Contents lists available at ScienceDirect

# Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



# Development and dominance of Douglas-fir in North American rainforests

Stephen C. Sillett<sup>a,b,\*</sup>, Robert Van Pelt<sup>a,b</sup>, James A. Freund<sup>b</sup>, Jim Campbell-Spickler<sup>a</sup>, Allyson L. Carroll<sup>a</sup>, Russell D. Kramer<sup>b</sup>

<sup>a</sup> Department of Forestry and Wildland Resources, Humboldt State University, Arcata, CA 95521, USA
<sup>b</sup> School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA

# ARTICLE INFO

Pseudotsuga menziesii

Allometric equations

Forest development

Crown structure

Keywords:

Tree size

Tree age

Biomass

Leaf area

# ABSTRACT

One of the five tallest tree species, Pseudotsuga menziesii has enormous economic and ecological importance, but rainforests dominated by this species are not as well understood as their drier montane counterparts. We climbed and measured 30 trees up to 97 m tall growing in coastal forests of the Olympic Peninsula and northern California to quantify structural attributes-leaves, bark, cambium, sapwood, heartwood, deadwood, biomass, growth increments, and age-and combined these with an equal number of trees up to 85 m tall growing in forests of the Cascade Mountains to develop allometric equations based on ground-level predictors. After comparing new equations to those previously published, we applied the best available equations for tall forests to predict aboveground quantities of all vascular plant species in 12 ha of Olympic and Cascade forests. The largest (117 Mg) and one of the oldest (615 years) trees we studied had the highest biomass increment  $(305 \text{ kg yr}^{-1})$ , but age had a negative effect on current and long-term growth increments. After accounting for variation in tree size and aboveground vigor, older trees produced less wood annually and grew less efficiently than younger trees. Size of P. menziesii trees increased more rapidly, and the proportion of biomass and leaf area in P. menziesii decreased more slowly, in Olympic than Cascade forests over six centuries following stand-replacing fire. Maximum aboveground biomass (1999 Mg ha<sup>-1</sup>) and carbon density (994 Mg ha<sup>-1</sup>) occurred in a Cascade forest with high abundance of three conifer species (P. menziesii, Tsuga heterophylla, Thuja plicata), but maximum *P. menziesii* biomass  $(1289 \text{ Mg ha}^{-1})$  occurred in an Olympic forest with 50 trees ha<sup>-1</sup> up to 90 m tall. Vulnerability to wood decay fungi and dependence on fire for stand dominance limit P. menziesii biomass accumulation in rainforests.

# 1. Introduction

Among the five tallest tree species, *Pseudotsuga menziesii* (Douglasfir) has by far the widest geographic distribution. The native range of the coastal variety—*menziesii*—extends from southern British Columbia to central California and from the immediate coast to the Cascade Mountains and Sierra Nevada, whereas the Rocky Mountain variety—glauca—extends from central British Columbia through eight western states and far into Mexico (Hermann and Lavender, 1990). The other four species capable of heights > 95 m—*Eucalyptus regnans, Picea sitchensis, Sequoia sempervirens, Sequoiadendron giganteum*—have much more limited distributions. The coastal variety (hereafter *P. menziesii*) includes some of the tallest trees ever measured and is the largest member of Pinaceae (Fig. 1). Along the California coast, *P. menziesii* cooccurs with *P. sitchensis* and *S. sempervirens* in the southernmost North American rainforests, where all three species exceed 95 m tall (Van Pelt et al., 2016). Here *S. sempervirens* dominates, achieving sizes (> 400 Mg aboveground biomass) and ages (> 2000 years) much larger than *P. menziesii* (Sillett et al., 2015a) and creating forests with global maximum biomass, carbon density, and leaf area (Van Pelt et al., 2016). The largest and oldest *P. menziesii* trees grow farther north than *S. sempervirens* in low elevation (< 500 m) rainforests of Washington and British Columbia (Van Pelt, 2001).

Logging during the 19th and 20th centuries made *P. menziesii* the most valuable timber species of all. A historical consequence of logging was that low elevation forests were cut first, leaving more remote, higher elevation forests for cutting later (Harris, 1984). Today unlogged forests dominated by *P. menziesii* occur scattered across its geographic distribution and mostly at middle elevations in the Cascade Mountains of Washington and Oregon. Intensive study of these mid-elevation, *P. menziesii*-dominated ecosystems revealed not only the key structural features of old-growth forests, but also their developmental trajectory following stand-replacing fires (Franklin et al., 1981, 2002; Spies and Franklin, 1991; Van Pelt and Nadkarni, 2004; Freund et al, 2015). Like

https://doi.org/10.1016/j.foreco.2018.07.006 Received 12 April 2018; Received in revised form 19 June 2018; Accepted 1 July 2018 0378-1127/ © 2018 Elsevier B.V. All rights reserved.

<sup>\*</sup> Corresponding author at: Department of Forestry and Wildland Resources, Humboldt State University, Arcata, CA 95521, USA. *E-mail address*: prof.sillett@gmail.com (S.C. Sillett).



Fig. 1. Historical photographs of P. menziesii. (a) The largest individual ever recorded, which grew at 440 m elevation in Lewis County, Washington, was reliably measured at 119.8 m tall and 469 cm DBH (Carder, 1995; Van Pelt, 2001). In addition to total height and lower trunk diameters, a diameter of 183 cm at 68.6 m above the ground was measured on the snapped top in 1908 and verified by an independent observer in 1924 (Boland 1927 photograph from McArdle and Meyer (1930)). (b) After the tree toppled in 1930, a 305-cm-diameter cross section was cut from a height of 18.4 m. This sample remains preserved today at the Wind River Arboretum and has 865 rings (Silen and Olson, 1992). (c) The only known photographic evidence of an entire tree larger than any P. menziesii alive today is of this 494-cm-DBH individual growing at 100 m elevation in Skagit County (Washington State Historical Society, Tacoma). Note people standing at tree bases for scale.

