₂] conditions has changed from 280 to 385 parts per
205 million (ppm) in the last 150 years, and is increasing at *ca.* 2 ppm per year (IPCC 2007).
206 This shifting ambient [CO₂] “baseline” is well recognized (Polley et al. 1993, Dippery et
207 al. 1995, Tissue et al. 1995, Cowling and Sage 1998; Ward et al. 1999b; Ward et al. 2000,
208 Ward 2005), but it nevertheless presents complications in interpretations of global change
209 biology experiments.

210 For example, in a recent study, Körner *et al.* (2005) observed the responses of *ca.*
211 100 year old temperate trees to [CO₂] of 530 ppm and found that elevated [CO₂]
212 stimulated carbon uptake by crowns of mature trees but did not increase tree growth or
213 litter production. However, the study by Körner *et al.* (2005) was *not* designed to
214 investigate, whether (1) trees have already showed a ‘treatment effect’ in response to the
215 30% increase in [CO₂] that has occurred over the past 150 years, and (2) whether 100
216 year old trees developing in concert with the Industrial Revolution might show a different
217 ‘treatment effect’ than trees that were already reproductively mature when the Industrial
218 Revolution began. Indeed, even untreated reference trees in the study by Körner *et al.*
219 (2005) were in a vigorous growth phase. To properly address this question would require
220 a pre-industrial [CO₂] treatment, along with a current-day ‘ambient’ control treatment,
221 imposed from early development through maturity. This is impracticable for several
222 reasons, which make it necessary to rely instead on observational data like that provided
223 by tree rings and modeling.

224

225

226 **Tree Ring Increases in the 20th Century**

227 Contrary to the view that old trees approach zero growth, these trees in the late 20th
228 century have the potential to exhibit similar increases in girth as those observed in their
229 early growth years (Figure 4). Indeed, the doubling of ring width (from *ca.* 1750 to *ca.*
230 1950) as trees grow larger implies a more-than doubling of area increment (Figure 4). At
231 this site (Lava Beds, Washington, USA), at least half of 14 trees that were *ca.* 600 years
232 old displayed mid-to-late 20th century increases in ring width. For trees at this site that
233 did not exhibit such strong growth responses, there are many reasons, including biotic
234 competition (*e.g.*, light), disease and disturbance. Whether the rate of increase in tree
235 girth at this site is due to elevated [CO₂] or other environmental variables, and whether or
236 not wood density decreased in the newest growth rings, it is clear that, contrary to
237 idealized growth curves, old trees have the capacity to exhibit sustained diameter growth
238 in old age.

239 The phenomenon of 20th century ring width increase has been noted by other
240 studies (*e.g.* La Marche *et al.* 1984, Jacoby 1986, Graybill 1987, Kienast and Luxmoore
241 1988, Graumlich 1991, Knapp *et al.* 2001). A particularly notable study was that of La
242 Marche *et al.* (1984), that found latter 20th century increases in ring widths in many-
243 centuries-old bristlecone pine trees (Figure 5). These results could not be explained by
244 temperature or precipitation variation over this time period, but were consistent with, and
245 attributed to the rise in atmospheric [CO₂]. While these data appear to represent
246 compelling circumstantial evidence for carbon fertilization of old growth trees, recent
247 work has shown that pan evaporation, the geometry of solar radiation, and forest carbon

248 gain have varied in concert over the last several decades (Roderick and Farquhar 2005;
249 Gu *et al.* 2005) and must also be considered as potential drivers of these responses.

250 The capacity of old trees to respond to environmental change has a key applied
251 consequence: interpretation of annual rings to detect climate change. A key initial step in
252 tree ring analysis is the detrending of biological growth curves, which are of secondary
253 interest (*e.g.* Esper *et al.* 2002). A continuing, central challenge in tree ring-based
254 climate analysis is to assess whether changes occur in the growth curves themselves, due
255 to [CO₂] or to other environmental changes. Several approaches have been developed to
256 meet this analytical challenge (Graumlich *et al.* 1991, Briffa *et al.* 1992, Knapp *et al.*
257 2001, Monserud and Marshall 2001, Esper *et al.* 2002). Notwithstanding their value in
258 separating climate change signals from biological growth in old trees, these techniques
259 face a fundamental challenge in attempting to separate (1) low frequency climate
260 variation from (2) a “low frequency” – often sigmoidal – tree growth curve, especially as
261 they may interact.

