

Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions

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ABSTRACT

Stand density reductions have been proposed as a method by which old-growth ponderosa pine (*Pinus ponderosa*) forests of North America can be converted back to pre-1900 conditions, thereby reducing the danger of catastrophic forest fires and insect attacks while increasing the productivity of the remaining old-growth individuals. However, the duration of productivity response of individual trees and the physiological mechanisms underlying such a response remain speculative issues, particularly in old trees. Tree-ring measurements of carbon isotope ratios ($\delta^{13}\text{C}$) and basal area increment (BAI) were used to assess the response of intrinsic water-use efficiency (the ratio of photosynthesis, A to stomatal conductance, g) and growth of individual >250-year-old-ponderosa pine trees to stand density reductions. It was hypothesized that reductions in stand density would increase soil moisture availability, thus decreasing canopy A/g and increasing carbon isotope discrimination (Δ). Cellulose- $\delta^{13}\text{C}$ of annual tree rings, soil water availability (estimated from pre-dawn leaf water potential), photosynthetic capacity, stem basal growth and xylem anatomy were measured in individual trees within three pairs of thinned and un-thinned stands. The thinned stands were treated 7 to 15 years prior to measurement. The values of $\delta^{13}\text{C}$ and BAI were assessed for 20 consecutive years overlapping the date of thinning in a single intensively studied stand, and was measured for 3 years on either side of the date of thinning for the two other stands to assess the generality of the response.

After thinning, Δ increased by 0.89‰ ($\pm 0.15\%$). The trees in the un-thinned stands showed no change in Δ (0.00‰ $\pm 0.04\%$). In the intensively studied trees, significant differences were expressed in the first growing season after the thinning took place but it took 6 years before the full 0.89‰ difference was observed. BAI doubled or tripled after disturbance, depending on the stand, and the increased BAI lasted up to 15 years after thinning. In the intensively studied trees, the BAI response did not begin until 3 years after the Δ response, peaked 1 year after the Δ

peak, and then BAI and Δ oscillated in unison. The lag between BAI and Δ was not due to slow changes in anatomical properties of the sapwood, because tracheid dimensions and sapwood-specific conductivity remained unchanged after disturbance. The Δ response of thinned trees indicated that A/g decreased after thinning. Photosynthetic capacity, as indexed by foliar nitrogen ([N]) and by the relationship between photosynthesis and internal CO_2 ($A-C_i$ curves), was unchanged by thinning, confirming our suspicion that the decline in A/g was due to a relatively greater increase in g in comparison with A . Model estimates agreed with this conclusion, predicting that g increased by nearly 25% after thinning relative to a 15% increase in A . Pre-dawn leaf water potential averaged 0.11 MPa (± 0.03 MPa) less negative for the thinned compared with the un-thinned trees in all stands, and was strongly correlated with Δ post-thinning ($R^2 = 0.91$). There was a strong relationship between BAI and modelled A , suggesting that changes in water availability and g have a significant effect on carbon assimilation and growth of these old trees. These results confirm that stand density reductions result in increased growth of individual trees via increased stomatal conductance. Furthermore, they show that a physiological response to stand density reductions can last for up to 15 years in old ponderosa pines if stand leaf area is not fully re-established.

Key-words: *Pinus ponderosa*; carbon isotopes; forest management; old growth; stem growth; tree rings.

INTRODUCTION

Ponderosa pine is a conifer with a widespread range in North America, occurring from central Mexico to southern Canada (Waring & Law 2001), and is an economically important species in both public and private forests. Prior to 1900, frequent ground fires removed competing understorey vegetation and maintained park-like stand structure in ponderosa pine forests. However, with the advent of fire exclusion around 1900, stand density (the number of individuals per unit ground area) has increased dramatically (Agee 1993). Fire exclusion has resulted in increased regeneration of understorey plants as well as invasion of shade-tolerant conifers, resulting in increased competition and

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reduced productivity of overstorey trees (Parsons & DeBenedetti 1979). Reductions in growth capacity of individual trees results in increased susceptibility to attack from insects such as the mountain pine beetle (*Dendroctonus ponderosae*) (Larrson *et al.* 1983; Waring & Pitman 1985). Of particular relevance to the public is the increased danger of catastrophic forest fires associated with the large fuel loads in the dense forests. Concern is mounting that the old-growth pine forests of western North America are in danger of disappearing due to fire and insect attack unless intervention via management techniques is employed.

Thinning of understorey competition to reduce stand density is a popular new management method because it effectively reduces within-stand competition while maintaining the presence, and increasing the vigour of old-growth trees (Waring & Pitman 1985; Newton & Cole 1987). However, the duration of the growth response is variable. Oren *et al.* (1987) observed that the thinning-induced growth response of young pine trees lasted for only a few years. Growth decline after the initial peak was associated with re-establishment of canopy leaf area index (*LAI*, m² leaf area per m² ground area) to pre-thinning levels. However, if a sufficiently large reduction in *LAI* occurs via thinning, stands may potentially respond for as long as 15 years (Latham & Tappeiner 2002).

The mechanism of growth response is also variable. In relatively dry ecosystems it seems likely that soil moisture availability should increase after partial removal of transpiring leaf area via thinning, thereby increasing water availability to the remaining trees. There is mixed evidence in support of this theory. Selective cutting resulted in increased soil water availability for *Pinus resinosa* (Sucoff & Hong 1974) and *Pinus contorta* (Donner & Running 1986). However, Waring & Pitman (1985) found large increases in growth efficiency in 120-year-old subalpine lodgepole pine (*Pinus contorta*) stands after thinning despite no changes in soil moisture availability. In young *Pinus radiata*, post-thinning growth increases occurred due to increases in nitrogen and light availability rather than increases in water availability (Warren, McGrath & Adams 2001). Finally, mature ponderosa pine trees in Arizona exhibited no thinning response (Leavitt & Long 1986).

If thinning does result in increased soil water availability then crown-scale stomatal conductance (*g*) should increase because foliage balances atmospheric demand for water vapour with the supply from the soil-plant hydraulic system via *g*. Diffusion of CO₂ into foliage is a function of *g*, thus photosynthetic carbon assimilation (*A*) should also increase if soil water availability increases. Such an increase in *g* and *A* may be a proximal mechanism of increased growth after thinning. If this is the mechanism of growth response, it should be recorded in the δ¹³C record of tree rings. Photosynthesis by terrestrial C₃ plants discriminates against CO₂ with ¹³C relative to CO₂ with ¹²C because ¹³C has a lower diffusivity through the stomatal pore and lower reactivity with the photosynthetic enzyme ribulose 1,5-bisphosphate carboxylase-oxygenase (Rubisco). This discrimination results in a decrease in δ¹³C of plant matter of

approximately 20‰ below that of atmospheric CO₂. Discrimination can be expressed mathematically as (Farquhar, Ehleringer & Hubick 1989):

$$\Delta = a + (b - a) \cdot \frac{C_i}{C_a} \quad (1)$$

where *a* is the fractionation associated with diffusion in air (4.4‰) and *b* is the net fractionation associated with carboxylation by Rubisco (27–29‰), and *C_i* and *C_a* are the intercellular and atmospheric partial pressures of CO₂, respectively. Discrimination is physiologically linked to gas-exchange because *g* and *A* regulate *C_i*:

$$C_i = C_a - \frac{A}{g} \quad (2)$$

A/g is also referred to as the intrinsic water use efficiency. Changes in *A/g* cause a proportional change in Δ. This will result in a change in δ¹³C because δ¹³C is related to Δ as (Farquhar, O'Leary & Berry 1982):

$$\Delta = \frac{\delta^{13}C_p - \delta^{13}C_a}{1 + \delta^{13}C_p/1000} \quad (3)$$

where δ¹³C_a and δ¹³C_p are the isotope compositions of the source air used for photosynthesis and from tree-ring cellulose, respectively. Because cellulose is immobile within tree rings once it has been deposited within the cell walls (Tans, deJong & Mook 1978), it can be analysed to provide an isotopic record at the annual time-step. Therefore, tree-ring cellulose can be used as a record of crown-scale *A/g*.