E. regnans but less extreme (Tng et al., 2012; Sillett et al., 2015b), P. menziesii requires fire for prolific regeneration in rainforests and generally fails to establish stand dominance unless much of the previous cohort is killed. If unable to reproduce, P. menziesii is gradually replaced by other species and will ultimately disappear from stands if the interval between fires is > 1000 years. Across a large portion of its native range, however, surviving old-growth forests have multiple P. menziesii cohorts as a consequence of moderate-severity fires that kill only some of the previous cohort and allow P. menziesii to re-establish (Zenner, 2005; Tepley et al., 2013). In the wettest part of its distribution, long fire-return intervals preclude development of localized seed sources and promote development of extensive forests dominated by other conifers with higher shade-tolerance and lower fire resistance, especially P. sitchensis, Tsuga heterophylla, and Thuja plicata (Franklin and Dyrness, 1988; Beach and Halpern, 2001; Van Pelt, 2001, 2007; Stolnack and Naiman, 2010).

Even if *P. menziesii* trees escape or survive fire over centuries, their crowns inevitably sustain injuries through the violence of storms. Arboreal investigations in Cascade forests of Oregon (Pike et al., 1977) and Washington (Ishii and Ford, 2001; Ishii et al., 2002, 2017; Van Pelt and Sillett, 2008) defined the development of *P. menziesii* crown structure. After a multi-decadal establishment period (Freund et al.,

2014), the cohort gains height rapidly, retaining model-conforming crowns until damaged. Following canopy closure, crown depths contract through self-pruning, and trees jostle for social position. Crowns of dominant trees eventually deepen via epicormic branching as neighbors succumb to mortality and light penetration of the canopy increases. Decapitation of treetops and branch tips in storms eventually leads to trunk reiteration and limb formation (see Sillett et al., 2018). Cumulative effects of damage and reiteration over centuries lead to individualized crown structures in old-growth forests. Decay fungi drive density-independent tree mortality during later centuries (Bible, 2001), ultimately determining *P. menziesii* longevity. Ring counts of felled trees reveal that maximum longevity of *P. menziesii* is > 1000 years in rainforests (Stoltmann, 1993; Carder, 1995), about twice as long as *P. sitchensis* and half as long as *S. sempervirens*.

Understanding of *P. menziesii* tree and forest development is biased towards the Oregon and Washington Cascades, where the vast majority of research on unlogged forests has occurred. These Cascade forests do not support trees as tall, large, or old as those known from coastal forests at lower elevations (Carder, 1995; Van Pelt, 2001). Except for a few protected areas on the western Olympic Peninsula and in northern California, coastal rainforests with trees > 95 m tall are virtually gone. To our knowledge, no intensive study of *P. menziesii* in these forests has

Characteristics of ten locations in Washington (WA) and California (CA) where 60 trees were climbed to develop allometric equations for *P. menziesii* along with independent location in Oregon (OR, 11). Locations within region are ranked by decades since stand-replacing fire (if known). California location (5) in Humboldt County is dominated by *S. sempervirens* in silvatic mosaic subjected to small-scale disturbances, where stand age becomes irrelevant (Van Pelt et al., 2016). Trees in one Olympic location (1) regenerated after clearcut logging in early 20th century. All other locations are dominated by *P. menziesii* presumably established after stand-replacing fires. Precipitation and temperature values reflect long-term averages (PRISM and Western Regional Climate Center). Ownerships include Washington Department of Natural Resources (DNR), United States Forest Service (USFS), National Park Service (NPS), and California State Parks (CSP). Trees indicate number of individuals climbed within reference plots established in eight locations with additional trees climbed near plots in three locations (2, 3, 4). Oregon location is aggregate of three plots established for study of spatial patterns in understory vegetation (Van Pelt and Franklin, 2000).

								Precipitation (cm)		Temperature				
Location	State	Region	Ownership	Stand age (decades)	Latitude (°N)	Longitude (°W)	Elevation (m)	Annual	Summer	Snow	Winter T <sub>min</sub>	Summer T <sub>max</sub>	Plot area (ha)	Trees
1	WA	Olympic	DNR	9	47.3	123.8	100	297	21	6	1	22	-	2
2	WA	Olympic	USFS	20	47.5	123.9	180	329	26	18	2	23	1.00	4
3	WA	Olympic	NPS	35	47.9	123.9	240	337	28	59	1	21	1.00	4
4	WA	Olympic	USFS	63	47.4	123.9	160	331	26	36	1	23	1.00	5
5	CA	Humboldt	CSP	-	41.4	123.9	60	175	5	0	3	20	-	15
6	WA	Cascade	USFS	10	45.7	122.0	580	241	12	233	1	18	0.58	6
7	WA	Cascade	USFS	16	45.8	121.8	730	235	11	254	0	18	0.68	6
8	WA	Cascade	NPS	28	46.7	121.6	620	172	11	365	-3	24	1.60	6
9	WA	Cascade	NPS	55	47.0	121.9	610	176	18	128	-1	20	2.30	6
10	WA	Cascade	USFS	65	46.1	122.0	410	278	17	65	1	25	2.92	6
11	OR	Cascade	USFS	48	44.2	122.2	860	232	15	295	-2	21	1.09	-

been made. Moreover, all existing allometric equations used to predict physical quantities of *P. menziesii* are based on trees < 85 m tall and < 3 m diameter. Intensive study of much larger *S. sempervirens* and *S. giganteum* revealed that biomass increments continue to increase with tree size for over 2000 years and that old age has little direct effect on tree-level productivity (Sillett et al., 2015a). Whether this is true in *P. menziesii*, and if coastal forests dominated by *P. menziesii* hold more biomass and leaf area than comparable Cascade forests, remain unknown.

