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Crown dynamics and wood production of Douglas-fir trees in an old-growth forest

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ABSTRACT

Large trees are the most prominent structural features of old-growth forests, which are considered to be globally important carbon sinks. Because of their large size, estimates of biomass and growth of large trees are often based on ground-level measurements (e.g., diameter at breast height, DBH) and little is known about growth dynamics within the crown. As trees increase in size, growth of the crown may not be reflected in DBH measurements contributing to inaccuracy of aboveground forest productivity. Here we present data from a 10-yr re-measurement of crown structure and branch/trunk growth of 400-year-old *Pseudotsuga menziesii* trees in an old-growth forest in western Washington, USA. In six study trees, 40–60% of branches occurred in the upper third of the live crown. Branch mortality over 10 years was highest in the lower third of the crown. Of live-branch mass (including leaf mass), 41–78% occurred in the middle third of the live crown. During the study period, live-branch mass increased in the upper half of the crown and there was little loss due to fragmentation or death. In contrast, increment of live-branch mass was negligible and live-branch mass decreased in the lower half of the crown. On average, 70–99% of the increment of live-branch mass per tree occurred in the upper half of the crown. Core samples taken from various heights indicated that trunks became less tapered with increasing age as a result of greater increments of upper-trunk radius during the most recent 10 years. Increment of live-branch mass contributed 42 and 66% of the whole-tree and upper-crown increments of mass, respectively, and its vertical distribution corresponded to that of leaf mass density. Increments of trunk mass contributed 88% of the lower-crown increment. Growth increments of the crown were not reflected in core samples taken at lower heights. Our estimates of trunk, branch, and leaf mass were consistently smaller than those calculated using empirical allometric equations based on tape-wrap measurements of DBH. Moreover, leaf mass decreased in four trees, whereas allometric equations predicted increases. Our results indicate that large *P. menziesii* trees can sustain wood mass production, especially in trunk and branches of the upper crown, while leaf mass change can be more dynamic, and that such growth dynamics of the crown are difficult to detect via DBH-based measurements.

1. Introduction

Although aboveground productivity of some forests declines with increasing stand age (Ryan et al., 1997; Binkley et al., 2002), old-growth forests are considered to be carbon sinks (Carey et al., 2001; Luyssaert et al., 2008) because large amounts of carbon continue to accumulate in the soil (Zhou et al., 2006) and above ground as coarse woody debris (Harmon and Hua, 1991; Jonsson, 2000). The decline in aboveground productivity was attributed to decreasing growth rate with increasing age and size of individual trees (Meinzer et al., 2011). However, recent studies based on direct measurements made by accessing the crown of large trees (Sillett et al., 2010; Sillett et al., 2015a,b) and long-term ground-level measurements of temperate and tropical tree species (Stephenson et al., 2014) reveal sustained or increasing biomass increments with increasing size, regardless of age. For example, in a *Quercus*-dominated deciduous forest in the Northeastern USA, the decrease in aboveground biomass accumulation in old forests was primarily due to the mortality of large dominant trees and not to declining growth of the surviving trees (Xu et al., 2012).

Large trees are the most prominent features of old-growth forests that characterize their structure (Franklin et al., 1981; Lindenmayer et al., 2012; Lutz et al., 2013). Because of their size, estimates of biomass and growth rates of large trees are often based on ground-level measurements, such as diameter at breast

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height (DBH) scaled to the tree level using empirically derived allometric equations (e.g., Jenkins et al., 2003; Stephenson et al., 2014). Only a handful of studies utilize multiple measurements made at various heights within the living crown (e.g., Gilmore and Seymour, 1996; Inoue et al., 2008; Sumida et al., 2013; Sillett et al., 2015a) and/or repeated measurements of crown growth and dynamics (e.g., Ishii and Kadotani, 2006; Sillett et al., 2015b). As trees age, the lower trunk becomes a platform upon which new trunks and branches are produced by reiteration, the production of repeating architectural units within a tree (Barthelemy et al., 1989; Ishii and Kadotani, 2006; Sillett and Van Pelt, 2007). Such dynamics of the crown may not be reflected in radial growth of the trunk at breast height. For example, in some species, radial growth may shift from lower to upper part of the trunk and branches with increasing size and age (e.g., Bouriaud et al., 2005; Sillett et al., 2010, 2015b; Sumida et al., 2013). This also suggests that, with increasing stand age, biomass production in the canopy may become an increasingly important component of forest productivity (Ishii and Kadotani, 2006).

The process of reiteration in tree crowns is analogous to the regeneration of trees in a forest stand (Sillett and VanPelt, 2000; Ishii and McDowell, 2002). In large trees, while radial increments at breast-height may decline, increments of wood volume, including the crown, may still be increasing as the crown rejuvenates through reiteration (Van Pelt and Sillett, 2008; Sillett et al., 2010). However, long-term dynamics of branch reiteration, growth, and death in the crown of large, old trees are poorly understood. While branch wood production may increase, branch death and disturbances may cause decreases in crown biomass (Ishii and Kadotani, 2006), just as tree mortality contributes to declining stand-level biomass (Xu et al., 2012). Thus, in order to understand the contribution of tree crowns to carbon stores of old-growth forests, there is a need for long-term monitoring of crown dynamics in large trees.

Pseudotsuga menziesii (Mirb.) Franco var. *menziesii* is a dominant component of many old-growth forests in the Pacific Northwest of North America (Spies and Franklin, 1991), where crown structure of large *P. menziesii* trees has been well studied (e.g., Pike et al., 1977; Clement and Shaw, 1999; Ishii and Wilson, 2001; Winter et al., 2002; Van Pelt and Sillett, 2008). Comparison of crown structure among *P. menziesii* trees ranging 50–650 years suggests that as trees age and experience repeated disturbance at various scales, multiple reiterations occur within crowns resulting in hierarchical levels of epicormic branches and reiterated trunks of various sizes and ages (Van Pelt and Sillett, 2008). In 400-year-old, *P. menziesii* trees in southwestern Washington, USA, nearly half of the primary branches are produced from epicormic buds and these reiterated branches contribute more than 25% of tree-level branch mass (Ishii and Wilson, 2001). Although growth rates and crown dynamics of large *P. menziesii* trees have been inferred from studies comparing crown structure among trees of various ages (e.g., Ishii and McDowell, 2002; Van Pelt and Sillett, 2008), long-term studies of crown dynamics are still lacking because they require repeated measurements made by tree climbing.

Here we present long-term data on crown dynamics of 400-year-old *P. menziesii* trees in an old-growth forest of western Washington, USA. We document branch growth, death, and recruitment over a 10-yr period by repeated measurements throughout tree crowns. We also use core samples collected at various heights along the main trunk to estimate rates of wood production dating back 100 years and to elucidate vertical distributions of trunk, branch, and leaf mass as well as their increments of growth. We also compared our estimates with those derived from DBH-based allometric equations (Jenkins et al., 2003), to determine how well growth dynamics of the crown can be predicted from ground-based measurements.

2. Materials and methods

The study was conducted in an old-growth *P. menziesii* – *Tsuga heterophylla* (Raf.) Sarg. forest of the Thornton T. Munger Research Natural Area, Wind River Experimental Forest, Gifford Pinchot National Forest in southwestern Washington, USA (45°82′N, 121°96′W; 352–379 m ASL). In 2010, the stand basal area (69.3 m^2 ha^{-1}) was dominated by *T. heterophylla* (47%), followed by *P. menziesii* (38%) (Lutz et al., 2014). The stand is believed to have established after a major fire disturbance in the area (Franklin and DeBell, 1988) and the *P. menziesii* trees are about 400 years old (Van Pelt and Sillett, 2008). Other tree species in the stand include (in order of basal area): *Thuja plicata* Donn ex D. Don, *Taxus brevifolia* Nutt., *Abies amabilis*. Dougl. ex Forbes, and *Abies grandis* (Dougl. ex D. Don) Lindl.