262

263 **Rings versus leaders: Girth versus height growth**

264 The universally-observed cessation of *height* growth in long-lived trees may promote a
265 simplistic inference that growth in general ceases in old trees. However, girth growth is
266 common in old trees and may even increase after centuries of stable or decreasing girth
267 growth. Regarding height, observations of the annual leader on old trees with apical
268 dominance show that they do approach zero (personal observations on 500 year old
269 Douglas-fir, Western hemlock, and Western red cedar trees), but the vertical position of
270 the leader can fluctuate inter-annually in response to inter-annual variation in soil or

271 atmospheric moisture (*e.g.* Koch *et al.* 2004). The cessation of height but not girth
272 growth is a provocative clue that height growth cessation in old trees may be due to
273 hydraulic (*e.g.* cell turgor, expansion, and gravity; Koch *et al.* 2004; Woodruff *et al.*
274 2004) or biomechanical limitations that do not constrain girth growth. This phenomenon
275 also raises interesting questions. Could increased atmospheric [CO₂] have caused a
276 gradual, albeit small increase in tree height over what would have obtained in the absence
277 of the industrial age rise in [CO₂]? More fundamentally, is continued girth growth of
278 functional benefit in old trees? At least two features of girth growth argue for potential
279 functional benefit: increased biomechanical support, and provision of new vascular tissue
280 to replace permanently dysfunctional vascular tissue (Thomas 1996).

281

282 **Simulating Old Tree Response to Environmental Change**

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

291 We used the DESPOT model (Buckley and Roberts 2006) to evaluate differences
292 in tree physiology and growth for a generalized conifer growing in an even-aged stand
293 over 400 years, comparing steady pre-industrial [CO₂] (280 μmol mol⁻¹) versus

294 monotonically increasing $[\text{CO}_2]$ (280-370 $\mu\text{mol mol}^{-1}$). Key attributes of this model that
295 made it appropriate for use here are that it: (1) simulates long term (centuries) tree growth
296 and carbon allocation; and (2) does not impose pre-determined constraints on carbon gain
297 or allocation. Instead, physiological constraints (*e.g.*, hydraulic, nutritional, and
298 metabolic) emerge and are modified as a result of optimal carbon allocation to maximize
299 net carbon gain (discounted by probability of mechanical failure). It allows for stand level
300 feedbacks; specifically, changes in stem density and canopy leaf area that may feedback
301 to influence individual tree growth and allocation.

302 Our model simulation predicts substantial changes in tree structure – increased
303 height, diameter, leaf area, and sapwood area - and reduced stand density over 400 years,
304 comparing trees growing through the Industrial Revolution with those growing through a
305 constant pre-industrial $[\text{CO}_2]$ environment (Table 1). This model predicts instantaneous
306 water use efficiency (*i.e.*, photosynthesis per unit transpiration) is higher today than in a
307 low $[\text{CO}_2]$ world, and this drives changes in tree carbon allocation and stand structure. It
308 also suggests an explanation for confounding results such as those of Körner *et. al*
309 (2005): namely, that the responses of leaf area production, stem growth and height
310 growth differ widely under different assumptions about stomatal physiology (Buckley
311 2008) because those assumptions greatly affect the adaptive landscape on which
312 alternative strategies for investing the extra CO_2 are parsed. These non-intuitive
313 predictions, and similarly non-intuitive results from enrichment experiments, suggest that
314 an understanding of tree response to climate change may require a more integrative and
315 dynamical conceptual perspective than currently used by physiologists.

316 Even these results are based on an extreme simplification of reality (*e.g.* constant
317 environment except for [CO₂]). A more sophisticated approach, but outside of the scope
318 of this study, would be to obtain species and site specific parameters for use in this
319 model, and utilize historical climate data instead of assuming steady climate and edaphic
320 (soil moisture, nutrition) conditions. This would allow an evaluation of the sensitivity of
321 the simulations to multiple environmental variables, including temperature, precipitation,
322 nitrogen deposition, and atmospheric [CO₂].