Here we make the first intensive measurements of P. menziesii in coastal rainforests (Washington and California) and evaluate the effects of tree structure and age on aboveground productivity for comparison with other tall species recently studied using the same methods. We then develop new allometric equations for P. menziesii in coastal and Cascade forests, compare them with existing equations, and apply the best available equations to all vascular plants within vegetation plots established in single-cohort, P. menziesii-dominated forests. We selected these locations to form a pseudo-chronosequence for examination of Olympic and Cascade forest development after stand-replacing fire. We have three specific questions: (1) How do P. menziesii trees in coastal forests differ from those reaching comparable heights in Cascade forests with respect to crown structure? (2) After accounting for variation in crown structure, does age have any additional effect on annual growth increments of P. menziesii? (3) In the centuries following disturbance, do P. menziesii-dominated forests develop similar canopy structures and rates of biomass accumulation in Olympic and Cascade locations?

# 2. Methods

#### 2.1. Overview

We combined crown mapping and limited destructive sampling to quantify branch components of 60 *P. menziesii* trees, used increment cores to determine trunk tissue volumes and densities, analyzed annual rings to quantify trunk ages and growth increments, and compiled intensive measurements of vegetation across 12 ha of forest. Our effort spanned spatial scales from leaf to plot, so we employed hierarchical sampling based on complete, nondestructive inventories as in previous work (Sillett et al., 2010, 2015a,b, 2018; Van Pelt et al., 2016). We paid special attention to within-tree variation to achieve a high degree of accuracy in aboveground estimates of leaves, bark, cambium, sapwood, heartwood, and biomass for use in developing allometric equations. Tree growth increments were calculated using a three-dimensional framework of physical measurements combined with crossdated annual ring widths. All aboveground vegetation within plots was measured in a spatially explicit manner to quantify biomass and leaves of vascular plants via allometric equations derived from this study and the published literature.

#### 2.2. Study area

From March 2014 to March 2016, we established three vegetation plots in P. menziesii-dominated forests of different age classes on the western Olympic Peninsula of Washington to quantify forest structure and initiate longer-term measurements of forest dynamics (see Plot measurements). These forests experience a maritime climate accentuated by cool, wet winters and warm, dry summers. Precipitation at low elevations occurs primarily as rain between October and April, exceeding 300 cm annually. Forests dominated by P. menziesii are usually confined to steep slopes above alluvial terraces where P. sitchensis and T. heterophylla prevail, except in a few isolated areas that experienced high-severity fire (Franklin and Dyrness, 1988). Typically occurring during summer on south-facing slopes (Huff and Agee, 1980; Van Pelt, 2007) or associated with dry east winds (Henderson et al., 1989), fires are rare in these forests. Wind is the predominant disturbance agent, usually happening in large-scale events with several hurricane-force storms recorded since 1788 (Henderson et al., 1989).

We selected published datasets for comparison with Olympic forests that included six locations in the western Cascade Mountains of Washington and Oregon. Within each location, plot-level measurements were taken for trunk diameter, height, and crown size of all trees as well as spatially explicit sampling of understory vegetation (Van Pelt and Franklin, 2000; Van Pelt and Nadkarni, 2004; Van Pelt and Sillett, 2008). These Cascade forests are dominated by *P. menziesii* and include substantial quantities of other conifers, especially *T. heterophylla* and *T. plicata*. The climate is maritime with cool, wet winters and warm, dry summers, but these forests receive less annual precipitation with greater proportions as snow than Olympic forests (Table 1). Prehistoric disturbance regimes in the Cascade forests we selected were characterized by single, high-severity wildfires leading to replacement of *P. menziesii* cohorts (Hemstrom and Franklin, 1982; Agee, 1993). We avoided forests with more than one *P. menziesii* cohort to isolate stands initiated after a single disturbance event.

#### 2.3. Tree selection

Over half of the P. menziesii trees we climbed grow within vegetation plots established in this and previous studies (Table 1). Each Olympic plot had three trees selected for detailed study, and six additional trees were chosen in nearby forests, including one regenerating after clearcut logging in the 20th century. In northern California, we selected 15 trees from old-growth forest in Prairie Creek Redwoods State Park dominated by S. sempervirens. We stratified selection of these trees on the basis of height such that five were 59-66 m, five were 73–80 m. and five were 91–97 m tall. In the Washington Cascades, we selected 30 trees from mid-elevation (410-730 m) P. menziesii-dominated forests of five age classes (Table 1). These trees were a subset of 70 trees from seven age classes (Van Pelt and Nadkarni, 2004), excluding individuals with dead tops as well as two forests deemed incapable of developing canopy heights > 70 m (i.e., Trout Creek and adjacent plantation; Van Pelt and Sillett, 2008). Thus, our dataset included 30 trees from coastal forests in Washington (climbed 2014-2016) and California (climbed 2006) and 30 trees from Cascade forests in Washington (climbed 2001-2002). The 60-tree sample included dominant and suppressed individuals in each region, excluding trees deemed unsafe to climb because of tiny branches, excessive lean, or extensive decay.

# 2.4. Crown mapping

Using modern arborist-style rope techniques, we crown-mapped trees as described previously (Van Pelt et al., 2004; Van Pelt and Sillett, 2008; Sillett et al., 2010, 2015a,b, 2018). Main trunks were tapemeasured for diameter at < 5-m intervals above buttressing. From top of buttress (TB), where the trunk is mostly round, to ground level, we converted tape diameter (tape D) to functional diameter (f-D) at multiple heights, including breast height (BH = 1.37 m), via footprint analysis (Van Pelt et al., 2016). Branches larger than a minimum diameter (4 cm) were measured for height above ground, base diameter, path length (i.e., distance along branch to the minimum diameter, including laterals and forks), horizontal extension, azimuth, slope in degrees relative to horizontal, and number of foliar units. Foliage of P. menziesii occurs in discrete units that can be counted to the nearest tenth unit with proper calibration. Because counting of foliar units occurred over 15 years by different sets of calibrated climbers, we quantified foliar units via independent dissections in Olympic, California, and Cascade locations (see Branch sampling). Broken branches, portions of appendages proximal to unbroken branches, limbs, and reiterated trunks were mapped as segments that each received base, top, and supplemental (if necessary) measurements of diameter and height as well as distance and azimuth from a mapped reference. We accounted for missing bark, cambium, and sapwood by visually estimating the dead proportion of each branch and segment. As described previously (Sillett et al. 2015b), we created computer models for each tree to screen for errors prior to making size calculations.