In 1998, we selected six *P. menziesii* trees for detailed measurement of crown characteristics (Table 1, Ishii and Wilson, 2001). The study trees were selected to represent the size distribution of *P. menziesii* trees in the stand based on data from the 4-ha permanent research plot established around the Wind River Canopy Crane (Ishii et al., 2000b; Shaw et al., 2004). Our sample included three each of emergent (E1, E2, E3) and co-dominant (C4, C5, C6) crown-class trees. During June–July of 1998 we accessed the crown of each tree using the "single-rope technique" for tree climbing. Detailed analyses of crown structure for these trees are presented elsewhere (Ishii and Wilson, 2001; Ishii and Kadotani, 2006).

In 1998, we tagged all live and dead primary branches attached to the main trunk of each tree (>0.5 m in length). For each branch, we measured the height above ground (h, m) using a tape measure that was stretched vertically along the trunk, branch diameter immediately outside the branch collar using a diameter tape, and branch length by extending a 2.5-cm-wide engineer's tape from the branch base to the farthest point away from the trunk (foliage for live branches and axis for dead branches). Measurements were not taken on branches in the top 1–2 m of each tree because they could not be reached safely. Then, in 2008, we re-measured all branch parameters to document growth, death, and loss. All branches were relocated and distinguished as live, dead, or broken since the previous measurement. We also documented branch recruitment by measuring new branches that had grown to be longer than 0.5 m in length. We strived to cause minimal damage during measurements. Branches that we destructively sampled and those that were damaged as a result of climbing activity were considered unchanged during the study period.

To estimate wood mass produced by the trunk, we measured trunk diameter at 5-m intervals. A total of 37 core samples up to 40 cm long were collected at multiple heights on main trunks in September 2008 when annual wood growth was complete and used to measure bark thickness and annual rings. From each tree, we collected a pair of cores at breast height (1.37 m, marked on each tree with a tag), a pair of cores just below base of the live crown, and two or three additional cores along the height gradient within the live crown. We measured bark radius (thickness) from a convex hull (as a tape wrapped around trunk) and not inside fissures. After extracting a core, bark thickness was measured to the nearest mm by inserting the probe of the borer back into the hole, finding cambium, and then using the probe to measure distance from cambium to the circumferential tape.

We prepared cores in the lab by gluing them onto wooden mounts and polishing them with progressively finer grit sandpaper. Individual growth rings were inspected and marked under the microscope. We scanned all cores at 1200 dpi using a flatbed scanner (Expression 10000XL, Epson Inc.) and measured growth rings to the nearest 0.001 mm resolution using WinDendro image analysis software (ver. 2005, Régent Instruments Inc., Quebec, Canada). Cores were cross-dated to assign calendar years to each

Table 1
Structural characteristics (measured in 2008) and growth increments (1998–2008) for six *P. menziesii* trees in an old-growth forest of southwestern Washington.

Tree	Tree height (m)	DBH (cm)	Height increment (m 10 yr^{-1})	DBH increment (cm 10 yr^{-1})
E1	59.4	153.5	0.7	3.8
E2	62.6	138.8	1.0	3.5
E3	61.7	130.4	0.6	3.5
C4	54.9	104.5	1.2	0.2
C5	51.4	93.9	0.6	2.6
C6	51.6	87.7	0.4	0.6

DBH (diameter at breast height) increments are based on repeated tape-wraps at 1.37 m above average ground level. Letters preceding tree numbers indicate canopy status (E: emergent, C: co-dominant).

ring via the list method (Yamaguchi, 1991), and cross-dating was confirmed via correlation analysis in COFECHA (Holmes, 1983). A total of 5467 annual rings were measured with two cores reaching the year 1780.

2.1. Numerical analysis

In order to compare data on branch dynamics among the six study trees, we calculated the relative height of each branch within the crown:

$$h_{rel} = (h - H_{LCB})/(H - H_{LCB}), \quad (1)$$

where H_{LCB} (height at live-crown base) is the height of the lowest live branch and H is tree height, so that h_{rel} = 1 at treetop and 0 at live-crown base.

We used nonlinear and stepwise regression in JMP (version 12, SAS Institute) to develop allometric equations for predicting branch dry masses (Table 2). Using 38 additional live branches (12–56 m height, 2–20 cm diameter, 1.1–8.2 m length) from ten *P. menziesii* trees (44–57 m tall, 89–171 cm DBH) in the same forest (Van Pelt and Sillett, 2008), we predicted live-branch mass (including leaves) as a stepwise power function of branch diameter and length. Because branch volume, not mass, was measured for 30 of these samples, we used a density of 500 kg m^{-3} (USDA ForestService, 1984) to convert fresh volume to dry mass. An additional 13 branches (21–57 m height, 3–20 cm diameter, 2–6 m length) sampled from the six study trees (Ishii and Kadotani, 2006) were combined with these 38 branches to predict the proportion of leaf mass relative to branch mass as a power function of branch length. To estimate the change in branch mass (kg yr^{-1}) over the 10-yr study period as a result of branch growth, branch death, and branch fall/fragmentation, we calculated branch and leaf masses for each tree based on repeated measurements of branch diameter and length for 1998 and 2008, respectively.

Branch mortality rate (yr^{-1}) over the study period was calculated as:

$$1 - (n_{2008}/N_{1998})^{0.1} \quad (2)$$

where N_{1998} is the total number of live branches in 1998, and n_{2008} is the number of surviving branches in 2008. Similarly, annual rates of branch recruitment and increase/decrease of branch/leaf mass (kg yr^{-1}) were calculated from branch production and growth/loss measurements in the crown of each tree.

We used direct measurements from the core samples to determine bark and wood radii of trunks. After computing average bark thickness for each pair of cores, we used stepwise regression in JMP to develop equations for predicting bark radius (r_B, m) from total radius (r, m), which is half of the tape-measured diameter, and relative height (H_r), which is measurement height divided by tree height. The resulting equation:

$$r_B = 0.0545r - 0.0486H_r + 0.0520 (N = 25,\ R^2 = 0.937), \quad (3)$$

was applied to all trunk diameter measurements to predict bark radii. Because some trees had unusually thin or thick bark for a given trunk diameter, we regressed measured against predicted bark radii and used slopes of linear relationships as scalars to adjust predicted values on a tree by tree basis.

To calculate increments of trunk volume for each tree, we combined the measured diameter with predicted bark radii and measured ring widths to compute wood radii backward in time at all heights. We used interpolation to compute ring widths at heights between core samples. At heights above the highest cores, ring width was assumed equal to that of the highest core. At heights below the lowest cores, ring width was calculated as the average

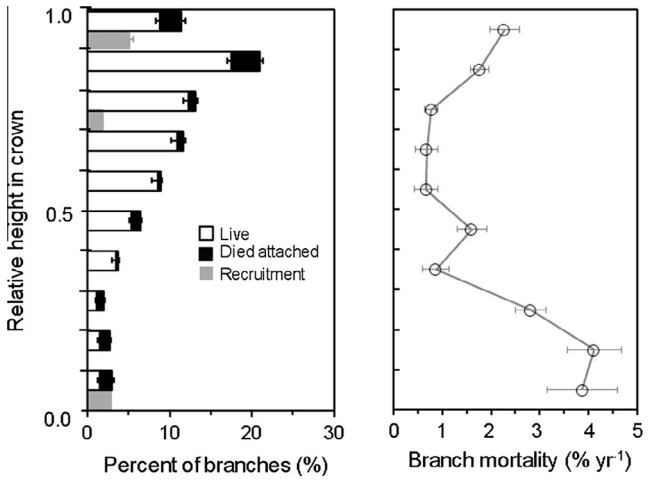

Fig. 1. Vertical distributions of the mean number of branches in 1998 (expressed as percentages in each height class relative to whole-tree) and mean mortality rate in each height class during 10-yr study period for six *P. menziesii* trees. Error bars indicate one standard deviation (n = 6).