A/g is negatively correlated with water availability (Dupouey *et al.* 1993; Ehleringer 1993; Livingston & Spittlehouse 1996) because *g* increases more in response to increasing water availability than the concomitant increase in *A* (Meinzer, Goldstein & Grantz 1993). However, in thinned forests this response may be mediated or even overwhelmed by a simultaneous increase in nutrient or light availability associated with disturbance (Warren *et al.* 2001). Alternatively, there may be no response of *A/g* to thinning (Leavitt & Long 1986), potentially due to a balancing effect of increased light or nitrogen (which should increase *A/g*) against the effect of increased soil moisture (which should decrease *A/g*).

The primary objectives of our study were: (1) to determine if growth responds to thinning in large, old ponderosa pine trees; (2) to determine if canopy gas exchange responds to thinning; and (3) if responses are observed, to determine the duration of such responses if *LAI* remained below pre-thinning levels. Through this analysis we were able to examine whether the linear relationship between growth and Δ observed by McNulty & Swank (1995) held for disturbed systems. We also investigated the relationship between canopy gas exchange and sapwood anatomy (Ponton *et al.* 2001) before and after stand density reductions. We used three different stands of 250-year-old-ponderosa pine trees, each of which had a section thinned with ≥61% of the basal area removed in the last two decades. Results are presented both at the individual tree level and stand level. Because this is a relatively dry region with low *LAI*

($\leq 2.5 \text{ m}^2 \text{ m}^{-2}$, Law *et al.* 2001), we expected that reductions in stand density would result in increased soil water availability and therefore increased Δ .

METHODS

Experimental design

Three separate stands dominated by approximately 250-year-old ponderosa pine (stands A, B and C) were selected to test the hypothesis that stand density reductions affect Δ . Portions of each stand were previously thinned, and had a pair of plots located within the control and thinned sections (within a few hundred metres of each other). Plots were located randomly but with a minimum of 100 m between each plot and the edge of the treatment (the harvest boundary). Plots were variable in size, but were large enough to ensure that a minimum of five overstorey trees were present within the plot. This resulted in plot sizes of 706–2153 m^2 . Five trees per plot were selected for measurement of Δ and other sapwood characteristics. Intensive measurements of leaf gas exchange and further detail measurements of the tree ring record (described below) were carried out at stand A only.

Study stands

Ponderosa pine stands were selected near Black Butte, OR (between 44°25' N and 121°40' W, and 44°30' N and 121°37' W). The three stands are located along an 18 km transect that runs from north to south. They are located at elevations between 960 and 1035 m and are on deep, sandy loam soils derived from volcanic ash. Ponderosa pine is the dominant overstorey tree species, comprising $\geq 80\%$ of the basal area at each stand. The area receives approximately 360 mm annual precipitation. Nearly all of the annual precipitation falls during the winter, with the summers characterized as warm and dry. The average leaf area index for forests in this area is $1.5 \text{ m}^2 \text{ m}^{-2}$ ground area (Law *et al.*

2001). This region has experienced fire exclusion since approximately 1910 and as a result, most forests are more heavily stocked with regenerating trees than was typical of pre-settlement conditions (Weaver 1943; Agee 1993).

Treatments

Details on tree sizes and the treatment sizes are given in Table 1. In each stand, the thinning treatments selectively left the largest trees with a wide spacing. A portion of stand A was selectively harvested in 1987. Regenerating ponderosa pines were present at low density in the thinned plot. In the un-harvested control portion of the stand, small ponderosa pines with diameter at breast height (*DBH*, 1.38 m height) ≤ 6 cm comprised 12% of the basal area and 91% of the number of stems. A portion of stand B was selectively harvested in 1993. The understorey was sparsely covered by regenerating ponderosa pine. The un-harvested control forest was heavily stocked with large ponderosa pines and grand fir trees (*Abies grandis*), but very few saplings or seedlings. A portion of stand C was selectively harvested in 1985. Regenerating ponderosa pines were present at low density. Ponderosa pines comprised nearly all of the trees in the un-harvested control forest. Also presented in Table 1 are estimates of whole-tree leaf area from the cored trees on each plot and plot level *LAI*. Leaf area and *LAI* were calculated using the allometric equations to predict sapwood area from *DBH* from Grier & Waring (1974) and leaf area from sapwood area from McDowell *et al.* (2002). These allometric equations are from trees in stands that were not thinned. Thus, application of these equations to the present study assumes no change in the allometric relationships associated with thinning and therefore, they should be used for reference only.

Growth measurements

Four increment cores, two collected with a 5 mm diameter bore and two with a 12 mm diameter bore, were removed

Table 1. Stand characteristics

Stand	Plot	<i>B.A.</i> cut ($\text{m}^2 \text{ ha}^{-1}$)	<i>B.A.</i> left ($\text{m}^2 \text{ ha}^{-1}$)	% <i>B.A.</i> removed	Peak <i>BAI</i> m^{-2} ground area ($\text{cm}^2 \text{ m}^{-2}$)	Sample trees <i>DBH</i> . (mean, range, cm)	Plot mean <i>DBH</i> (cm)	<i>LAI</i> ($\text{m}^2 \text{ m}^{-2}$)	Leaf area per tree (m^2)
A	Control	0	31.47	0	0.0169	58.4 (45.5–84.1)	58.4	1.56	200.5
	Thinned	18.49	11.45	61	0.0305	74.8 (53.7–87.6)	74.8	0.49	191.2
B	Control	0	60.00	0	0.0302	79.2 (70.2–87.4)	43.6	3.17	210.0
	Thinned	39.14	8.45	82	0.0158	72.0 (65.0–78.1)	72.0	0.37	74.95
C	Control	0	43.19	0	0.0205	63.0 (56.8–69.4)	46.6	2.06	137.3
	Thinned	34.85	12.23	74	0.1828	69.4 (61.8–85.2)	69.4	0.53	165.4

Basal area is presented per unit ground area. The amount of basal area removed from each plot (*B.A.* cut) was assessed by measuring the mean diameter of every stump within the plot and then correcting stump basal area to basal area at ~ 1.38 m using stand-specific relationships of basal area at stump height to basal area at ~ 1.3 m height. Peak *BAI* per m^2 ground area is the peak plot average *BAI* for the thinned plots and the average *BAI* of control plots for the corresponding year. Mean *DBH* is from all trees within a plot ≥ 6 cm *DBH*. It differs from sample trees mean *DBH* only when there were more trees within the plot than were sampled. The *DBH* of trees ≤ 6 cm *DBH* is provided in text when applicable. Leaf area per tree is for the five-cored trees per plot. Leaf area and leaf area index are calculated using the allometric equations to predict sapwood area from *DBH* from Grier & Waring (1974) and leaf area from sapwood area from McDowell *et al.* (2002), and assumes no change in the allometric relationships associated with thinning.

from each of the five sampled trees at ~1.38 m height to measure ring widths and basal area increment (*BAI*). Cores were dated and ring widths were measured to the nearest 0.001 mm under 40× magnification (Olympus SZ-4045; Tokyo, Japan) with a linear-encoded measurement stage (Velmex, Bloomfield, NY, USA). The instrument was calibrated daily. Ring widths were converted to *BAI* over the last 20 years using tree-specific *DBH* (inside bark) and assuming concentric circularity.

Carbon isotope composition

We focus on Δ as a measure of canopy gas exchange rather than $\delta^{13}\text{C}$ because the $\delta^{13}\text{C}$ of atmospheric CO_2 has become progressively depleted during the last century due to fossil-fuel burning (Keeling *et al.* 1989) thus complicating the isotope record. Because Δ accounts for changing $\delta^{13}\text{C}_a$ (Eqn 3), we are able to examine directly how disturbance affected tree physiology without confounding of $\delta^{13}\text{C}_a$. We calculated Δ with Eqn 3 using tree-ring $\delta^{13}\text{C}$ and $\delta^{13}\text{C}_a$ from

Moana Loa, Hawaii for the corresponding years (Keeling *et al.* 1989; see Table 2 for further references). One 12-mm-diameter core collected on the north side of the bole at ~1.38 m height was used from each of the five trees on all six plots for carbon isotope analyses. After drying, annual rings (including both late- and early-wood) were carefully dated for the period of 1980–99 and separated with a sharp blade. Because our focus was on the annual response of Δ to reductions in stand density, we did not attempt to separate early-wood from late-wood (i.e. Livingston & Spittlehouse 1996). Samples were ground using a Wiley mill to pass a 0.2-mm-mesh. Cellulose was extracted from the ground tree rings using the method described by Leavitt & Danzer (1993). Cellulose $\delta^{13}\text{C}$ was analysed using an isotope ratio mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) at the Integrated Stable Isotope Research Facility (ISIRF) at Environmental Protection Agency in Corvallis, OR. Precision for $\delta^{13}\text{C}$ was assessed using a National Institute of Standards and Technology-certified standard, with an average standard deviation of 0.08‰ ($n = 36$).