# 2.5. Branch sampling

In the Olympic trees, we defined foliar units as branches or portions of branches < 4 cm diameter. Thus, larger branches had multiple foliar units, while individual smaller branches arising from segments or the main trunk had < 1. From treetop to lowest living branch, crowns of 10 trees were divided into quartiles on the basis of height, and one foliar unit was randomly selected from each quartile to yield 40 destructive samples of exactly 4 cm basal diameter distributed across the height gradient (28–87 m). After removal with a hand saw, we bagged foliar units and lowered them from the crown for dissection in the laboratory, where stems were cut at 1-cm diameter intervals to isolate size classes of unbranched pieces that were then laid end to end for measurement of non-overlapping path length to the nearest cm. From freshly cut ends of randomly selected pieces of each foliar unit, we used paired caliper measurements to quantify bark and wood radii at 1-cm diameter intervals as well as piece length. After computing fresh volumes, bark and wood portions were oven-dried at 101 °C to compute densities. We subsampled twigs < 1 cm diameter by randomly selecting about a third of the material for measurements of distal diameter-average of five caliper readings beneath terminal buds-and path length. Ten fresh leaves were randomly selected from each subsample, digitally scanned at 600 dpi to quantify silhouette area, oven-dried, and weighed to compute specific leaf area ( $m^2 kg^{-1}$ ). For twigs < 1 cm, all material of each foliar unit was oven-dried and weighed, and mass ratios were used to convert subsample to total path length. After drving, leaves were manually separated from twigs and weighed separately. All these measurements were combined to compute the following quantities for each foliar unit: bark volume, wood volume, bark mass, wood mass, bark area, cambium area, leaf mass, leaf area, and number of leaves. We used 40-sample means and standard errors as multiples to calculate foliar unit quantities of all branches on Olympic trees.

In California and Cascade locations, smaller foliar units were recognized while mapping trees, so we based calculations on independent samples. In California, 23 foliar units averaging 1.7 cm basal diameter were collected from 14 trees 20-89 m above the ground. At two Cascade locations (9, 10), 38 foliar units averaging 2.5 cm basal diameter were collected from 15 trees 21-79 m above the ground. These foliar units were dissected using methods similar to the Olympic effort except that samples were not separated into 1-cm-diameter pieces for measurements of path lengths, radii, and densities. We used Olympic data to predict these quantities separately for California and Cascade foliar units (Appendix A). At three Cascade locations (6, 7, 8), foliar units were not counted, because foliage quantities in the previous study were based on equations resulting from dissection of branches 2-10 cm basal diameter whose leaves were removed, dried, and weighed (Van Pelt and Sillett, 2008). Here we predicted the number of foliar units per branch in these locations as a power function of basal diameter using data from 22 branches (Appendix A). The vertical gradient of specific leaf area was inconsistent among locations, so we used independent equations to convert leaf mass to area for foliar units at Olympic, California, and Cascade locations (Appendix A).

Tissue components of branches > 4 cm diameter were predicted using equations derived from dissection of freshly fallen material. We used a hand saw to collect pieces (4–25 cm diameter, 14–41 cm length) from 25 branches (16 Olympic, 9 California). After measuring each piece for length and diameter, we used paired caliper measurements to quantify bark, sapwood, and heartwood radii at cut ends. These data were used to develop equations for predicting bark and wood radii as functions of total radius (Appendix A). After calculating fresh volumes, bark and wood portions were oven-dried at 101 °C to compute densities (Appendix A).

#### 2.6. Trunk sampling

From the 15 Olympic trees, we collected 205 increment cores from main trunks in pairs at BH, TB, and 10–20 m height intervals up to 87.5 m. Attempts were made to reach pith at all height intervals except BH and TB, and single cores were collected when the borer reached cambium on the opposite side of the trunk. As described previously, increment cores were mounted, sanded, digitally scanned to quantify ring widths, and crossdated (Carroll et al., 2014), yielding 41,180 annual rings extending back to the year 1412. Bark radius from each core was measured by inserting a probe into the hole, finding cambium, and measuring distance along probe from cambium to the convex hull of a diameter tape. Sapwood radii were measured from cambium to heartwood using color differentiation at the sapwood/heartwood boundary. Heartwood radii were computed as total radius minus average bark radius minus average sapwood radius at each sampling height. Average wood and heartwood radii (m) were regressed against trunk total radius



**Fig. 2.** Density of *P. menziesii* sapwood and heartwood as quadratic functions of height. Values are means  $\pm 1 S_E$  (N = 4–13 trees per height interval). Equations are in Appendix A.

(m) or height (m) to predict these radii at all heights (Appendix A), and bark radius was computed as total radius minus wood radius. After regressing measured against predicted radii, we used linear relationships to adjust predicted values for each tree, which improved calculations for trees with unusually thin or thick bark or sapwood for a given trunk size (Sillett et al., 2015a).

We collected additional cores at 10-m height intervals from 13 trees (excluding 4, 14) to quantify wood density. Freshly collected cores were separated into sapwood and heartwood portions and immediately sealed in airtight tubes. After determining fresh volumes of cores by the Archimedes principle, cores were oven-dried at 101 °C and weighed to the nearest 0.0001 g. Average sapwood and heartwood densities at 10-m height intervals (N = 4-13 trees) were then regressed against height (N = 8 heights up to 80 m), yielding separate equations to predict wood densities as functions of height (Fig. 2, Appendix A) for the 47 trees we did not core-sample. Wood densities of the 13 sampled trees were predicted using tree-specific equations or means if no relationship between height and density was evident. Because main trunk bark density could not be determined via core sampling, we used handsaw, chisel, and hammer to remove six bark samples (1072-7364 cm<sup>3</sup>) from various trunk diameters (27-129 cm) of freshly fallen trees > 1 m DBH near the Sol Duc River in Olympic National Park. After oven-drying at 101 °C and weighing, we obtained a mean tissue density of  $317 \text{ kg m}^{-3}$  for bark, compared to mean densities of 363 and 400 kg m<sup>-3</sup> for sapwood and heartwood, respectively (Appendix A).