323

324 **Future Research Opportunities**

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

332

333 *Evaluating impacts of multiple environmental variables on old tree function*

334

335 Variation in water, nutrient availability, pollutants, [CO₂] and/or temperature may
336 independently and interactively impact plant function (Luo, Canadell and Mooney 1999,
337 Oren *et al.* 2001), including in old trees. To make progress in deconvolving and
338 synthesizing old tree response to multiple environmental changes, judicious choices of

339 old trees for study can be critical. For example, old growth coniferous forests of the
340 Pacific Northwest often experience low soil nutrient status, particularly N. Moreover, N
341 deposition in montane forests of the Pacific Northwest has been remained near pre-
342 industrial levels (Holland *et al.* 1999). Trees from such a condition, possibly compared to
343 trees closer to anthropogenic sources of N, but otherwise exposed to similar
344 environments, could be used to evaluate the influence of environmental changes in N as
345 part of a suite of environmental changes including [CO₂]. Similarly, old trees that
346 differed throughout their lives in access to soil water or in seasonal temperature variation
347 could be compared and contrasted in their response to the industrial rise in [CO₂]. In
348 particular, trees that experience moderate temperatures year round (*e.g.*, old growth
349 forests of the Pacific Northwest, or tropical regions) may be expected to show greater
350 response to post-industrial age [CO₂] than trees that are severely temperature limited.

351 Finally, selection of tree species for these studies is crucial, especially regarding
352 life history traits. In particular, trees that remain canopy dominants throughout their
353 lifetimes (*e.g.* Douglas-fir in the Pacific Northwest United States), or are otherwise
354 naturally open-grown (*e.g.*, palm species like *Washingtonia robusta* H. Wendl.) may be
355 especially tractable study subjects. This trait simplifies environmental history through
356 maintenance of a similar light environment during the same time that atmospheric [CO₂]
357 has risen.

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362 *Old questions applied in a new context*

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364 Several topics of current research interest in global change biology have yet to be
365 examined specifically in old trees, and have direct relevance to the questions addressed in
366 this paper. For example, there are no studies to our knowledge that have examined how
367 tree foliar and reproductive phenology varies with both age *and* environmental change,
368 although phenology has been shown to vary with tree age (*e.g.* Augsburger 2004, Lugo
369 and Rivera Batlle 1987) and climate (*e.g.* Myneni et al. 1997) and [CO₂] (Springer and
370 Ward 2007 and references therein). However, the interactive effects of phenology,
371 ontogeny, and environmental change remains unexplored.

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

378

379 *New Technologies*

380

381 Over the last several decades, environmental treatment and measurement techniques have
382 been developed that provide new insights into old tree response to environmental change.
383 Canopy access to the tops of large, old trees (*e.g.*, Shaw *et al.* 2004) has opened up new
384 research opportunities. Moving canopy science from observation to environmental

385 manipulation is likely the wave of the future. For example, the webface technology
386 (Körner *et al.* 2005) could be implemented on very old trees, including those showing
387 post-maturity growth declines. This technology could also supply pre-industrial levels of
388 [CO₂] to crowns of old trees as a way to ‘set the clock back’ on the environment that old
389 trees experienced for most of their life, thereby allowing examination of the ‘normal’
390 baseline environmental condition and physiological response of ancient trees, and
391 consequently providing knowledge of whether these trees have likely already experienced
392 an Industrial Age “treatment effect”. Whole tree chamber technology (*e.g.* as described
393 in Phillips *et al.* 2004) or desert FACE technology (Jordan *et al.* 1999) could feasibly be
394 placed over very old, but relatively small trees like millennium-aged bristlecone pines (or
395 even in bonsai trees), to vary [CO₂] from pre-industrial to present, and future levels.

396 After nearly two centuries of industrialization, there is now a confluence of
397 factors – rapidly depleting stocks of old trees, exponential global environmental change,
398 and technological advances in canopy access and monitoring – that make the study of old
399 tree growth and physiology increasingly compelling and timely. We have shown here
400 that old trees have the capacity to grow well past a post-maturity growth decline. Yet the
401 understanding of old tree responses to the environment remains necessarily speculative,
402 because (1) there is ultimately no substitute for time in experiments on centuries-old
403 organisms; and (2) canopy access to tall, old trees remains a formidable challenge. For
404 these reasons, modeling and observational studies will continue to prove essential to our
405 assessments of the capacity of old trees to respond to environmental change.