Symbol	Definition	Units	Source
A	net photosynthesis	$\mu\text{mol m}^{-2} \text{s}^{-1}$	This study
A_s	sapwood area	μm^2	This study
$A_{\text{lumen}}/A_{\text{sapwood}}$	lumen area/sapwood area ratio	unitless	This study
a	fractionation due to diffusion	‰	1
b	enzymatic fractionation	‰	1
BAI	basal area index	cm^2	This study
C_i	leaf-internal CO_2	$\mu\text{mol mol}^{-1}$	This study
DBH	diameter at breast height	m	This study
EW/LW	early-wood : late-wood ratio	unitless	This study
g	stomatal conductance	$\text{mol m}^{-2} \text{s}^{-1}$	This study
g_w	stomatal conductance to water vapor	$\text{mol m}^{-2} \text{s}^{-1}$	This study
g_c	stomatal conductance to CO_2	$\mu\text{mol m}^{-2} \text{s}^{-1}$	This study
J_{max}	electron transport limited A	$\mu\text{mol m}^{-2} \text{s}^{-1}$	This study
K_c	Michaelis–Menton constant: CO_2	Pa	2, 3
K_o	Michaelis–Menton constant: O_2	kPa	2, 3
k_{sp}	sapwood hydraulic conductivity	10^{-12}m^{-2}	This study
$[N]$	nitrogen concentration	%	This study
η	dynamic viscosity of water	$(\text{kg m}^{-2} \text{s}^{-1})$	4
O_x	oxygen concentration	kPa	2
P_i	leaf-internal CO_2	Pa	This study
r	lumen radii	μm	This study
R_d	respiration	$\mu\text{mol m}^{-2} \text{s}^{-1}$	This study
T_{air}	air temperature	°C	This study
T_{max}	air temperature (maximum)	°C	5
V_{cmax}	carboxylation limited A	$\mu\text{mol m}^{-2} \text{s}^{-1}$	This study
WUE_i	intrinsic water-use efficiency (A/g)	$\mu\text{mol mol}^{-1}$	This study
Δ	carbon isotope discrimination	‰	This study
$\delta^{13}\text{C}$	carbon isotope ratio	‰	This study
$\delta^{13}\text{C}_a$	$\delta^{13}\text{C}$ of atmospheric CO_2	‰	6 ^a
τ	specificity of rubisco for O_2/CO_2	$\mu\text{mol m}^{-2} \text{s}^{-1}$	2
$\Psi_{\text{pre-dawn}}$	predawn leaf water potential	MPa	This study ^b

Table 2. List of symbols, definitions, and sources used in this paper

Sources are: 1, Farquhar *et al.* (1989); 2, Harley *et al.* (1992); 3, Ellsworth (2000); 4, Jones (1992); 5, Oregon Climate Service; 6, Keeling *et al.* (1989). ^a $\delta^{13}\text{C}_a$ data obtained from the Institute of Arctic and Alpine Research (INSTAAR) at the University of Colorado (CU), and the National Oceanic and Atmospheric Administration (NOAA), Climate Monitoring and Diagnostics Laboratory (CMDL), Carbon Cycle Group. ^bLeaf water potential gravity corrected to ground height (0.01 MPa m^{-1}).

Photosynthetic capacity

Photosynthetic capacity can influence Δ by increasing or decreasing A , and therefore C_i/C_a . We used two approaches to determine whether thinning affected photosynthetic capacity. First, we used foliar nitrogen concentration [N] as an indicator of photosynthetic capacity (Field & Mooney 1986; Livingston *et al.* 1998). Second, photosynthetic capacity was assessed using response curves of photosynthesis to internal $[CO_2]$ ($A-C_i$ curves). Foliar [N] was measured on foliage from three trees in each of the control and thinned plots in each stand (total of 18 samples). Year 2000 foliage was collected with a shotgun in the autumn of 2000 from relatively exposed, south-facing branches located in the middle or upper third of the crown. Samples were dried at 65 °C for 48 h, ground with a mortar and pestle, and analysed with an elemental analyser (Model 1108EA; Carlo Erba Milan, Italy). Precision was better than 0.1% around a NIST standard. The $A-C_i$ curves were measured at stand A only on five trees in the control and five trees in the thinned forests on overcast days in June 2000. Branches were severed with a shotgun and the cut ends were submerged immediately into water and re-cut. The $A-C_i$ curves were measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA) equipped with a blue-red artificial light source. The cuvette irradiance was 1400 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; photosynthesis of ponderosa pine A saturates at irradiance levels near 800 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Hadley 1969). The $A-C_i$ curves were generated by changing the cuvette CO_2 in the following order: 40, 30, 20, 10, 40, 60, 80, 100, 120, 160 and 200 Pa. After each exposure to a new CO_2 level, foliar A was allowed to reach steady state (cuvette CO_2 coefficient of variation <2%) prior to measurement. Six measurements were made per sample per CO_2 -level over a period of 60 s after the steady state had been reached. The maximum catalytic activity of Rubisco (V_{cmax}) and the maximum electron transport rate (J_{max}) were calculated from the $A-C_i$ curves using non-linear, least-squares regression to fit the values of these parameters to the equations of the Farquhar, von Caemmerer & Berry (1980) photosynthesis model (Harley *et al.* 1992). Parameters were temperature-corrected to 25 °C using the equations of Leuning (1997), and the activation energies measured for *Pinus taeda* (Ellsworth 2000).

Water potential

We estimated soil water availability in the root zone using pre-dawn measurements of leaf water potential ($\Psi_{\text{pre-dawn}}$) of five overstorey ponderosa pines per plot on all six plots. Foliage samples were removed from the lower branches of each crown using a shotgun and measured within 3 min with a Scholander-type pressure chamber (PMS, Corvallis, OR, USA). These leaf water potential measurements were corrected for gravitational potential (0.01 MPa m^{-1}). We assumed that night-time transpiration was negligible. Measurements were made on 10 June, 9 July, and 13 August 2000.

Sapwood anatomy

At stand A, two 12-mm-diameter cores were removed per tree at ~ 1.38 m height in winter 2001 for analysis of tracheid lumen dimensions, early-wood : late-wood ratios, and wood density. One core was used for tracheid anatomy measurements to be used for calculation of potential hydraulic conductivity; the other core was used for the early-wood : late-wood ratio and wood density measurements. For tracheid lumen dimensions, cross-sectional samples including all annual rings from year 2000 back to 1980 were removed with a sliding microtome and fixed on glass slides with a 70% ethyl alcohol solution. The tracheid lumen areas were determined using a digital imaging and analysis system [Roper Scientific Coolsnap camera v 1.7.3 (Trenton, NJ, USA) with a Nikon Eclipse 400 compound microscope (Tokyo, Japan), with Scion Image 1998 (Fredrick, MD, USA) public domain-image processing and analysis program]. Lumen areas were measured across the entire early-wood section of each ring from 1980 to 1999. Tracheid densities were determined as a proportion of total early-wood sapwood area.

Tracheid density and lumen areas within the sapwood were used to estimate potential saturated hydraulic conductivity ($k_{\text{sp}} \times 10^{-12} \text{ m}^2$) according to Poiseuille's law:

$$k_{\text{sp}} = \frac{\left[\frac{\pi}{8\eta} \cdot (\sum r^4) \right]}{A_s} \quad (4)$$

where r is the radius of a circle having the same area as the corresponding tracheid, A_s is sapwood area, and η is the dynamic viscosity of water ($\text{kg m}^{-2} \text{s}^{-1}$). This is considered an estimate of maximum potential conductivity because it assumes no differences in tracheid length or friction due to bordered pits, tracheid tapering or xylem cavitation.