# 2.7. Size calculations

Crown mapping and sampling yielded spatially explicit information for all aboveground tree components. We used these data to compute surface areas, volumes, and masses of bark, cambium, wood, and leaves as described previously (Sillett et al., 2015a,b) with size calculations differing for branches, segments, and main trunks. We calculated main trunk bark, sapwood, and heartwood masses by applying predicted densities to the midpoint height of each trunk frustum.

After summing the number of foliar units per tree and computing foliage quantities as multiples (see *Branch sampling*), we estimated path length of branch components larger than foliar unit basal diameters using an empirical equation ( $R^2 = 0.791$ ) derived from dissecting 434 branches of 15 species, including *P. menziesii* (R. Van Pelt, unpublished).

Pathlength (cm) = 
$$0.529773 \times BD^{1.605359} \times (d^{-1} - D^{-1}),$$
 (1)

where BD is basal diameter (cm) of branch, d is distal diameter (cm) of 1-cm interval, and D is basal diameter (cm) of 1-cm interval.

For California and Cascade trees, we applied this equation to estimate path lengths of 2–3 and 3–4 cm diameter intervals for each branch and thus bridge the gap between foliar units and components > 4 cm diameter at these locations. Above 4 cm diameter for all trees, we partitioned branch path length into 1-cm diameter intervals using Eq. (1), computed the proportion of each size class, and multiplied these proportions by measured path length > 4 cm diameter to estimate length of each size class. We combined the resulting path lengths with measured and predicted radii and densities to compute volumes, surface areas, and masses of bark, cambium, sapwood, and heartwood for all branch components > 4 cm diameter.

Tissue components of segments were quantified by applying conic equations to measured lengths, measured radii for total volume and bark area, and predicted radii for cambium, sapwood, and heartwood. Visually estimated dead proportions were used to downscale living components. Dead volume was computed as the sum of dead bark and dead wood to ensure that total volume equaled the sum of bark, wood, and dead volume. We converted volumes to masses using the following measured densities for branches > 4 cm diameter: bark = 408, wood = 544, total = 501 kg m<sup>-3</sup> (Appendix A), where total density was used to convert dead volume to mass.

# 2.8. Age calculations

Increment cores not reaching pith often yielded sufficient evidence in ring curvature to estimate number of years to pith and thus determine trunk age as the sum of annual rings, but this was impossible on large trees. We developed equations to predict ring width as power functions of wood radius at 10, 20, 30, 40, and 50 m using data from all 15 Olympic trees. After subtracting bark, the sampled portion of each trunk's wood radius was determined for year of sampling and all crossdated years by subtracting ring widths sequentially. Prior to this we averaged ring widths for each pair of cores. The resulting time series (N = 75) of ring widths (mm) and wood radii (m) extending to the innermost rings reached by coring were divided into quartiles, whose averages were computed and used to develop equations at each height (Table 2). These equations used all available evidence to provide reasonable estimates of ring widths as pith was approached. When pith was not reached by coring, the remaining wood radius was divided into annual increments by sequentially subtracting predicted ring widths, and trunk age was determined by counting all measured and predicted ring widths from cambium to pith. We regressed height (x) at 10-m intervals up to 50 m against trunk age (y), and the y-intercept of this linear relationship became the estimate of tree age (i.e., trunk age at ground level).

*Tree structure, age, and recent growth*—As in our previous studies of *P. menziesii* (Van Pelt and Sillett, 2008) and other tall species (Sillett et al., 2010, 2015a,b), a primary matrix of aboveground attributes describing tree size, branches, and tissue ratios was generated for the 60 trees and subjected to principal components analysis using a correlation cross-

#### Table 2

Annual ring widths can be predicted as power functions of wood radii at multiple trunk heights in *P. menziesii* of Olympic rainforests. Equations take the form  $y = ax^b$ , where y = ring width (mm) and x = wood radius (m).

Height (m)	а	b	Ν	$R^2$
50	0.3906	-0.9632	40	0.71
40	0.5353	-0.8656	44	0.73
30	0.5580	-1.0031	44	0.74
20	0.6290	-1.0878	46	0.75
10	0.7656	-1.0827	46	0.76

Principal components summary of aboveground structural attributes in *P. menziesii*. Eigenvalues, variance, and *P* values corresponding to first two principal components (PC1, PC2) are given with Pearson correlations (*r*) between tree scores and attributes. The strongest correlation for each variable is highlighted in bold. Transformations used to satisfy assumptions of multivariate normality are indicated by daggers ( $\dagger$ , square root;  $\ddagger$ , cube root). CV is the coefficient of variation.

Pseudotsuga menziesii ( $N = 60$ trees)	PC1	PC2
Eigenvalue	8.64	3.57
Variance (%)	57.6	23.8
<i>P</i> -value	< 0.0001	< 0.0001
Total mass (Mg)‡	0.983	-0.103
Heartwood volume (m <sup>3</sup> )‡	0.978	0.126
Sapwood volume (m <sup>3</sup> )‡	0.963	-0.071
Cambium (m <sup>2</sup> )†	0.952	0.260
Bark area (m <sup>2</sup> )†	0.936	0.307
Leaves (millions)‡	0.910	0.316
Maximum branch diameter (cm)	0.909	-0.098
Dead volume (m <sup>3</sup> )‡	0.859	0.313
Mean branch diameter (cm)	0.852	-0.183
CV branch diameter	0.619	-0.030
Cambium area: leaf area ratio	0.105	-0.764
Number of branches	-0.349	0.765
Heartwood area: cambium area ratio	0.475	-0.781
Leaf area density $(m^2 m^{-1})$	0.365	0.803
Cambium area in appendages (%)	-0.131	0.842

products matrix (Table 3). Prior to analysis, variables exhibiting excessive skewness, kurtosis, or bivariate nonlinearity with other variables were power-transformed such that skewness averaged 0.40, kurtosis averaged -0.08, and there was no pronounced bivariate nonlinearity. After using randomization tests to determine statistical significance (McCune and Mefford, 2011), we interpreted significant principal components by examining correlations between tree scores, tree age, and growth increments.