406

407

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415

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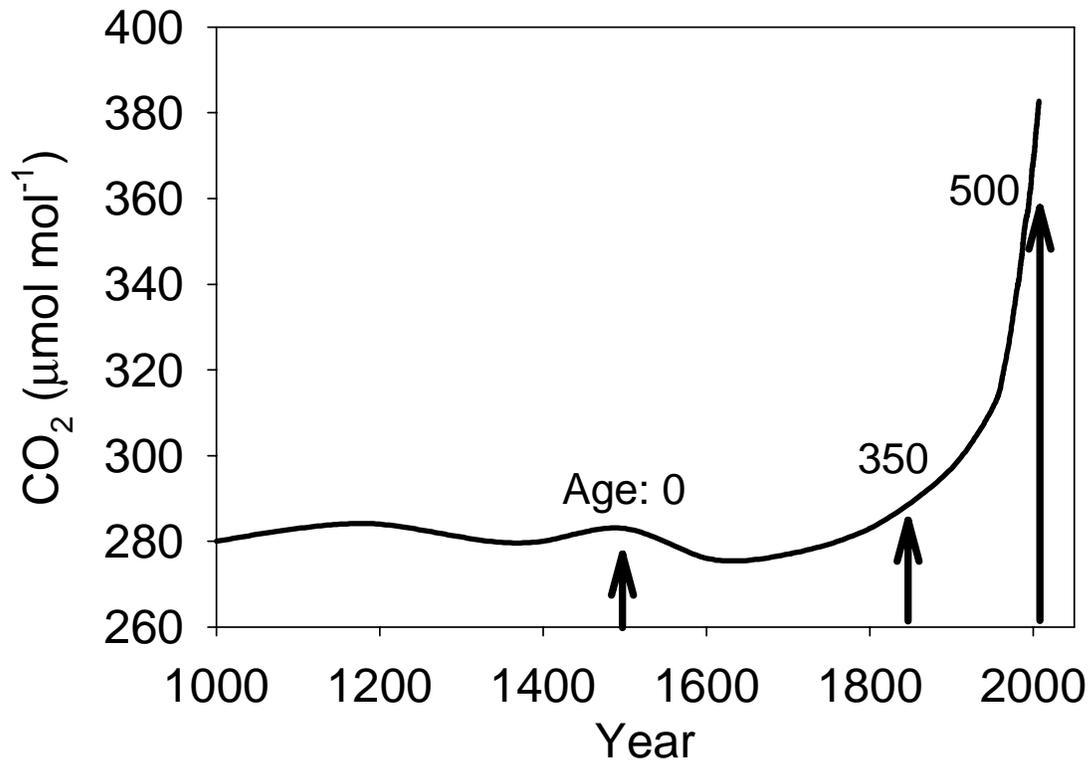
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- 633

633 **Figures**

634



635

636 **Figure 1.** Change in mean global atmospheric carbon dioxide over the last millennium.