Table 2
Allometric equations to predict oven-dry masses of six *P. menziesii* trees. Equations are based on 38 dissected branches. All equations were of the form: $aD^b + cL^d$, where D is branch diameter (cm) and L is branch length (m). Live branch mass includes leaf mass.

Dependent variable	a	b	c	d	R^2
Live branch mass (kg)	1.13×10^{-4}	4.44	3.07×10^{-2}	3.57	0.988
Dead branch mass (kg)	7.57×10^{-3}	2.24	2.51×10^{-1}	1.67	0.798
Proportion leaf mass	5.98×10^{-1}	-8.06×10^{-1}	2.19×10^{-1}	−1.09	0.849

of two quantities derived from core samples: (1) ring width of the lowest core and (2) the ring-width: wood radius ratio at the lowest core height multiplied by the wood radius at that height. This procedure maintained a consistent rate of taper change and accounted for wood investment in buttress formation (Sillett et al., 2015a).

After determining wood radii of the trunk of each tree at all heights for all cross-dated years, we generated time series of two annual growth increments—ring width (radial) and wood volume—using equations for conic frusta. Because uppermost frusta on trunks with intact treetops lengthened with height growth over time, we reduced lengths in proportion to ring widths of uppermost cores down to known tree-top heights revealed by pith locations.

For comparison among trees, increments of trunk radius and wood volume at each height were converted to those at h_{rel} with heights below the live crown expressed as negative values. Because the length of the vertical sections of trunk used for calculating increments of trunk wood-volume varied among study trees depending on the interval of core sampling, we computed increments per vertical meter of trunk ($m^3\ m^{-1}$) using the length of each trunk frustum. Volume estimates were converted to wood mass using wood density as for branches. Based on these calculations, we were able to estimate trunk increments up to the middle of the live crown as far back as the year 1900 for all six study trees. In order to infer recent changes in growth patterns, we calculated increments of trunk radius and mass during the study period based on the difference in trunk radius between 2008 and 1998 (10-yr growth) and compared this to the 100-year increment (1908–2008).

To assess whether growth dynamics of the crown can be inferred from conventional ground-based measurements, we compared our estimates of trunk, branch, and leaf mass and their

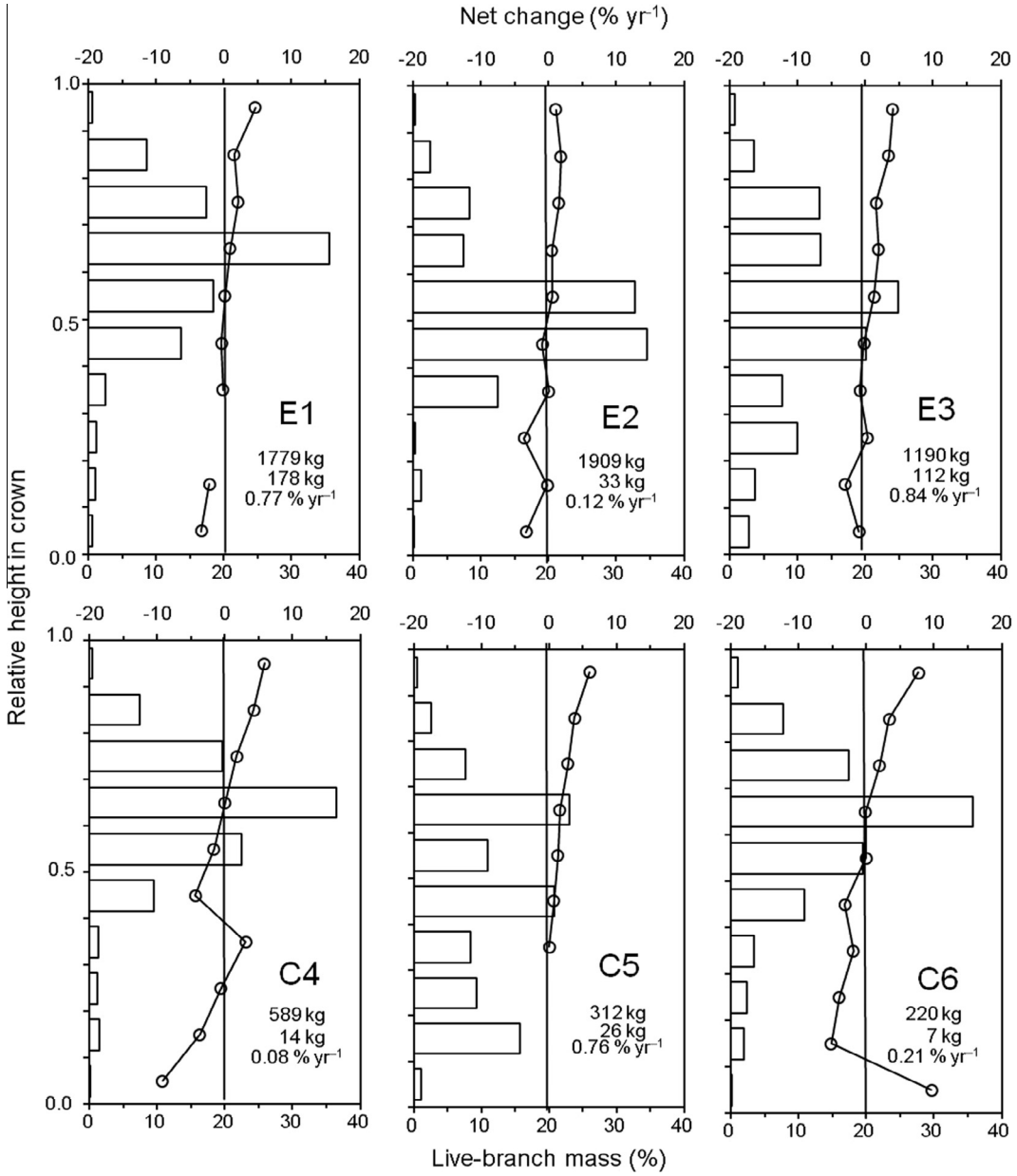

Fig. 2. Vertical distributions of live-branch mass (bars, including leaves, % relative to total branch + leaf mass in 1998) and its net rate of change (lines) for six *P. menziesii* trees. Vertical line indicates 0 net change. Missing data indicate where a single branch in height class died during study period (decrease rate = −100%). Numbers in each frame indicate branch and leaf mass in 1998, net increase during study period, and annual rate of increase per tree.

increments with those derived from DBH-based allometric equations (Jenkins et al., 2003). Equations for estimating total aboveground biomass and component ratios for trunk wood, branches, and leaves (Tables 4 and 6 of Jenkins et al., 2003) were used to estimate changes in trunk, branch, and leaf mass for each tree during the study period. We applied Jenkins' equations using tape-wrapped measurements of DBH and wood diameters derived from core samples at breast height from each tree for 1998 and 2008. Mass estimates for 1998 were subtracted from those for 2008 to obtain increments of mass.

Table 3
Branch and trunk masses in 1998 and mass change during 10-yr study period for six *P. menziesii* trees.