The annual ring wood density and early-wood : late-wood ratios were measured using an X-ray densitometer (Enraf-Nonius FR-590, 545; Delft, The Netherlands). Prior to density measurement, one core per tree was oven dried at 40 °C for 3 days. Density was measured every millimetre along the length of each core, and then converted to whole-ring densities with DendroScan software (UBC Press, Vancouver, BC, Canada). The boundaries between early-wood and late-wood were distinguished by abrupt, large changes in wood density.

Modelling A from Δ and $A-C_i$ functions

Assimilation-weighted A was estimated from tree-ring calculations of Δ and $A-C_i$ relationships. Equation 2 can be solved for C_i using cellulose-derived Δ . Using the equations of Farquhar *et al.* (1980), A in the carboxylation-limited region of the $A-C_i$ curve is:

$$A = V_{\text{cmax}} \cdot \left(\frac{C_i}{C_i + k_c \cdot (1 + O_x/k_o)} \right) \cdot \left(1 - \frac{0.5 \cdot O_x}{\tau \cdot C_i} \right) - R_d \quad (5)$$

where V_{cmax} is derived from the measured $A-C_i$ curves and C_i is obtained from tree-ring $\delta^{13}\text{C}$:

$$C_i = C_a \left(\frac{\delta^{13}C - \delta^{13}C_a - a}{b - a} \right) \quad (6)$$

All parameters used in these equations are described in Table 2. Electron transport-limited A is thought to occur only at C_i over 25 Pa (Harley *et al.* 1992), and examination of our $A-C_i$ curves verified that, at the low C_i levels recorded in the tree rings (< 20 Pa), electron transport was less limiting than carboxylation capacity. Triose phosphate utilization may also limit A , but we found no evidence of such limitation in the analysis of our $A-C_i$ curves; therefore we did not incorporate this limitation into our calculations.

We assumed that V_{cmax} was invariant among thinning treatments or years because we found no difference in V_{cmax} or leaf [N] between treatments (see Results) and because our values were very similar to estimates from $A-C_i$ curves measured on old ponderosa pines in a nearby region in the early 1990s (B.J. Bond, unpublished results). However, modelling A and g over varying temperature conditions requires correction of V_{cmax} to the average air temperature during photosynthesis. We corrected V_{cmax} for each year from 1980 to 1999 using a relationship between air temperature measured at mid-canopy height at an Ameriflux site near our forests (Law *et al.* 2001) and maximum temperature measured at the Sisters Ranger Station (15 km distant) from day of year 110–243, 1997. This is the period in which stem growth occurs in this region (Cleary & Waring 1969; R.H. Waring, personal comm.). Daily average air temperature in the forest from 0900 to 1500 h (T_{air} , the period of maximum photosynthesis, Law *et al.* 2000) was related to maximum air temperature at the Ranger Station (T_{max}) as:

$$T_{\text{air}}(^{\circ}\text{C}) = 0.44 \times T_{\text{max}} - 13.93, R^2 = 0.66 \quad (7)$$

The relationships between T_{air} and Ranger Station average temperature or minimum temperature were not as strong (R^2 values of 0.51 and 0.19, respectively). We then modelled T_{air} from 1980 to 1999 using daily T_{max} records from the Ranger Station. We assumed that needle temperature equalled air temperature.

We also modelled g for the sake of completeness. Stomatal conductance for each year was modelled by combining and re-arranging Eqns 1, 2 and 5:

$$g_w = \left[\frac{A}{C_a - \left(C_a \left(\frac{\Delta - a}{b - a} \right) \right)} \right] \cdot 1.6 \quad (8)$$

Our estimate of g was derived from CO_2 variables expressed as mole fractions, therefore the factor 1.6 is necessary to convert g for CO_2 (g_c) to g for water vapour (g_w). In this model, g_w is not independent of A and therefore inferences on the interaction between A and g_w are impossible. However, the model allows us to examine retrospectively how A or g_w varied after thinning.

Statistics

The physiological responses to stand density reduction were tested using a blocked analysis of variance with

repeated measures, in which the three stands make up the blocks and average pre- and post-thinning BAI , Δ or tracheid anatomy of annual tree rings from 1980 to 1999 is the repeated measure. $\Psi_{\text{pre-dawn}}$ was analysed as a blocked, repeated-measures analysis of variance. Foliar [N] was analysed as a blocked analysis of variance and $A-C_i$ parameters were compared using a paired t -test. The relationships between BAI , Δ , g_w , and A were examined via non-linear regression, including exponential, power and polynomial functions. Our statistical criteria for selecting equations included 95% confidence intervals, correlation coefficients and mean square error. If these criteria were similar, we chose the simplest model. Autocorrelations were not examined explicitly because of our limited time-series (Monserud & Marshall 2001); however, correlations between lagged parameters including BAI , Δ , g_w , and A were examined using linear regression.

RESULTS

Overall response to stand density reduction

Average tree BAI exhibited a large increase in response to stand density reductions in each forest (Table 1, Figs 1 & 2a). The pre-thinning BAI did not differ between control and thinned treatments for any forest ($P = 0.98, 0.57, 0.99$ for stands A, B and C, respectively, $n = 5$ trees per treatment and stand), but increased dramatically after thinning in all three forests ($P < 0.01$ for each stand). At stand A, the value of BAI of the trees remaining after thinning increased from a mean BAI of 18.3 cm^2 before thinning to a peak value of 45.1 cm^2 after thinning (increase of 124%). At stand B, BAI increased from a pre-thinning mean of 15.4 to a peak of 39.6 cm^2 (increase of 109%), and at stand C BAI increased from 14.6 before thinning to a peak value of 57.4 cm^2 (increase of 303%). When analysed as a blocked analysis of variance with repeated measures, the increase in average tree BAI was significant for all three thinned stands ($P < 0.01$), but the effect of stand (block) was not significant ($P = 0.54$).

The growth responses to stand density reductions were associated with significant increases in Δ . At stand B, Δ of the thinned trees increased from 16.25 to 16.86‰ after thinning ($P < 0.01$), whereas no change occurred in the control trees (Fig. 1). At stand C, Δ of the thinned trees increased from 15.46 to 16.43‰ after thinning ($P < 0.01$), whereas no change in Δ occurred in the control trees (Fig. 1).

At the intensively measured stand (stand A), where we measured average tree BAI and Δ for 20 consecutive years, both parameters increased after thinning (Fig. 2). As mentioned above, BAI more than doubled after thinning; however, the growth response did not begin until 4 years after the thinning occurred, and did not reach a maximum until 7 years after thinning (Fig. 2a). The temporal dynamics were different for Δ . A slight response in Δ was apparent 1 year after the thinning took place, followed by maximum Δ 6 years after the thinning (Fig. 2b). There was no significant decline in Δ 12 years after the thinning. No apparent

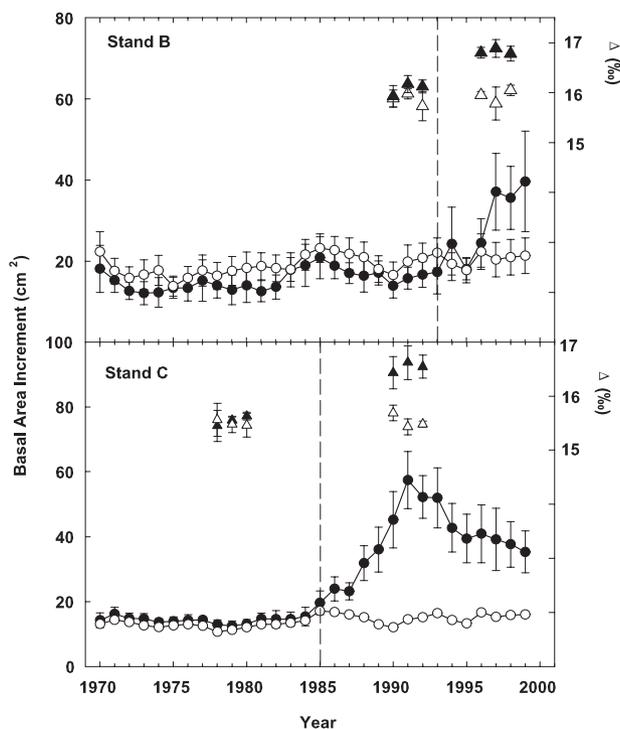


Figure 1. Basal area index (*BAI*, cm^2) of trees from the control stand (open circles) and the thinned stand (filled circles) from stand B (upper panel) and stand C (lower panel) from before and after the thinning. Carbon isotope discrimination (Δ , ‰) for the same trees is shown in the upper portion of each figure, with open triangles representing trees from the control stand and filled triangles representing trees from the thinned stand. The Δ values for stand B are averages of five trees for tree rings from 1990 to 1992 and 1996 to 1998. The Δ values for stand C are averages of five trees for tree rings from 1978 to 1980 and 1990 to 1992. The date of thinning for stand B is 1993, and for stand C is 1985 (indicated by dashed lines). Bars are standard errors, and the sample size was five trees per plot.

change in Δ of control trees was detected during the two decades. The Δ response was a common and significant response of all three forests when analysed as a blocked analysis of variance ($P < 0.01$), but there was no difference among stands ($P = 0.11$).