637 Arrows indicate the ages of a contemporary 500-year-old tree during this period.

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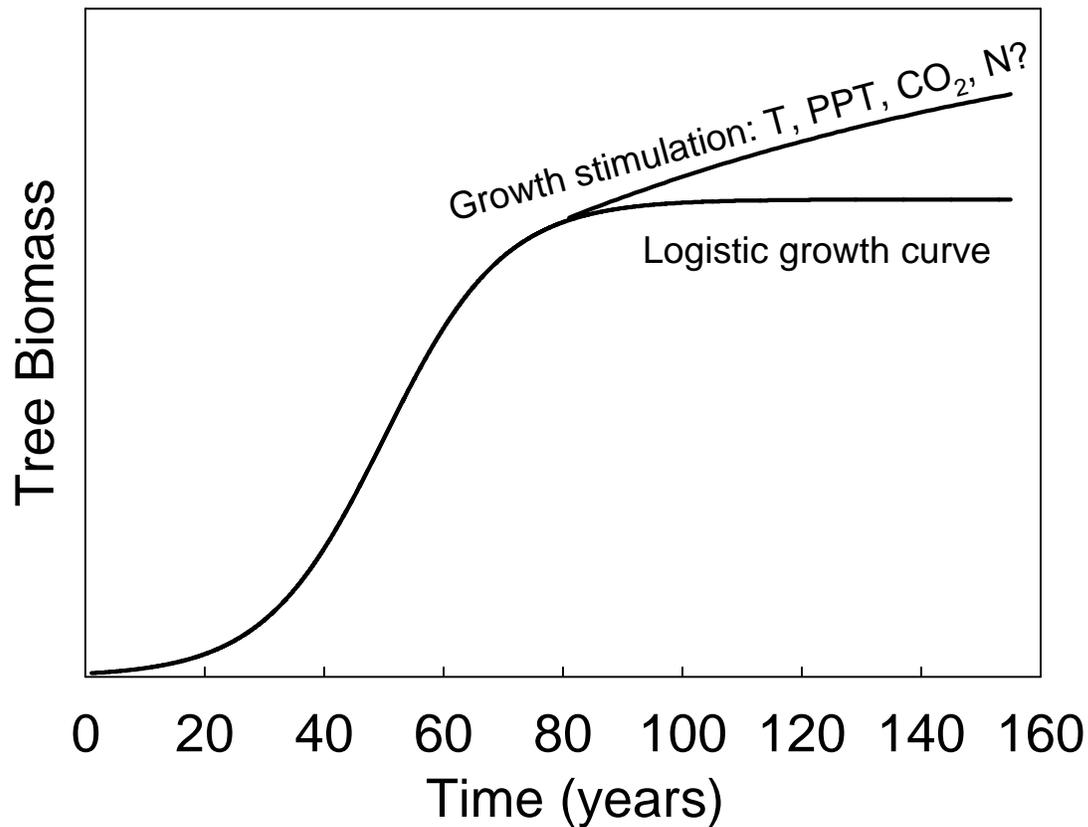
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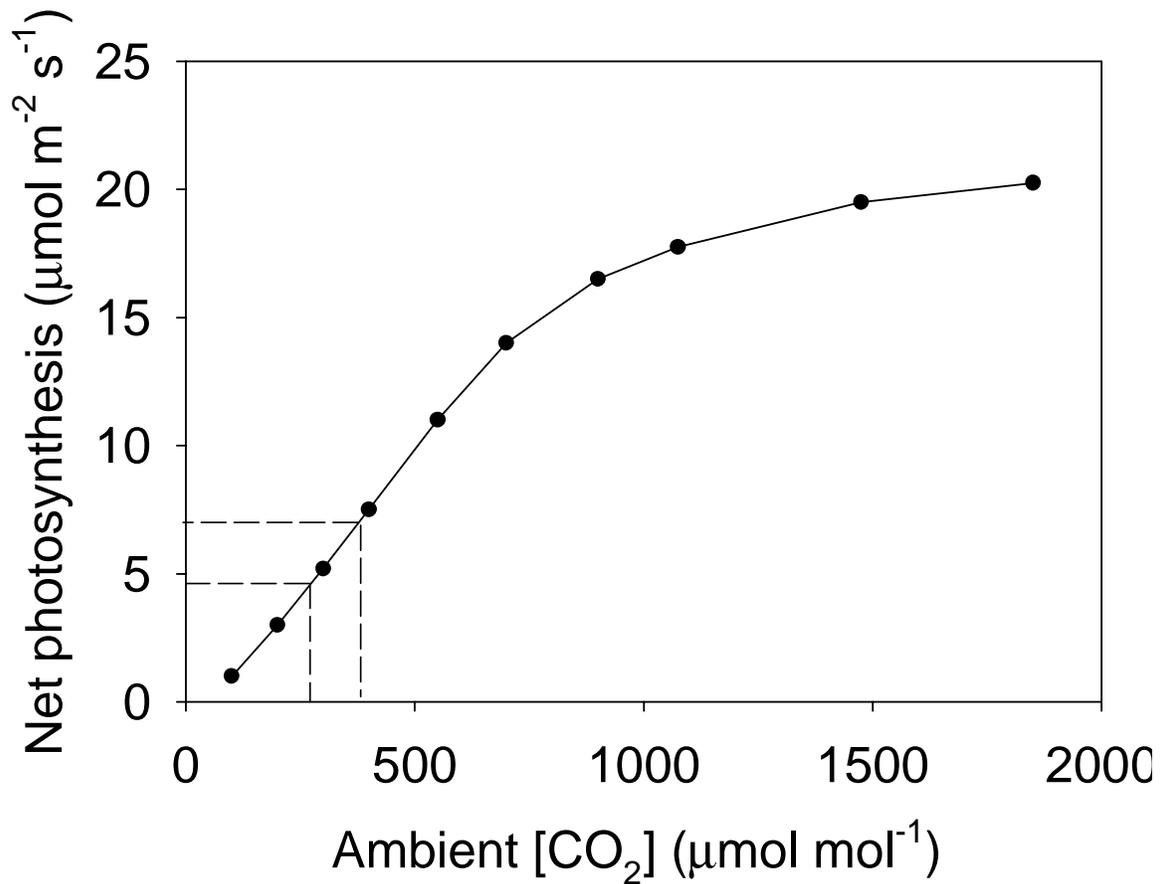