For the 15 Olympic trees, three annual growth increments—main trunk wood volume increment (WVI,  $m^3 yr^{-1}$ ), main trunk specific volume increment (SVI, mm yr<sup>-1</sup>), and aboveground growth efficiency (GE, kg kg<sup>-1</sup> yr<sup>-1</sup>)—were computed as annual averages for the five-year period 2010–2014. As described previously, the measured taper of each main trunk was combined with predicted bark radii and measured ring widths to compute wood radii backwards in time, calculate annual growth increments, and establish a timeline for growth analysis (Sillett et al., 2015a). Growth efficiency was calculated as the ratio of above-ground biomass increment to leaf mass, where aboveground biomass was predicted as a linear function of main trunk wood volume ( $R^2 = 0.996$ , Appendix A) in 2010 and 2014, and biomass increment was computed as one-fifth of the predicted size difference.

Using a likelihood framework, we compared models representing all combinations of predictors—tree age and significant principal components—on the basis of  $AIC_c$  and Akaike weights. If the best model had > 90% of Akaike weight, it alone was used to draw inferences, but if model selection was ambiguous, we examined evidence for each parameter by calculating the  $AIC_c$ -weight-averaged model from those models necessary to achieve a cumulative Akaike weight > 90%. We used model averaging to inflate standard errors on parameters and produce an unconditional standard error that incorporated uncertainty in both parameter estimation and model selection (Burnham and Anderson, 2002).

#### 2.9. Long-term growth analysis

We computed WVI of the 15 Olympic trees as far back as dendrochronology allowed using the complete set of main trunk measurements as previously described (Sillett et al., 2015a). These wholetrunk growth records reached the 15th century in two trees (6, 9), 16th century in one tree (5), 17th century in three trees (11, 12, 15), 18th century in three trees (4, 7, 13), 19th century in four trees (3, 8, 10, 14), and 20th century in two trees (1, 2). For long-term analysis, we selected eight trees with WVI time series reaching the year 1750 to avoid confounding growth trends with changing sample size. Prior to analysis, we converted WVI to a size-independent metric of trunk productivity known as the residual wood volume increment (RWVI) described previously (Sillett et al., 2015a).

# 2.10. Developing allometric equations

A central objective of this study was development of allometric equations to predict aboveground quantities of P. menziesii using ground-based measurements-DBH, DTB, and crown volume-deemed useful in other tall species (Sillett et al., 2015a,b; Van Pelt et al., 2016). To facilitate future research—and recognizing that TB occurs below BH in small trees—we developed equations (N = 193 trees) to predict f-DBH as power functions of tape DBH as well as equations to predict DTB as power functions of DBH (Appendix A). Crown volume was calculated as either a paraboloid ( $\pi/2 \times$  crown depth  $\times$  crown radius<sup>2</sup>) or ellipsoid  $(4\pi/3 \times \text{crown depth}/2 \times \text{crown radius}^2)$  depending on observed shapes, where crown depth was the vertical distance from treetop to base of live crown, and crown radius was the average horizontal distance from trunk pith at ground level to crown edge in 4-8 cardinal or subcardinal directions. We considered main trunk sapwood cross-sectional area (SA) as a predictor given its strong, linear relationship to leaf quantities in P. menziesii and other tall conifers (Van Pelt and Sillett, 2008; Sillett et al., 2015a). Since only the 15 Olympic trees were core-sampled at multiple heights, we calculated SA at BH (SABH) to take advantage of other trees cored only at BH. We also developed an equation to predict SABH as a function of f-DBH and crown volume without core-sampling ( $R^2 = 0.789$ , Appendix A).

During equation development using JMP 13 (SAS Institute Inc.), we examined scatterplots of 16 rigorously measured dependent variables—total mass, crown mass, bark mass, wood mass, dead mass, total volume, bark volume, sapwood volume, heartwood volume, dead volume, bark area, cambium area, heartwood area, leaf mass, leaf area, number of leaves—against ground-level predictors. We used power-function transformations to linearize bivariate relationships between predictors and dependent variables (if necessary), applied stepwise regression to identify worthwhile combinations of predictors, and manually checked various combinations for goodness of fit such that final equations—excluding those yielding negative size predictions for small samples—had only well-defined parameters (i.e.,  $S_E$  < half the estimate).

We compared final (N = 60) allometric equations to those based on half the trees—30 from coastal forests (Olympic, California) and 30 from montane forests (Cascade). Independent equations predicting aboveground biomass and leaf mass were developed for each set of trees and used to predict attributes of the other set (Appendix A). This permitted calculation of bias as the slope of the linear function (intercept = 0) relating predicted to measured variables, where slope < 1 indicates underestimation, slope > 1 indicates overestimation, and slope = 1 is unbiased. We used bias and  $R^2$  to determine if considering coastal and montane trees as one population for *P. menziesii* allometry was justified.