Photosynthetic capacity and water availability

Photosynthetic capacity, assessed using foliar [N] and $A-C_i$ curves, was unchanged by thinning (Table 3). Foliar [N] values averaged 1.11%, and did not vary with thinning or stand [blocked analysis of variance (ANOVA), $P = 0.41$ and $P = 0.26$, respectively]. The $A-C_i$ parameters V_{cmax} and J_{max} were also unresponsive to thinning at stand A (paired t -test, $P = 0.97$ and $P = 0.51$, respectively). The value of $\Psi_{\text{pre-dawn}}$ was significantly less negative at the thinned stands throughout the summer of 2000 (repeated measures blocked ANOVA, $P < 0.01$, Table 4). As the summer drought progressed the value of $\Psi_{\text{pre-dawn}}$ became more negative at

both control and thinned stands, but the relative rankings between treatments did not change at any date or stand. There was a strong relationship between stand-average $\Psi_{\text{pre-dawn}}$ and stand-average Δ after thinning (Fig. 3).

Sapwood anatomy

Sapwood anatomy was unresponsive to stand density reductions (Table 5). There was no response of tracheid lumen diameters calculated as the straight mean or the 'hydraulic' mean (equivalent to $\Sigma \text{diameter}^4 / \Sigma \text{diameter}^5$; Pockman & Sperry 2000) between the thinned and control trees after thinning ($P = 0.50$ and 0.60 , respectively). Potential hydraulic conductivity of sapwood calculated from Eqn 4 also did not respond to thinning ($P = 0.72$), nor did the early-wood : late-wood ratio ($P = 0.94$). The lumen surface area per unit sapwood area was invariant with stand density reduction ($P = 0.93$). The wood density did not respond to thinning ($P = 0.12$). Correlations between anatomical parameters and Δ (as carried out by Ponton *et al.* 2001) were not examined due to the lack of variation in anatomical parameters.

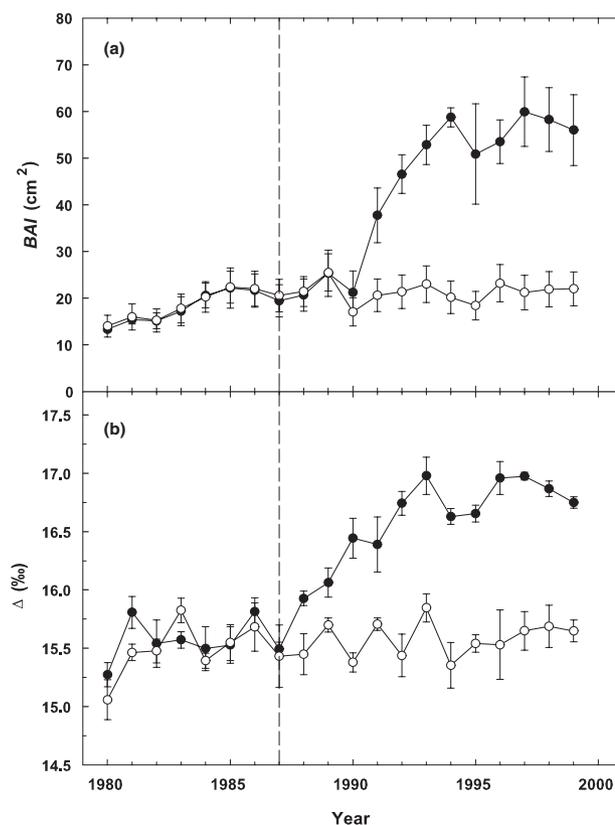


Figure 2. (a) *BAI* and (b) Δ of trees from the paired thinned and control portions of stand A. Trees from the thinned stand are indicated by closed symbols and from the control stand are indicated by open symbols. The date of thinning is indicated by the dashed line. Values are means with standard errors.

Table 3. Foliar nitrogen concentration ([N], percentage dry mass) from old ponderosa pine trees in three paired thinned and un-thinned stands, and the parameters V_{cmax} and J_{max} from $A-C_1$ curves from trees located at the paired thinned and un-thinned plots at stand A

Stand	Treatment	[N]	V_{cmax}	J_{max}
A	Control	1.11 (0.04)	42.8 (2.6)	100.7 (6.8)
	Thinned	1.12 (0.10)	42.7 (3.0)	104.6 (9.8)
B	Control	1.11 (0.02)		
	Thinned	1.10 (0.07)		
C	Control	1.20 (0.06)		
	Thinned	1.09 (0.04)		

V_{cmax} and J_{max} are presented in $\mu\text{mol m}^{-2} \text{s}^{-1}$, and are temperature corrected to 25 °C (Leuning 1997). Values in parentheses are standard errors ($n = 3$ trees).

Modelled A and g_w

At stand A, A and g_w for each tree were modelled for the period of 1980–99 using Eqns 5 & 8, respectively. The value of A/g_w calculated from the model, which equals Eqn 5/ (Eqn 8 \times 1.6) was identical to A/g_w from the traditional equations of Farquhar *et al.* (1989), thus verifying the accuracy of the calculations. A significant response of A/g_w occurred during the year after the thinning (Fig. 4). The value of A/g_w decreased from approximately 112 $\mu\text{mol mol}^{-1}$ to 97 $\mu\text{mol mol}^{-1}$ over 6 years, and stayed at this low level until 1999, 12 years after thinning. This response was associated with increases in both A and g (Fig. 5a & b). A reached a maximum 5 years after thinning and stayed at that level through the sixth year, whereas g_w did not reach its maximum value until year six. The decrease in A/g_w after thinning was associated with a 25% increase in g_w relative to the 15% increase in A (Fig. 5c).

The increase in A after thinning preceded the increase in average tree BAI by approximately 3 years (Fig. 6). BAI did not begin increasing generally until 4 years after the thinning occurred, and reached its maximum 1 year after A . It appears that after 9 years following the harvest, A and BAI oscillated in unison. To quantify the lag between average

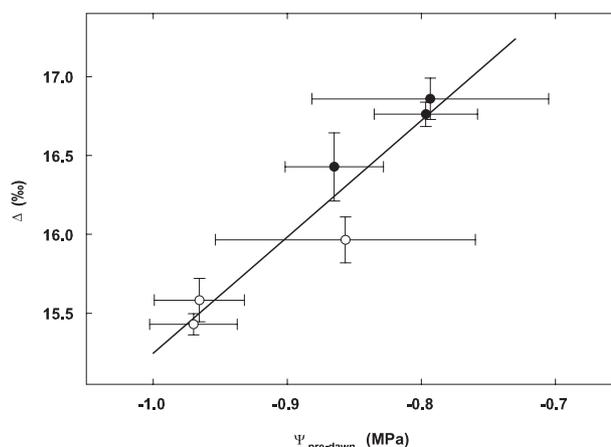


Figure 3. Mean Δ versus mean $\Psi_{\text{pre-dawn}}$ for trees in the thinned and controls stands at stands A, B and C. Δ is calculated as the mean for a given stand for all years post-thinning, and $\Psi_{\text{pre-dawn}}$ is calculated as the mean of all measurements for a given stand in 2000. Control stands are indicated by open symbols and thinned stands are indicated by closed symbols. Bars are standard errors. The equation is: $\Delta = 7.38 \cdot \Psi_{\text{pre-dawn}} + 22.63$, $R^2 = 0.91$, $P = 0.003$.

tree BAI and A , we regressed BAI against A using A from concurrent years or lagged 1 to 4 years behind BAI ; that is BAI from year X was regressed against A at year X_0 , X_{-1} ... X_{-4} . Pearson correlation coefficients for regressions of BAI versus A were 0.86, 0.92, 0.87, 0.89 and 0.86, with time lags of 0, 1, 2, 3 and 4 years, respectively. This indicated that BAI was best correlated with A in the previous year. However, analysis of the 95% confidence intervals about each correlation indicated that the correlations were not statistically different (Sokal & Rohlf 1987). The lack of significant differences is due in part to variation in the length of the lag period; namely a 3 year lag between A and BAI in the first 4 years, a 1 year lag at 6 to 8 years after thinning, and a zero year lag 9 to 12 years after thinning (Fig. 6).