Tree	Mass (kg)				Mass change (kg 10 yr^{-1})				
	Branches			Trunk	Live branches			Dead Branches	Trunk
	Live	Leaves	Dead		Live	Died	Fallen	Fallen	
E1	1779	184	124	12,965	284 (16)	−5 (−0.3)	−101 (−6)	−31 (−25)	527 (4.1)
E2	1909	198	143	13,140	154 (8)	−9 (−0.5)	−112 (−6)	−37 (−26)	546 (4.2)
E3	1190	134	96	11,390	176 (15)	−2 (−0.3)	−61 (−5)	−20 (−21)	533 (4.7)
C4	589	101	97	6250	84 (14)	−3 (−0.5)	−67 (−1)	−30 (−31)	447 (7.1)
C5	312	43	63	8915	40 (12)	−2 (−0.7)	−12 (−4)	−27 (−43)	261 (4.8)
C6	220	43	94	5315	24 (11)	−1 (−0.5)	−17 (−8)	−18 (−33)	169 (3.2)

Live branch mass includes leaf mass. Figures in () indicate percentages relative to 1998.

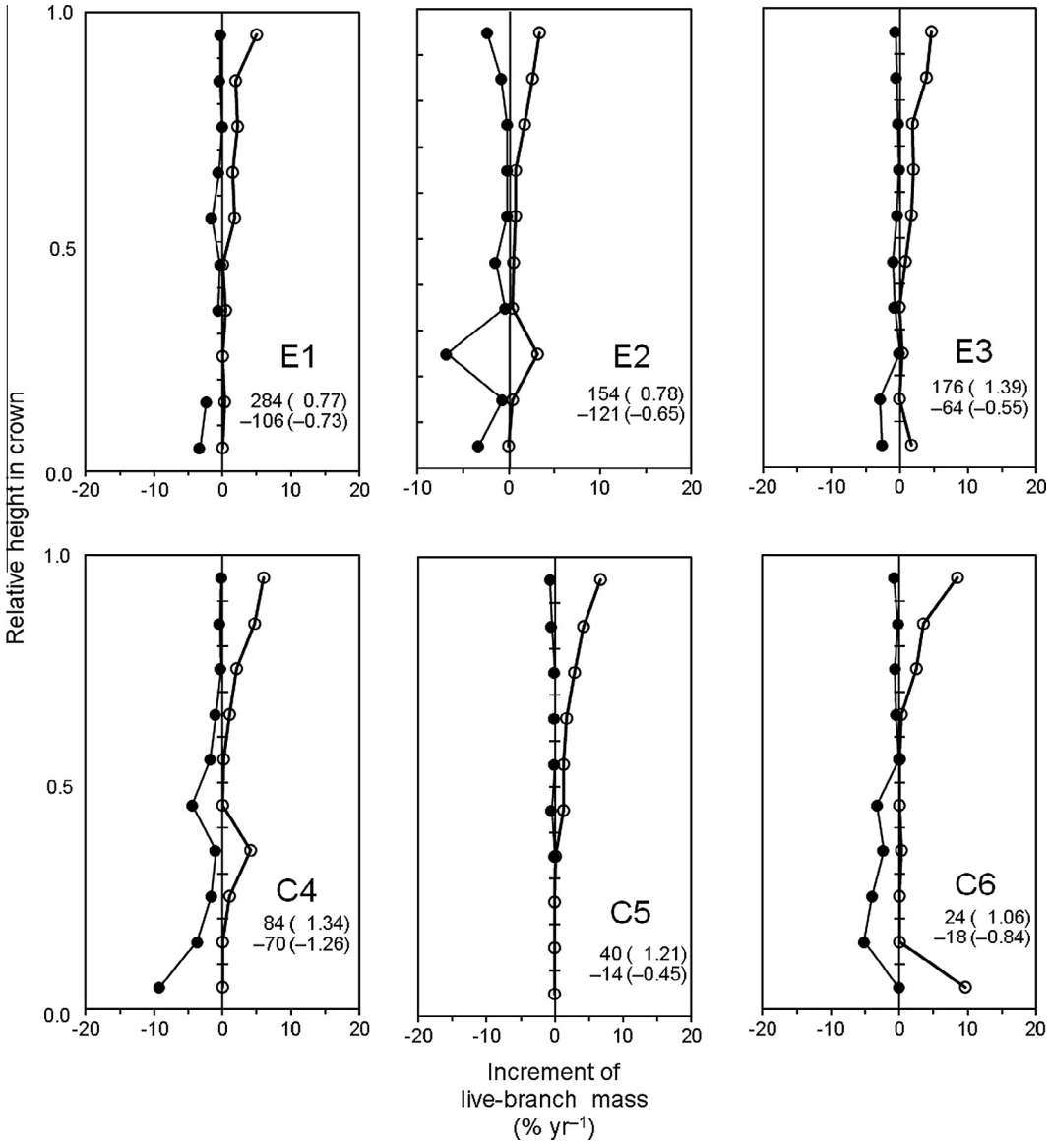

Fig. 3. Growth (○) and loss (●) increments (% relative to 1998) of live-branch mass (including leaves) during 10-yr study period along height gradient in six *P. menziesii* trees. Missing data indicate where a single branch in height class died during study period. Positive/negative numbers in each frame indicate increase/decrease of branch mass per tree (kg) during the study period followed by annual rates (% yr^{-1}) in parentheses.

3. Results

Branches were most numerous in the upper third of the crown (h_{rel} > 0.7), which contained 40% of all branches on six trees (Fig. 1). During the study period, 16.4% of live branches died attached to the trunk or fell from the crown. The mean branch mortality rate per tree was 1.7% yr^{-1}. A large snag fell in 2002, breaking several live branches in the lower crown of two trees (C4 and C5). If we exclude this stochastic event, branch mortality rate was 1.2% yr^{-1}. Branch mortality rate decreased from approximately 2.0% yr^{-1} at h_{rel} > 0.8 to less than 1.0% yr^{-1} at 0.8 > h_{rel} > 0.5. Branch mortality rates were higher (2.8–4.1% yr^{-1}) at h_{rel} < 0.3. Branch recruitment occurred through extension growth of existing branches in the upper crown and initiation of epicormic branches in the lower crown. The mean branch recruitment rate per tree was 0.4% yr^{-1}. In total, there was a net decrease (−1.3% yr^{-1}, including loss due to tree-fall damage) in the number of live branches.

Whole-tree live-branch mass (including leaf mass) ranged from 220 to 1909 kg per tree, of which 41–78% occurred in the middle crown (0.7 > h_{rel} > 0.3, Fig. 2). Increments of live-branch mass ranged from 24 to 284 kg per tree over 10 years, nearly half of which was canceled by branch death and branch fall/fragmentation (Table 3). Live branches that died attached (1–9 kg per tree) contributed to dead branch mass, but loss of dead branches that fell from the crown was greater (18–37 kg per tree). Of the increment of live-branch mass per tree, 70–99% (mean = 88%) occurred in the upper half of the live crown, resulting in net increase of live-branch mass in the upper half of the crown (Fig. 3). Whereas in the lower half of the crown, increments of live-branch mass were low and decreases due to mortality resulted in net decrease of live-branch mass. Vertical distribution and patterns of change in leaf mass generally paralleled those of live-branch mass (Fig. 4). Decreases in leaf mass in the lower crown were more marked than for live-branch mass (Fig. 5), resulting in net decrease of whole-tree leaf mass in four trees (E2, C4, C5, and C6).