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646 **Figure 2.** One possible realization of altered tree growth due to changes in
647 environmental variables. The logistic growth trajectory in this figure is highly idealized
648 and commonly assumed (Weiner and Thomas 2001), and the departure from logistic
649 growth here illustrates the concept that growth of old trees may be affected by
650 environmental change. Resource availability (T= temperature; PPT = precipitation; N =
651 nitrogen availability) increases around approximately year 90 in this illustration.

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655 **Figure 3.** Typical response of leaf net photosynthesis (measured as net CO₂ uptake) to656 ambient [CO₂] in the crowns of 500-year-old Douglas-fir trees. Vertical lines indicate657 pre-industrial and current [CO₂]. Corresponding horizontal lines show a *ca.* 30%

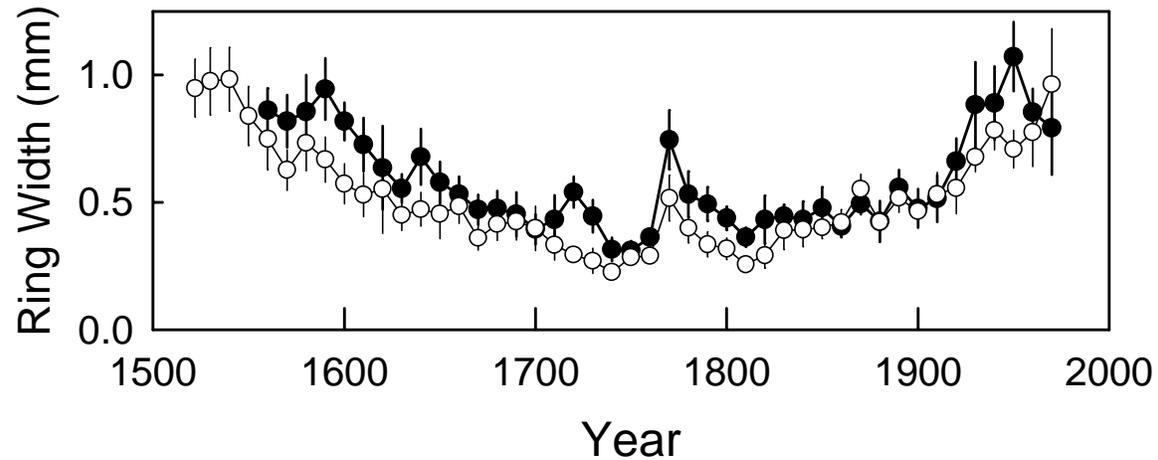
658 difference in net photosynthetic rate. Data from Wind River, Washington, June 22, 1999,

659 during conditions of saturating light. Site and sampling details are described in