The lag between canopy-scale A and growth resulted in a non-linear relationship between growth and photosynthesis (Fig. 7). There was no relationship between BAI and A for the control trees (regression P -values >0.05). However,

Stand	Treatment	June 2000	July 2000	August 2000
A	Control	-0.92 (0.03)	-0.95 (0.04)	-1.03 (0.03)
	Thinned	-0.74 (0.05)	-0.78 (0.02)	-0.87 (0.03)
	<i>Difference</i>	<i>0.18</i>	<i>0.17</i>	<i>0.16</i>
B	Control	-0.71 (0.03)	-0.82 (0.03)	-1.04 (0.06)
	Thinned	-0.66 (0.04)	-0.76 (0.04)	-0.96 (0.02)
	<i>Difference</i>	<i>0.05</i>	<i>0.06</i>	<i>0.08</i>
C	Control	N/A	-0.93 (0.05)	-1.01 (0.05)
	Thinned	N/A	-0.82 (0.03)	-0.91 (0.05)
	<i>Difference</i>		<i>0.11</i>	<i>0.10</i>

$\Psi_{\text{pre-dawn}}$ is gravity corrected (0.01 MPa m^{-1}). The difference between $\Psi_{\text{pre-dawn}}$ of trees in the thinned and control stands is given in italics. N/A indicates data not available. Values in parentheses are standard errors ($n = 5$ trees).

Table 4. Pre-dawn water potential ($\Psi_{\text{pre-dawn}}$, MPa) of foliage collected from old ponderosa pine trees at three thinned and control stands

Parameter	Control Pre-thin	Control Post-thin	Thinned Pre-thin	Thinned Post-thin
Diameter ^a (μm)	18.57 (0.42)	18.86 (0.44)	20.99 (0.69)	19.26 (0.57)
Diameter ^b (μm)	22.82 (0.42)	22.88 (0.50)	25.12 (0.70)	24.11 (0.70)
k_{sp} (10^{-12} m^2)	3.08 (0.23)	3.13 (0.22)	4.6 (0.48)	3.5 (0.34)
EW/LW	2.23 (0.67)	2.12 (0.34)	1.68 (0.17)	1.77 (0.12)
$A_{\text{lumen}}/A_{\text{sapwood}}$	0.21 (0.01)	0.20 (0.01)	0.24 (0.01)	0.20 (0.01)
Density (g cm^{-3})	0.37 (0.01)	0.38 (0.01)	0.40 (0.01)	0.43 (0.01)

Parameter abbreviations are defined in Table 2. Estimates of significance from repeated measures analysis of variance gave P -values > 0.10 for all parameters. ^aMean lumen diameter. ^bHydraulic mean diameter. See text for calculation details.

the thinned trees showed a significant ($\alpha = 0.05$) non-linear increase in BAI as A increased. Similar non-linear relationships existed for BAI versus g and Δ (data not shown).

DISCUSSION

Our results show that the growth and physiology of old ponderosa pine trees are responsive to stand density reductions. BAI and Δ showed large and consistent increases in response to disturbance (Figs 1 & 2). The observation that growth increased after thinning is not unique; in fact, foresters throughout the world rely on thinning-induced growth response for increasing stem-wood yield of young to mature (< 100 -year-old) forests. However, some foresters and scientists (but notably, not dendrochronologists) have assumed that old trees are intrinsically limited and are unable to respond to thinning. This assumption is caused partially because most studies of old-growth forests have focused on volume growth of entire stands rather than of individual trees (as pointed out by Latham & Tappeiner 2002). Indeed, the plot-level responses (BAI per unit ground area) were not consistently greater for the thinned stands (Table 1) because large increases in growth per tree of thinned stands are partially swamped out by the reduced number of individuals per unit ground area. At the individual level, however, our data suggests that old trees do have the potential to increase growth dramatically after stand density reductions. Similar growth responses have been observed in 120-year-old lodgepole pine trees (Waring & Pitman 1985) and 160- to 650-year-old ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) trees (Latham & Tappeiner 2002). Likewise, dendrochronologists have long recognized that the growth of old trees is responsive to change in their environment (Fritts 1976) and to stand density reductions associated with insect attacks (Fritts & Swetnam 1989).

The observation that Δ of old trees responds to reductions in stand density is more unique. Leavitt & Long (1986) found no response of Δ or growth to thinning in old ponderosa pines. They measured tree-ring $\delta^{13}\text{C}$ for the first 4 years after thinning, so it is possible that the response occurred more than 4 years after the disturbance. Alternatively, changes in photosynthetic capacity may have balanced the effects of increased g , or, the basal area reduction

Table 5. Sapwood anatomical parameters from Stand A. Mean values pre- and post-thin are presented for the control and thinned trees, with standard errors in parentheses

may have been too small to have an effect. Few other studies have examined the response of crown gas exchange in old trees to thinning. For young *Pinus radiata* trees, Walcroft *et al.* (1996) and Warren *et al.* (2001) observed decreased Δ with reduced stand density – the opposite of our observation. Both of these studies concluded that increased light and nitrogen availability in thinned stands caused a greater increase in A than g , resulting in reduced Δ . However, stands in those studies had much higher LAI than those of our study, up to 4.7 m^2 leaf area per m^2 ground area in the case of Warren *et al.* (2001). Light availability did not change significantly for the trees in our study because the measured trees were canopy dominants in relatively low LAI stands prior to thinning; therefore, illumination of their crowns would not have changed substantially via thinning. Furthermore, increased light availability acts to drive Δ down, the opposite of what we observed.

It appears that changes in water availability were the dominant control over the growth and gas exchange response in our study. Soil moisture (as estimated by $\Psi_{\text{pre-dawn}}$) increased after thinning for up to 15 years (Table 3), while photosynthetic capacity per unit leaf area remained unchanged (Table 4). We note that these parameters were

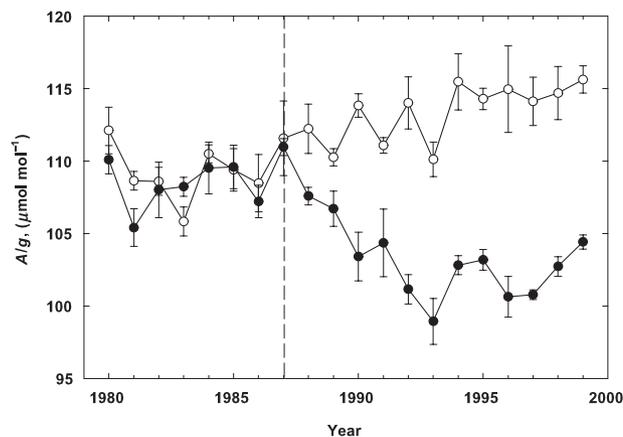


Figure 4. A/g , where g is conductance to water vapour rather than CO_2 , for trees from the control stands (open symbols) and thinned stands (closed symbols) trees at stand A. Bars are standard errors, and the year of thinning is indicated by the dashed line.