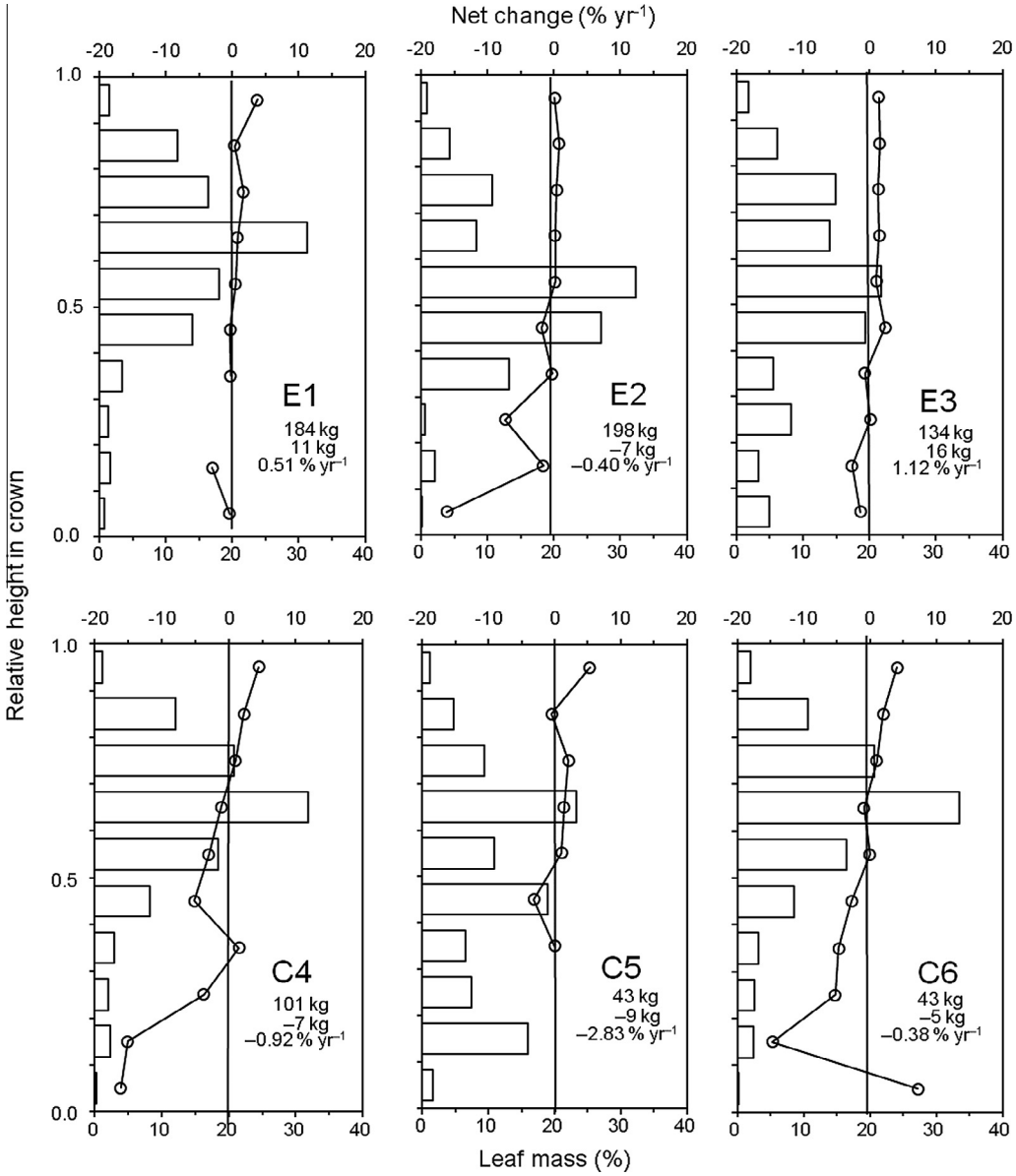

Fig. 4. Vertical distributions of leaf mass (bars, % relative to total leaf mass in 1998) and its net rate of change (lines) for six *P. menziesii* trees. Vertical line indicates 0 net change. Missing data indicate where a single branch in height class died during study period (decrease rate = −100%). Numbers in each frame indicate leaf mass in 1998, net increase/decrease during the study period, and annual rate of net increase/decrease per tree.

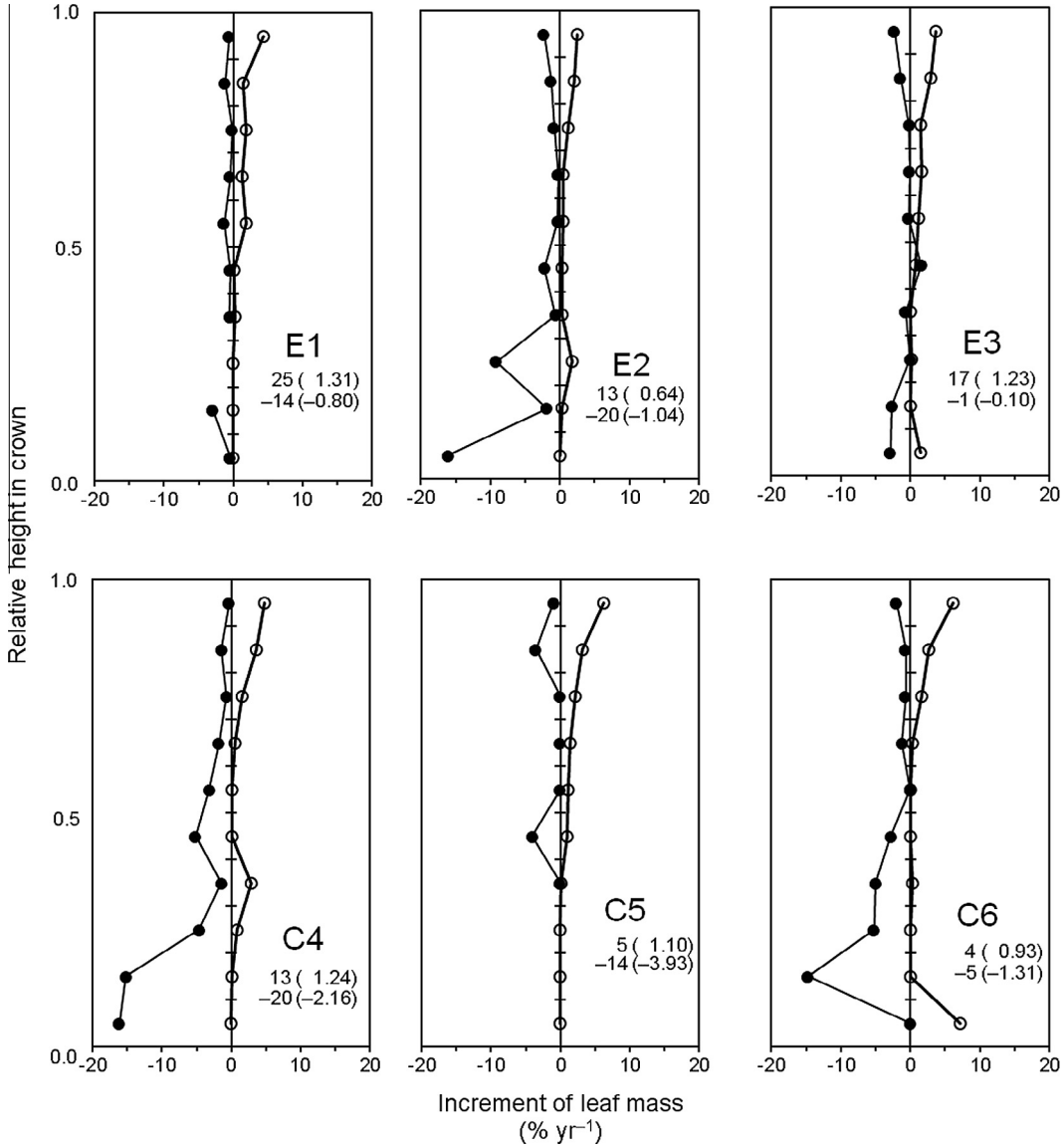

Fig. 5. Growth (○) and loss (●) increments (% yr^{-1} relative to 1998) of leaf mass during 10-yr study period along height gradient in six *P. menziesii* trees. Missing data indicate where a single branch in height class died during study period (decrease rate = −100%). Positive/negative numbers in each frame indicate increase/decrease per tree leaf mass (kg) during the study period followed by annual rates (% yr^{-1}) in parentheses.