Final allometric equations to predict *P. menziesii* quantities were applied in vegetation plots at nine locations (Table 1). For other species in the plots, we used previously published equations (Means et al., 1994; Jenkins et al., 2004, Van Pelt et al., 2016) that relied on measurements of stem diameter, crown size, and other predictors (see *Plot measurements*). Biomass was converted to carbon mass using measured proportions of live plant tissues (wood, bark, leaves) and log decay classes (Ares et al., 2007) as described previously (Van Pelt et al., 2016). Because we sought to quantify total aboveground quantities of leaves, bark, and wood, existing equations for an important conifer

species-T. plicata-were modified to overcome the lack of available allometrics for large trees. Aboveground biomass of T. plicata was computed as the sum of trunk mass and crown mass, which were predicted as exponential functions of DBH (Means et al., 1994). Bark mass was predicted using the proportion of total mass that is bark for equivalent size T. heterophylla (Van Pelt et al., 2016), leaf mass was predicted using the proportion of total mass that is leaf for equivalent size Sequoiadendron giganteum (Sillett et al., 2015a), wood mass was computed as the difference between predicted total mass and the sum of bark and leaf masses, and leaf area was computed as the product of predicted leaf mass and specific leaf area (SLA; Law and Berner, 2015). To facilitate future research, we developed a calculation template for aboveground quantities of T. plicata that includes these equations (Appendix B). We used corresponding wood, bark, and foliage carbon proportions of S. sempervirens (Van Pelt et al., 2016) to compute carbon masses of T. plicata.

#### 2.11. Plot measurements

Vegetation plots were installed in nine locations (Table 1). Plot sizes differed with single plots of exactly one hectare each installed in Olympic locations (2, 3, 4; this study), four plots of variable sizes (depending on tree height) installed in each of five Washington Cascade locations (6 = 0.144 ha, 7 = 0.169 ha, 8 = 0.400 ha, 9 = 0.575 ha, 10 = 0.730; Van Pelt and Nadkarni, 2004), and three plots (0.396, 0.3705, and 0.3235 ha) installed in the Oregon Cascade location (Van Pelt and Franklin, 2000). Field methods were similar to those described previously for California (Van Pelt et al., 2016) and Cascade (Van Pelt and Nadkarni, 2004) locations. Here we emphasize methods used to install the Olympic plots.

Complete inventories were made of live trees  $\geq 5$  cm DBH in plots 316.23 m long by 31.62 m wide. Live trees were identified by species, tagged, and Cartesian coordinates were mapped with reference to a central tape using laser rangefinders to survey horizontal distance to pith of each tree. All mapped values were later adjusted to slope-corrected horizontal distances using a digital elevation model as described previously (Van Pelt et al., 2016). Measurements of height, height to crown base, 4–8 crown radii, diameter at tag, and tag height above both the high and low points of ground were collected for each tree. If the tree had a broken top, the diameter was either measured or visually estimated, and if the highest leaf was either above or below the treetop, this was also measured.

The central tape was used as a transect to quantify downed woody debris < 30 cm diameter across plot length via line-intercept sampling (Brown, 1974). Each Olympic plot had 316 m of transect for small wood, whereas transect lengths were scaled to 12 times the dominant tree height in Cascade plots, ranging from 480 m at location 6 to 1080 m at location 10. Woody debris < 25 cm diameter was not measured at one Cascade location (11). All downed woody debris  $\geq$  30 cm diameter was mapped over entire Olympic plots, identified to species, assigned a decay class from 1 to 5 (Triska and Cromack, 1980), and measured for length and end diameters. Sizes and coordinates of logs were then cross-referenced with stem maps during field measurements as an error-checking procedure. Broken or heavily decayed logs had independent measures of log height and width. Longer logs received 1-3 additional mid-point diameter measurements. Tip-ups and other tree base features were mapped individually with height, width, and depth of the root plate recorded. Hollows and other features that reduced volumes of mapped pieces were also measured. Logs were individually mapped in only one Cascade location (11). Woody debris  $\geq$  30 cm diameter in the other Cascade locations (6, 7, 8, 9, 10) was quantified using line-intercept sampling only.

Standing woody debris (i.e., snags and stumps taller than 0.5 m) was mapped across whole plots, including direct or estimated measurements of top diameter. End diameters and lengths of each piece of woody debris were used for volume calculations. Stumps were modeled as cylinders below the lowest measurement of diameter. Straight sections of logs and snags were modeled as conic frusta with either circular or elliptical cross-sections. Long logs often had multiple decay classes present, so these portions were separated prior to calculating mass. Volumes of dead material were converted to masses via published densities for individual species and decay classes (Appendix C).

Small trees and shrubs were subsampled using a belt transect along the plot centerline. In this way, a 10% subsample was obtained from each plot for all shrubs  $\geq$  50 cm tall and trees < 5 cm DBH yet  $\geq$  50 cm tall, which were measured for basal diameter, height, and crown size. We used 1-m-diameter circular plots to tally woody vegetation < 50 cm tall and to estimate % cover by species for all herbaceous vegetation, including ferns. Circular plots were spaced at 4 m, yielding 80 samples per plot.

Finally, stem maps showing trees, snags, logs, bark mounds, and topographic features were generated during sampling. This ensured that error-checking could be conducted in the field, and maps could be updated accordingly. At least two updated versions of stem maps were error-checked via hardcopies prior to completion of plot measurements. We then linked Olympic plots to real Earth coordinates via high-resolution LiDAR data (Quantum Spatial, Inc.) as described previously (Van Pelt et al., 2016).

# 3. Results

#### 3.1. Tree structure and age

Intensive measurements permitted quantification of tree structure with minimal accumulation of error (mean tree-level  $S_E$  2–8%) despite the 60-tree sample spanning a wide size range—height 35–97 m, f-DBH 41-429 cm, aboveground biomass 0.9-117.5 Mg, and leaf area 137-4180 m<sup>2</sup> (Appendix D). The oldest trees in both Olympic and Cascade forests exceeded 600 years. Trees < 100 years in Olympic and < 300 years in Cascade forests had model-conforming crowns with many small branches, no limbs, and few (if any) trunk reiterations; older trees had deeper, ellipsoidal crowns with larger branches, limbs, reiterated trunks, and individualized structure (Fig. 3). Whereas some trees > 300 years retained simple, model-conforming crowns (e.g., 56), others (e.g., 11) developed complex, highly reiterated crowns. California trees (16-30) had relatively sparse crowns with fewer but larger appendages than Olympic or Cascade trees of similar size. These trees were not core-sampled at multiple heights, so ages were not determined. Most of these trees probably established after fires in 1714 or 1777 (Brown and Swetnam, 1994; A.L. Carroll, unpublished data), and all had bark and branch-whorl characteristics typical of younger trees (Van Pelt, 2007) so were likely < 300 years.