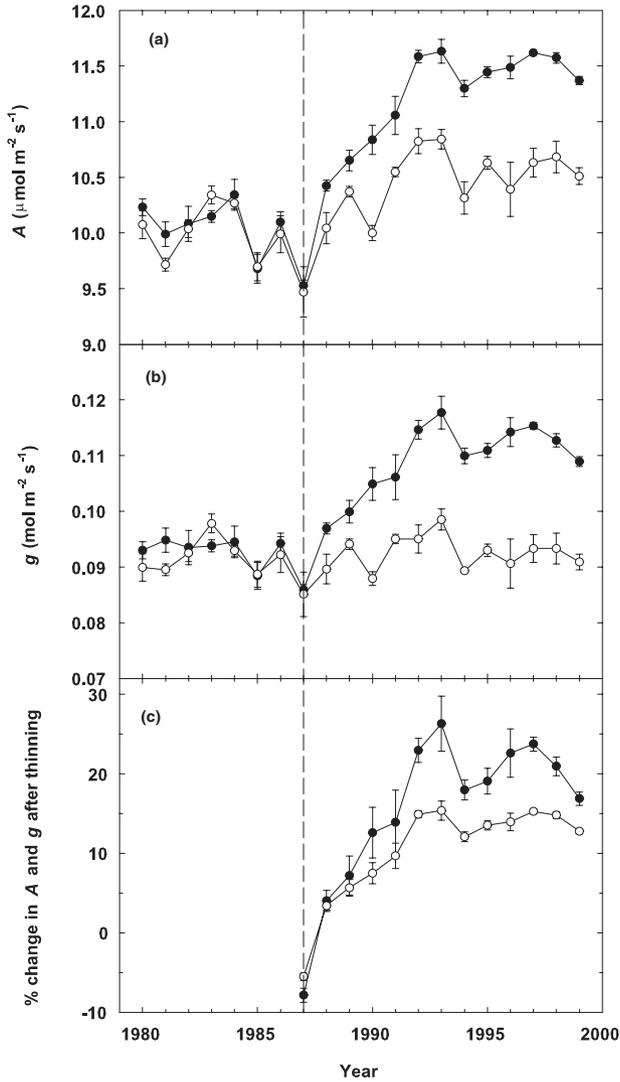


Figure 5. (a) A and (b) g calculated from Eqns 5 and 8 for the trees from the control stands (open symbols) and thinned stands (closed symbols). (c) The percent change in A (open symbols) and g (closed symbols) for trees in the thinned plot at stand A. The percent change is calculated as: $(\text{pre-thin mean} - \text{post-thin mean}) / \text{pre-thin mean}$, where the pre-thin mean is the mean of A or g from 1980 to 1986. The date of thinning is indicated by the dashed line. Bars are standard errors.

measured at variable times after thinning (7, 13 and 15 years after thinning for stands B, A, and C, respectively), and the responses between those years, particularly in the first 7 years, remains in question. Nonetheless, the strong correlation between Δ and $\Psi_{\text{pre-dawn}}$ ($R^2 = 0.91$; Fig. 3) suggests that less than 10% of the variation in Δ is attributable to variables other than $\Psi_{\text{pre-dawn}}$. Strong relationships between soil water availability and Δ have been observed when climate alone drives the variation in soil water availability (i.e. Dupouey *et al.* 1993; McNulty & Swank 1995; Livingston & Spittlehouse 1996). Our result suggests that Δ responds to variation in soil water availability due to disturbance as well.

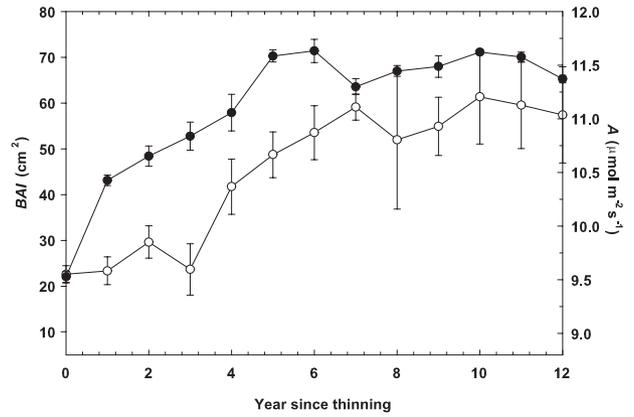


Figure 6. BAI (open symbols) and A (filled symbols) from the control and thinned trees at stand A. The stand was thinned in 1987. Bars are standard errors.

Our application of the biochemistry model of Farquhar *et al.* (1980) to tree-ring $\delta^{13}\text{C}$ records provided estimates of A and g_w that were similar to those measured on 250-year-old trees at a stand approximately 3 km from stand B (Hubbard, Bond & Ryan 1999). Hubbard *et al.*'s gas exchange measurements were made on mature foliage during the period in which stem-wood growth occurs (July to September), which may partially explain the similarity in A and g . The model that we used is highly constrained by the $\delta^{13}\text{C}$ time-series along with independent measurements of photosynthesis and temperature. The model provided logical behaviour of A and g_w in response to increased water availability; that is, g_w responded more than A (Fig. 5c). This result agrees with both theory and observations (Cowan 1985; Meinzer *et al.* 1993; Buckley, Farquhar & Mott 1999). The model application differs from other studies (i.e. Wal-

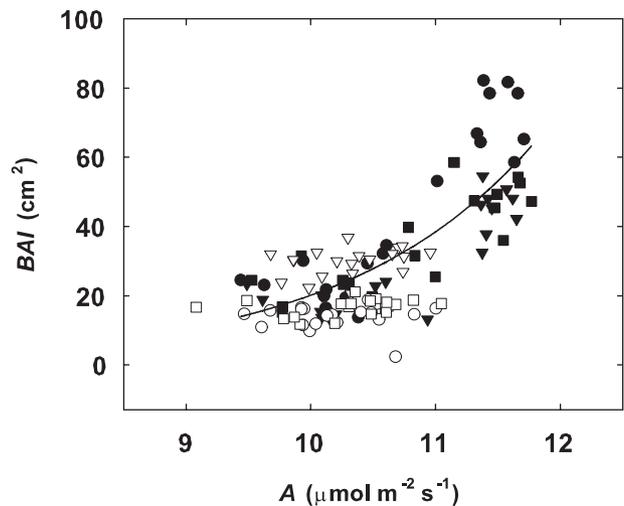


Figure 7. BAI versus A for control trees (open symbols) and thinned trees (closed symbols) from stand A. Both exponential and single parameter power regressions gave similar fits with significance at $\alpha = 0.05$, but for simplicity we present the exponential regressions: $BAI = 0.031e^{(0.647 \cdot A)}$, $r = 0.92$.

croft *et al.* 1997; Berninger *et al.* 2000), which utilized the Farquhar model as an independent method for interpreting the $\delta^{13}\text{C}$ time-series. These differences include: (1) our objective, which was to retrospectively examine the effects of A on Δ and stem growth; and (2) our approach, which was to combine together independent data to glean new information, rather than compare model output with the $\delta^{13}\text{C}$ data. An important point to make is that the gas exchange parameters are derived from C_i calculated from $\delta^{13}\text{C}$ of stem-wood cellulose, which may be $\sim 2\%$ offset from whole-leaf tissue (Leavitt *et al.* 2002). Equations 1, 2, 6 and 8 were originally conceptualized for whole-leaves, and so the parameters would be slightly offset if whole-leaf $\delta^{13}\text{C}$ had been utilized. Another important point about this model is that the estimate of g_w is highly dependent on A , so they must be interpreted as dependent variables (as they are physiologically, Wong, Cowan & Farquhar 1979; Meinzer *et al.* 1993). This prevents us from making inferences about the separate roles of A and g_w on Δ . The estimates of A and g_w are independent of BAI , however, and thus can be used to examine the relationships between carbon uptake and growth.

The 1 year lag between canopy gas-exchange and the date of thinning in Fig. 6 suggests that moisture availability increased 1 year after thinning and allowed greater crown-scale g_w and therefore greater canopy-level A . However, the 4 year delay in the onset of growth is puzzling, particularly in light of the immediate photosynthetic response. This is not an anomaly associated with stand A, as stand B also took 4 years to respond after thinning, and stand C showed a small response the first year followed by a large response 3 years after thinning (Fig. 1). Thinning 'shock' is often observed in mesic conifer species, and is associated with foliage loss due to desiccation in the first few years after thinning (i.e. Harrington & Reukema 1983); however, this is rarely observed in ponderosa pine. There are several other potential explanations for the time lag including shifts in carbon allocation and changes in hydraulic architecture. In these regards, we speculated that increased soil moisture availability from thinning would be associated with production of sapwood rings with larger tracheid diameters, more tracheid area per unit sapwood area, and a greater early-wood : late-wood ratio, all of which should lead to greater k_{sp} . However, this hypothesis was rejected: none of the sapwood specific parameters changed after thinning (Table 5). Ponton *et al.* (2001) found a strong correlation between early-wood vessel surface area and Δ , however, they were studying ring-porous *Quercus* species that typically rely on the current year xylem for the majority of water transport. Ponderosa pine is the opposite: it has relatively deep sapwood, most of which is conductive to water transport (F.C. Meinzer personal comm.), therefore the advantage gained by growing large tracheids is small. Furthermore, cavitation induced by freeze-thaw cycles is probably a determinant of tracheid diameter for temperate conifers (Sperry & Sullivan 1992), and the occurrence of freeze-thaw cycles is not likely to be altered by thinning.