In the three emergent trees, 10-yr mean increments of trunk radius varied little with height, whereas the 100-yr mean increments were lower in the upper trunk, resulting in a growth-rate reversal near live crown base (Fig. 6, arrows). In the three co-dominant trees, 10-yr mean increments of trunk radius were higher in the upper-trunk (Fig. 7), whereas 100-yr mean increments were lower in the upper-trunk (C4) or varied little with height (C5, C6). There were greater differences between 10- and 100-yr mean increments of wood mass in the upper than lower trunk. In all six trees, increments of breast-height wood diameters derived from core samples did not agree with those derived from repeated tape-wraps (compare numbers in Figs. 6 and 7 with Table 1). The 10-yr mean increments of breast-height wood diameter and whole-trunk wood mass were both greater than the 100-year mean increments.

Increments of trunk radius and mass at breast height were correlated with those at live-crown base and mid-crown (Table 4). In contrast, increments in the upper-trunk were not correlated with those at lower heights. Furthermore, increments of live-branch mass were not correlated with increments of trunk mass.

Trunk masses estimated from tape-wrap measurements of DBH were consistently larger than our estimates, while those estimated from wood diameter of core samples were consistently smaller (Fig. 8). Branch and leaf masses estimated from DBH and wood diameter were both consistently larger than our estimates. Increments of trunk mass estimated from DBH and wood diameter were larger than our estimates, with the exception of C4 and C6. In these two trees, both DBH and wood diameter increased by less than 1 cm during the study period. Increments of branch and leaf mass estimated from DBH and wood diameter were consistently larger than or estimates and positive for all trees, whereas our estimates of increment of leaf mass were negative for four trees.

Increment of live-branch mass (including leaves) contributed 42 and 66% of the whole-tree and upper-crown increment, respectively, and its vertical distribution corresponded to that of leaf mass density (Fig. 9). Increments of trunk mass contributed 88% of the lower-crown increment. Growth efficiency (increments of live-branch and trunk mass relative to leaf mass) of the six trees ranged 0.35–0.66 per tree.

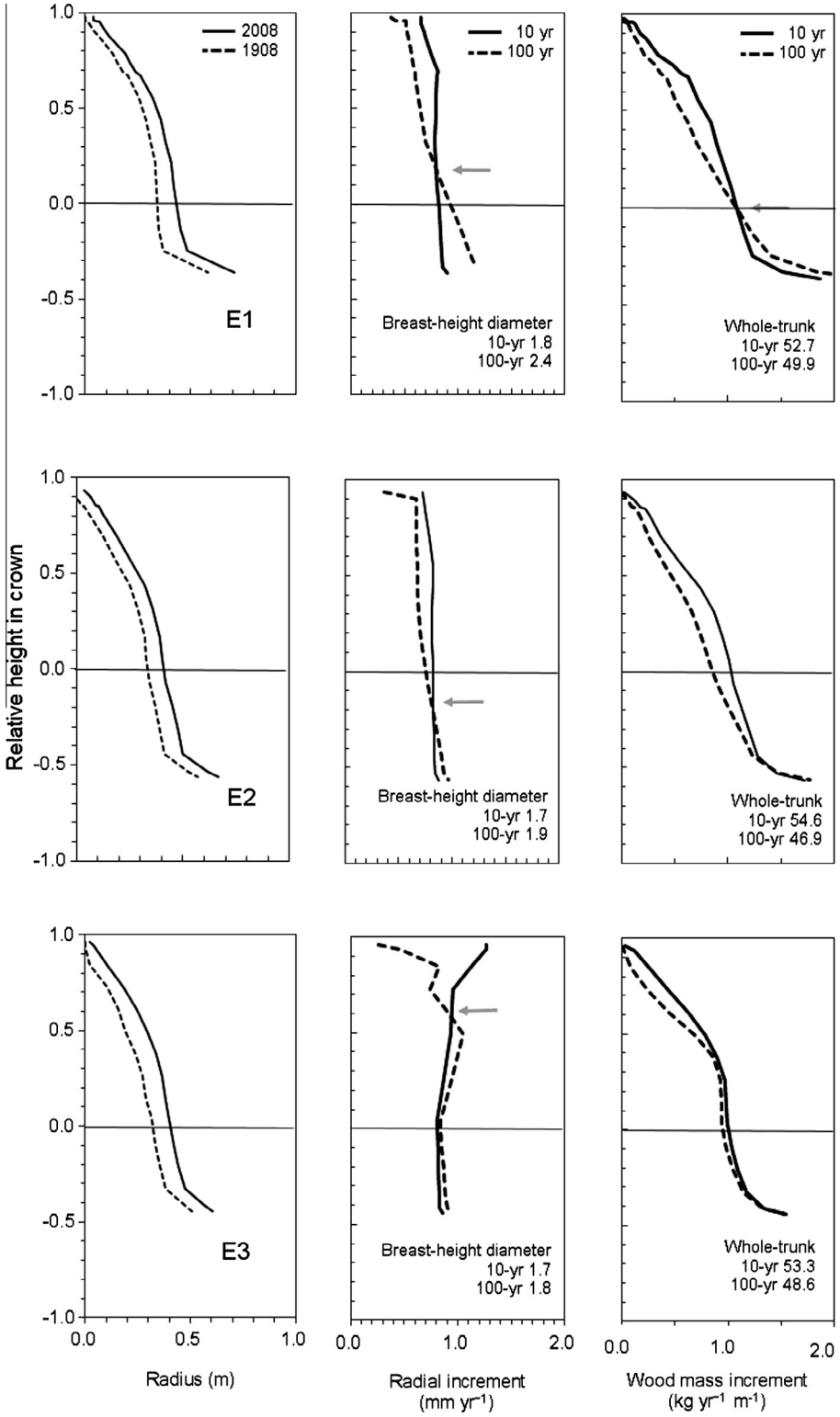

Fig. 6. Vertical changes in trunk radius, increments of trunk radius and increments of wood mass (per vertical meter) during 10-yr study period (1998–2008) and over 100 yr (1908–2008) for three emergent *P. menziesii* trees. Arrows indicate height above which 10-yr increment of trunk radius is greater than 100-yr mean. Numbers in each frame indicate mean annual increments of wood diameter at breast height and of whole-trunk wood mass over 10 and 100 yrs.

4. Discussion

We observed a net decrease in the number of branches on six *P. menziesii* trees over a 10-yr study period. Live-branch mass, however, increased because increments of mass in the upper crown more than compensated for losses in the lower crown. Moreover, increments of live-branch mass were highest in the upper crown and not in the middle-crown where greatest live-branch/leaf mass occurred. Whole-tree live-branch mass and its increment varied nearly ninefold among trees (220–1909 kg in 1998 and 284–24.5 kg, respectively). In contrast, there was much less variation among trees in increments of live-branch mass (0.77–1.39% yr^{-1}).