660 McDowell *et al.* 2002.

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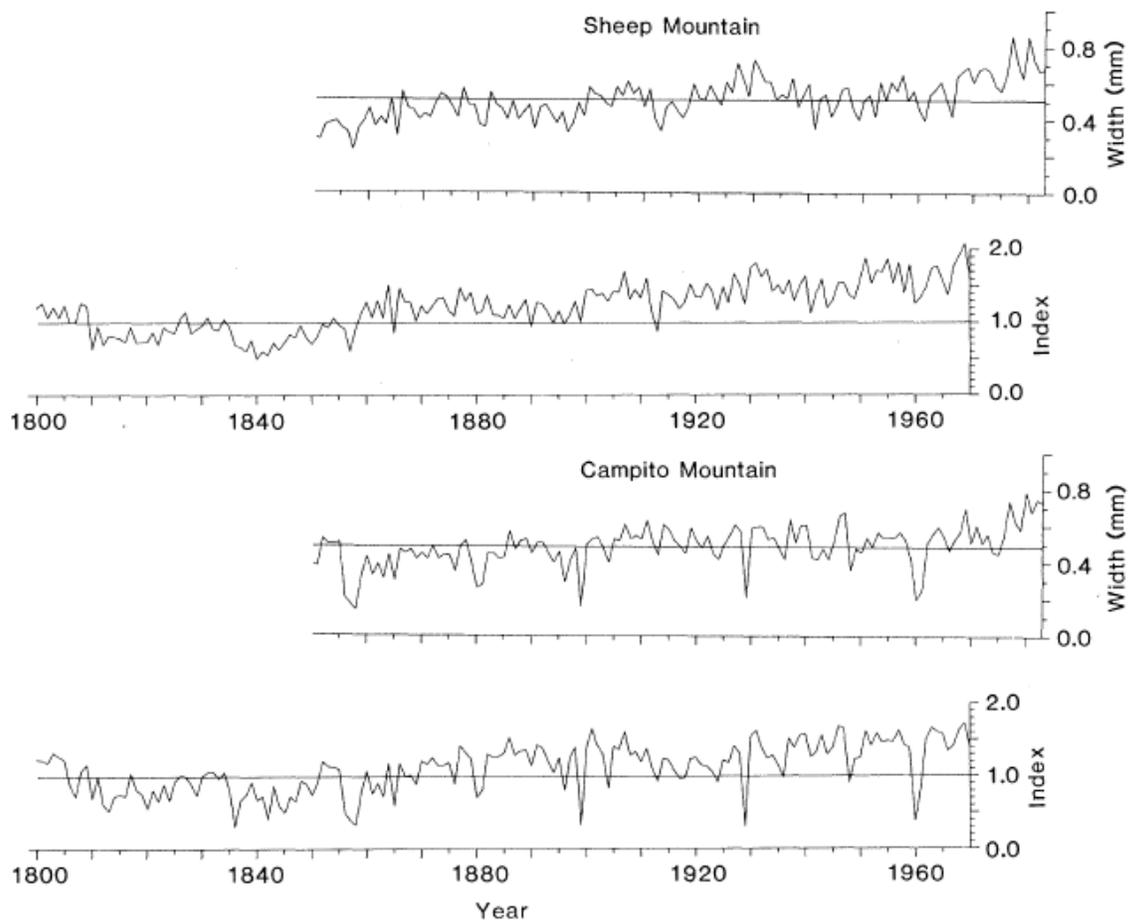
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664 **Figure 4.** Ring width chronology from a *ca.* 500-year-old dominant Douglas-fir tree at
665 Lava Beds, Washington, *ca.* 10 km from where the leaf level data were taken in Figure 3.
666 Each symbol is a decadal average, with standard deviations from 10-year averages.
667 Symbols correspond to two tree cores from different sides of the tree. Data obtained from
668 the NOAA paleoclimate web page (originally collected by L. Brubaker).

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Figure 5. Ring width time series in bristlecone pine trees from two sites in California,

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showing increases in the latter part of the 20th century that were uncorrelated with climate

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variation (temperature and precipitation data not shown). Data represent averages of 13 –

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15 trees in each site. In each of two sites above, the upper time series in the upper panel

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supplements the longer time series in the lower panel of each site (which was obtained for

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a previous study), and shows ring widths (mm) instead of a standardized ring width index

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(dimensionless; see www.ncdc.noaa.gov/paleo/treeinfo.html), because standardization

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procedures can confound environmental variation from biological growth. Figure

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reproduced from LaMarche *et al.* (1984). (Permission is pending from Science Magazine

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682

Variable	Percent Change with [CO ₂] Rise
Tree height	+9
Tree diameter	+9
Tree sapwood area	+36
Tree leaf area	+43
Stem density	-12

683

684 **Table 1.** Simulated differences in tree properties after 400 years, comparing constant 280
685 $\mu\text{mol mol}^{-1}$ [CO₂] with monotonically rising [CO₂] from 280-370 $\mu\text{mol mol}^{-1}$ (rate step =
686 0.23 $\mu\text{mol mol}^{-1} \text{y}^{-1}$). Input parameters used for this simulation are for a generalized
687 conifer tree, under unchanging climate conditions. Positive values of percent change
688 correspond to fertilizing effects of elevated [CO₂]. The simulations assume no effect of
689 [CO₂] on photosynthetic capacity or foliar or wood respiration rates (see text for
690 discussion of those assumptions).