Conservation of mass requires that the 'extra' carbon

acquired during the 3 years between the increase in A and the increase in BAI must have been allocated somewhere. We speculate that this lag between A and BAI (Figs 6 & 7) is associated with increased root growth. Leaf area typically increases dramatically after thinning; however, this response is usually associated with a concomitant increase in sapwood area (Brix & Mitchell 1983; Whitehead, Edwards & Jarvis 1984). Although sapwood area and presumably leaf area increased dramatically after 4 years, it is not apparent that they responded in the first 3 years. The potential carbon sinks remaining are reproductive tissues, respiration, insect and pathogen defence, and below-ground. We have no information on reproduction or respiration from these stands, but we have no compelling reason to believe that carbon allocation to these sinks would change in response to thinning (until growth increased, at which time respiration would also increase). Carbon allocation to defence typically takes 3 years to respond to thinning (T. Schowalter, personal comm.) similar to the lag in stem-wood growth. However, Waring & Pitman (1985) found a large increase in pine beetle (*Dendroctonus ponderosae*) resistance of old trees within 1 year after thinning. It remains unclear if carbon allocation to defence could explain the lag in growth. Root growth typically declines with increasing water availability (Ryan *et al.* 1996; Waring & Running 1998; Ewers, Oren & Sperry 2000). However, we suspect that during the first few years after thinning, carbon allocation to roots actually increased for the thinned trees. Urban, Lieffers & MacDonald (1994) found that trees along forest edges increased their growth of structural roots in the immediate years following harvest, but no increased growth was observed in the trunk (at breast height) until 3 to 9 years later. This may aid in structural resistance to the increased wind load associated with forest clearing (Urban *et al.* 1994). Although the proximal cause for elevated growth of structural roots may be wind loading, increasing root biomass also benefits trees by increasing the soil volume that may be explored during periods of scarce water supply and supports greater foraging for nutrients. This may explain how an increase in leaf area occurs without a dilution of foliar [N] (Table 3). Increased root growth in the immediate years after thinning would have also increased whole-tree conductance (Sperry *et al.* 1998; Magnani, Mencuccini & Grace 2000). This may have caused a feed-forward response in which increased whole tree conductance leads to increased g_w and A , which feeds back into increased root growth. This is consistent with the rise in A in years 1989 and 1990, when sapwood growth had not yet responded (Fig. 6). This cycle may still be continuing 15 years after thinning. The increased amount of sapwood from larger rings will also lead to increased whole-tree conductance; however, if leaf area increased concomitantly then whole-tree conductance should eventually plateau at a new level. Judging from Fig. 6, this new level occurs between 6 and 8 years after thinning. This theory deserves attention in future studies of physiological response to site disturbance.

The non-linear relationship between A and BAI (Fig. 7)

and between Δ and *BAI* differs from the linear relationship observed by McNulty & Swank (1995). In both studies, variation in growth and Δ was due to variation in soil water availability; however, in their study, water availability varied with climate and in ours it varied due to step reductions in transpiring leaf area. The step reduction caused the multi-year lag between *A* and Δ versus growth, forcing the non-linear relationship. Climate-induced variation, on the other hand, would not cause a multi-year lag because water availability would vary dramatically from year to year, swamping out the carry-over effects from previous years. This suggests that, while disturbance may act similarly to climate in driving a relationship between water availability and Δ , they may cause different long-term relationships between carbon assimilation and growth.

Correlations and auto-correlations between ring width or $\delta^{13}\text{C}$ in year *X* with climate, ring widths, or $\delta^{13}\text{C}$ in year X_{+1} have been observed in many tree-ring studies (Leavitt & Long 1988; Brooks, Flanagan & Ehleringer 1998; Monserud & Marshall 2001). These correlations are typically attributed to storage of photosynthate over winter or from photosynthate production by older foliage (Monserud & Marshall 2001). Alternatively, these correlations may also be due to structural changes in year *X* that carry over to affect physiological behaviour in year X_{+1} . Such 'carry-over effects' have been demonstrated in *Pseudotsuga menziesii* var. *glauca* forests (McDowell, Balster & Marshall 2001) and *Pinus taeda* forests (Ewers *et al.* 1999), in which fertilization or irrigation in early years leads to changes in coarse root biomass and water transport capacity in later years when treatment conditions have been removed. In our study, if the architectural components regulating whole-tree conductance are affected favourably by increased soil moisture in year *X*, such as through stand density reductions or increased precipitation, then canopy-scale g_w may be higher in year X_{+1} . This would lead to a correlation between the wet climate of year *X* and the $\delta^{13}\text{C}$ of year X_{+1} . Such a mechanism is supported by our observations of a feed-forward interaction between g_w , *A* and *BAI*.

There are important implications of these results. First, the observation that $\Psi_{\text{pre-dawn}}$, canopy gas exchange, and subsequent growth remain elevated as long as stand level *LAI* remains reduced (Table 1, and Oren *et al.* 1987) means that forest managers can effectively manipulate old-growth stands on an infrequent basis. The advantages to old-growth ecosystems are that susceptibility to fires, insects, and drought can be mitigated, and tree-level productivity can be enhanced with minimal mechanical damage associated with the harvest. Second, the strong growth and Δ response to stand density reductions re-affirms the caution that dendrochronologists have used in selecting trees that have not experienced substantial disturbance (Fritts 1976; Cook & Kairiukstis 1990; Fritts 1991). Stand density reductions cause patterns in tree rings that appear similar to periods of wetter than normal climate, i.e. both cause increased Δ and growth (Stuiver, Burk & Quay 1984; Stuiver & Braziunas 1987). Therefore, site disturbances such as windthrow, fire, floods, insect-induced mortality, and in recent centu-

ries, harvest, may be misinterpreted in the tree-ring chronology as representative of cool, wet periods. Given this source of variation in the isotopic record, future research in paleo-gas exchange should consider methodologies to avoid misinterpretation, including utilizing individual trees that are not subject to changes in stand density, examination of tree rings for abrasions or fire scars, and careful cross comparison to other chronologies when available (Fritts 1976). Also, the addition of $\delta^{18}\text{O}$ analysis of stem cellulose may allow us to separate the effects of disturbance versus changes in the moisture regime, as $\delta^{18}\text{O}$ of cellulose is partially dependent on humidity (Roden, Lin & Ehleringer 1999). Lastly, the variable lag between Δ and growth suggests that shifts in carbon allocation co-occur with changes in gas exchange after increases in soil water availability. Future work should quantify the interaction between resource availability, carbon assimilation and carbon allocation.

ACKNOWLEDGMENTS

We are grateful to Justin Soares for careful and diligent field and laboratory assistance. This work benefited from insightful advice and review by Steve Leavitt, Susan Lambrecht, Michael Ryan, Tim Schowalter, Richard Waring, Don Zobel and two anonymous reviewers. This research was funded in part by a grant to B.J.B., M.G. Ryan, M. Williams and E. Rastetter from the Western Regional Center (WESTGEC) of the National Institute for Global Environmental Change (NIGEC) through the US Department of Energy (Cooperative Agreement No. DE-FC03-90ER61010). J.R.B. and the isotopic analyses were funded by the US Environmental Protection Agency. Any opinions, findings and conclusions or recommendations expressed herein are those of the authors and do not necessarily reflect the view of the DOE. This manuscript has been subjected to the EPA's peer and administrative review, and it has been approved for publication as an EPA document. Mention of trade names, or commercial products does not constitute endorsement or recommendation for use.

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Received 15 July 2002; received in revised form 25 October 2002; accepted for publication 29 October 2002