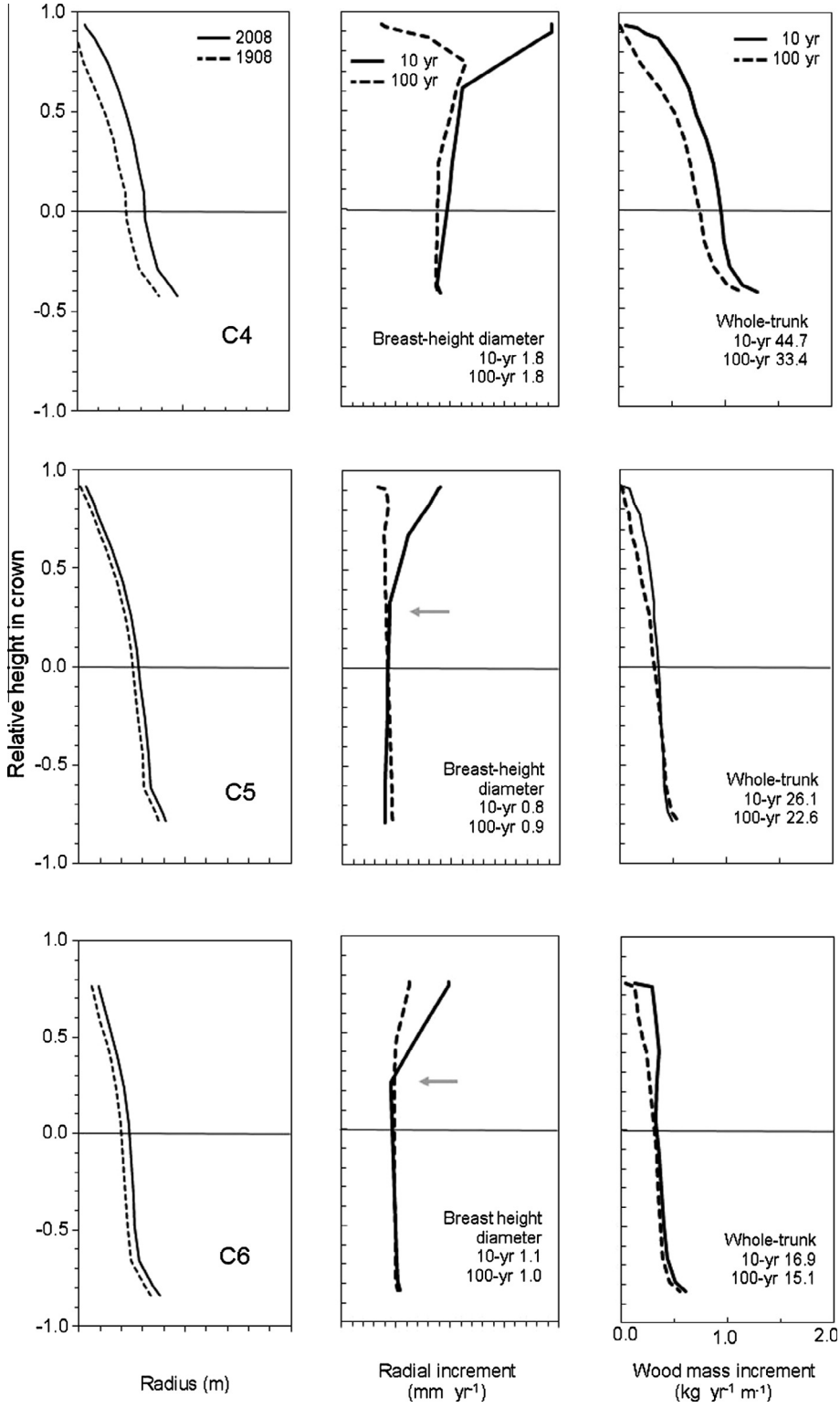

Fig. 7. Vertical changes in trunk radius, increments of trunk radius and increments of wood mass (per vertical meter) during 10-yr study period (1998–2008) and over 100 yr (1908–2008) for three co-dominant *P. menziesii* trees. Arrows indicate height above which 10-yr increment of trunk radius is greater than 100-yr mean. Numbers in each frame indicate mean annual increments of wood diameter at breast height and of whole-trunk wood mass over 10 and 100 yrs.

It is well documented that trunks become less tapered with increasing age (e.g., Makela, 2002; Sumida et al., 2013). In this study, increments of trunk wood mass changed from bottom-heavy to approximately even (no vertical trend) in emergent trees, while in co-dominant trees, it changed from approximately even to top-heavy. In co-dominant trees, increments of trunk radius in the upper crown were markedly higher than at breast height, indicating sustained diameter growth of the upper-trunk. Although statistical inference is limited due to small sample size (6 trees), increments of trunk radius and mass in the upper trunk and branches were not reflected in similar increments at breast height. In large trees of *Eucalyptus regnans* F. Muell.

Table 4
Pearson's correlation coefficients among 10- and 100-yr increments of trunk radius (lower half) and mass (upper half) and correlations between trunk radius and increments of live-branch mass (including leaves) at various heights for six *P. menziesii* trees.

Trunk radius/mass	Trunk radius/mass				Live-branch mass	
	BH	LCB	Mid-crown	Upper-trunk	Lower-crown	Upper-crown
10-yr						
BH		**0.967**	**0.814**	−0.239	0.496	0.785
LCB	**0.942**		**0.913**	−0.196	0.537	0.655
Mid-crown	**0.829**	**0.946**		0.090	0.391	0.507
Upper-trunk	0.284	0.541	0.106		−0.654	−0.158
Lower-crown						0.032[a]
100-yr						
BH		**0.836**	0.628	−0.209		
LCB	**0.970**		**0.935**	−0.373		
Mid-crown	**0.850**	**0.939**		−0.257		
Upper-trunk	0.015	0.084	0.276			

BH: breast height, LCB: live-crown base.
Numbers in bold indicate significant correlations ($P < 0.05$, $n = 6$).
[a] Correlation coefficient between increments of live-branch mass of the lower- and upper-crown.

and *Sequoia sempervirens* D. Don, basal area increments decrease slowly or do not change with increasing age, while aboveground wood production increases (Sillett et al., 2010), reflecting the contribution of upper-trunk and branches to increments of whole-tree mass. These observations suggest that growth dynamics of large trunks at breast height are not likely to reflect those of the upper crown. Furthermore, increments of diameter derived from tape-wraps did not agree with increments of wood diameter, resulting in over-estimation of aboveground mass calculated using allometric equations. Tape-wraps include the bark, whose thickness can vary with season (Gould et al., 2011), adding uncertainty. With increasing tree age, the relative position of breast-height measurements becomes lower, such that in very large trees, measurements made at breast height often include the buttressed or rapidly tapering base of the trunk. Measurements made above such irregularities (e.g., above the buttress), are better predictors of whole-tree size changes (Sillett et al., 2015b).

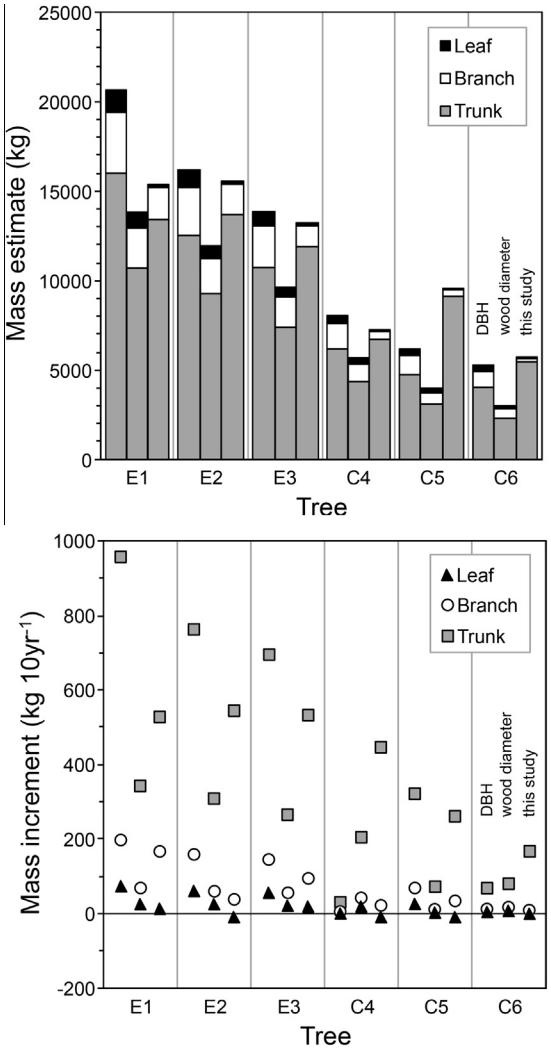

Fig. 8. Comparison of trunk, branch (excluding leaves), and leaf mass and their increments estimated by three different methods. Columns for each tree shows estimates by tape-wrap measurements of DBH (left) and wood diameter at breast height from core samples (center) using allometric equations of Jenkins et al. (2003) compared to measurements of this study (right).

Our estimates of branch and leaf mass were much smaller than estimates derived from allometric equations utilizing DBH and wood radius. Comparison of estimates suggests that effects of bark described above, resulted in over-estimation of aboveground mass. Our data also suggested that allometric relationships among trunk, branch, and leaf masses are likely to change with tree size. Although allometric equations of Jenkins et al. (2003) include data from trees up to 213 cm DBH, they also include numerous young trees whose branch/leaf mass are large relative to trunk mass (Maguire and Batista, 1995). This may have shifted the regression line upward, contributing to over-estimation of branch/leaf mass of the six study trees. Because branch length was the best predictor of leaf mass, according to our analyses, decreases in leaf mass observed during the study period reflect decreases in branch length. Reductions in branch length occur frequently in large trees as a result of crown disturbances, disrupting allometric relationships among branch dimensions (Ishii et al., 2000a). On the other hand, DBH increases cumulatively, which could result in large discrepancies between actual leaf mass and those derived from DBH-based allometric equations. The stochastic nature of some aspects of crown dynamics, such as disturbance, may explain why increments of branch mass were not accurately predicted from breast-height or other measurements of trunk growth in the study trees. In large trees of *Sequoia sempervirens* D. Don and *Sequoiadendron giganteum* (Lindl.) Buchh., for example, trunk growth is depressed during recovery periods following fire damage, presumably as trees rebuild crowns to recover leaf area (Sillett et al., 2015a).

Branch growth of young conifers exhibits a predictable vertical pattern (e.g., Kershaw et al., 1990; Maguire and Hann, 1990; Maguire et al., 1994; e.g., Maguire and Bennett, 1996). This is because branch height in young conifers corresponds to branch age as new branches are continuously produced at the top of the tree and grow to shade older branches below producing a vertical

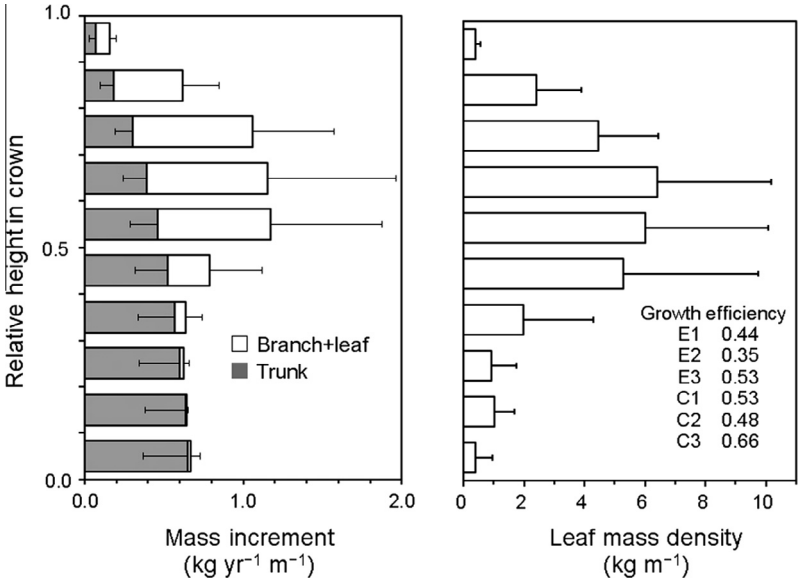

Fig. 9. Increments of live-branch mass (including leaves) and trunk mass as well as leaf mass density (mass per vertical m) during 10-yr study period for six *P. menziesii* trees. All variables are expressed per vertical meter of crown. Error bars are one standard deviation (n = 6). Numbers in the right frame indicate growth efficiency (kg branch and trunk mass increment per kg leaf mass per tree) for each tree.

gradient of decreasing light intensity (Ishii et al., 2000a; Makela, 2002). In large trees, on the other hand, disturbances create gaps in the crown, where light intensity may increase locally (Ishii and Wilson, 2001) and promote branch growth. In addition, production of epicormic branches by reiteration rejuvenates the lower-crown (Kennedy et al., 2004; Ishii et al., 2007). In angiosperm trees, epicormic branch production is associated with declining increments of trunk radius (Nicolini et al., 2003; Colin et al., 2012). In tall trees, a negative relationship between trunk growth and branch growth as a result of shifting resource allocation may disrupt vertical trends in branch wood production.

Shade tolerance of *P. menziesii* is intermediate among co-occurring conifers (Minore, 1979). Because of their emergent/co-dominant canopy status, the upper crowns of the six study trees are well illuminated. The vertical distribution of leaf area and wood mass production suggests that high photosynthetic production in the upper crown contributes to high increments of branch/trunk mass relative to leaf mass in the upper crown. Upper-crown branches on an emergent tree are also strong sinks for carbon allocation (Kramer et al., 2014). The correlative inhibition hypothesis (Takenaka, 2000; Sprugel, 2002), where shaded branches are actively self-pruned to allocate growth and resources to well-illuminated upper-crown branches, could explain why increments of branch mass were low or negative in the lower crown. Such vertical trends and correlative inhibition effects are likely to be weaker for more shade-tolerant species. Among *P. menziesii* trees ranging 50–650 years old, increments of trunk radius at breast height were unrelated to tree size but significantly correlated with the ratio of total cambium surface area to leaf area, suggesting that whole-tree carbon balance (i.e., resource allocation) may determine a tree's growth potential (Van Pelt and Sillett, 2008).

Our results corroborate recent observations of sustained or increasing mass production with increasing size in large trees (Sillett et al., 2010; Stephenson et al., 2014). Among 140 *S. sempervirens* and *S. giganteum* trees up to 116 m tall and 3240 years of age that were climbed and intensively measured, there was little or no evidence for negative effects of old age on tree-level mass increments, and old trees were just as responsive to environmental changes as young trees (Sillett et al., 2015a). Because tree growth is a cumulative process, increasing leaf area and cambium area lead to increasing mass increments as trees gain size, regardless of age (Enquist et al., 1999). In this study, aboveground growth efficiencies of the six study trees were comparable to those reported for other tall conifers (Sillett et al., 2015a). Our results suggest that large *P. menziesii* trees can sustain high growth rates, accumulating wood mass in the trunk and branches, while there can be dynamic fluctuations in leaf mass. Such trends in crown dynamics are difficult to detect from DBH measurements alone.

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