Two principal components from analysis of 15 aboveground structural attributes retained 81% of the information among 60 trees (Table 3). PC1 was a gradient expressing variation in overall tree and appendage size. Big trees with large, segmented appendages were at one extreme, whereas small, model-conforming trees were at the other extreme (Figs. 3 and 4). PC2 was a gradient expressing variation in tissue ratios, leaf area density (i.e., leaf area per meter of crown depth), number of branches, and proportion of cambium in appendages. Suppressed trees with few appendages, low leaf area density, and relatively high respiratory demands for their size were at one extreme, whereas dominant trees with numerous appendages, high leaf area density, and relatively low respiratory demands for their size were at the other extreme (Figs. 3 and 4). We referred to this size-independent dimension of tree structure in other tall species as aboveground vigor or apparent vigor (Sillett et al., 2010, 2015a,b). Here we use aboveground vigor to re-emphasize that our measurements excluded roots. Trees from Olympic and Cascade forests spanned most of the PC1 and PC2 gradients, but trees from S. sempervirens-dominated forests were restricted to the lower 40% of the PC2 gradient (Fig. 4). Among the 15 Olympic trees whose ages were determined by core-sampling, age increased with



**Fig. 3.** Crown structures of 60 *P. menziesii* trees ranked by height within region and depicted as scale models showing trunks and appendages in orthographic view. Main trunks (black) and segments (red) are portrayed as conic frusta using end diameters. Branches (green) are displayed as cylinders with thickness equal to basal diameter. Dead appendages are shown in gray. Blue numbers correspond to trees in Fig. 4 and Appendix D. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

size and decreased with aboveground vigor such that the effects of PC1 and PC2 on age were additive, allowing prediction of *P. menziesii* ages in Olympic forests ( $R^2 = 0.85$ , Appendix A).

# 3.2. Effects of tree structure and age on recent growth

Core-sampling of the 15 Olympic trees permitted estimation of tree age and calculation of annual growth increments with strong relationships to tree structure evident in other tall species (Sillett et al., 2010, 2015a,b). As expected, main trunk wood volume increment (WVI) increased with tree size (r = 0.65, P = 0.004), main trunk ring width (SVI) increased with aboveground vigor (r = 0.53, P = 0.02), and projected leaf area had the strongest individual correlation with biomass increment (r = 0.80, P = 0.0002). WVI also increased with aboveground vigor (r = 0.68, P = 0.003), and aboveground growth efficiency (GE) decreased with tree size (r = -0.58, P = 0.01).

We isolated effects of tree structure and age on growth by modeling growth increments as linear functions of PC1, PC2, and age. Age was a negative predictor in the top models for WVI, SVI, and GE (Table 4). Evidence for a slowing effect of age on all three growth increments was unambiguous. Age explained > 30% of growth variation, and age predictors were negative even after adding unconditional standard errors



**Fig. 4.** Locations of 60 *P. menziesii* trees in ordination space defined by principal components of 15 aboveground structural attributes (Table 3). Numbers correspond to trees in Fig. 3 and Appendix D.

Summary of tested models for predicting annual growth increments of 15 *P. menziesii* trees in Olympic rainforests. Dependent variables are main trunk wood volume increment (WVI, m<sup>3</sup> yr<sup>-1</sup>), main trunk specific volume increment (SVI, mm yr<sup>-1</sup>), and aboveground growth efficiency (GE, kg kg<sup>-1</sup> yr<sup>-1</sup>) averaged over five years (2010–2014). Model predictors are noted for positive (+) and negative (-) correlations with dependent variables and selected from independent dimensions of aboveground structure (PC1 and PC2, Table 3) as well as tree age (Age). Models are ranked by the selection criterion (AIC<sub>e</sub>). Number of estimated parameters (*K*), Akaike weight (*w<sub>i</sub>*), and goodness of fit (*R*<sup>2</sup>) are listed for each model.

Dependent variable	Model	AIC <sub>c</sub>	K	w <sub>i</sub>	$R^2$
WVI	+PC1 – Age	-27	4	0.8273	0.735
	+PC1 + PC2 - Age	-22	5	0.0860	0.737
	+PC1 + PC2	-20	4	0.0348	0.595
	+ PC2	-20	3	0.0273	0.461
	+ PC1	-19	3	0.0171	0.426
	+PC2 + Age	-17	4	0.0070	0.499
	+ Age	-12	3	0.0005	0.075
SVI	+PC2 – Age	26	4	0.5242	0.720
	-PC1 + PC2	27	4	0.3884	0.709
	-PC1 + PC2 - Age	30	5	0.0702	0.732
	+PC1 – Age	35	4	0.0072	0.505
	-Age	35	3	0.0063	0.350
	+ PC2	36	3	0.0031	0.284
	-PC1	40	3	0.0005	0.093
GE	-Age	-0.3	3	0.5831	0.475
	– PC2 – Age	2.3	4	0.1558	0.515
	- PC1	3.1	3	0.1034	0.339
	+PC1 – Age	3.5	4	0.0868	0.476
	+PC1 - PC2 - Age	4.7	5	0.0471	0.583
	-PC1 + PC2	6.9	4	0.0153	0.339
	-PC2	8.1	3	0.0085	0.078

(Table 5). Evidence for tree size effects on SVI and GE and aboveground vigor effects on WVI and GE was ambiguous. Predictors explained only small proportions of growth variation and had unconditional standard errors that included zero (Table 5).

# Table 5

Parameters of linear models predicting annual growth increments of 15 P.
menziesii trees in Olympic rainforests. Dependent variables and predictors are
described in Table 4. Values are best estimate (Est), standard error ( $S_E$ ), and
percentage variance explained (Var) for each dependent variable.

Dependent variable		PC1	PC2	Age	Intercept
WVI	Est	0.7824	0.0029	-0.0007	0.0404
	$S_E$	0.1683	0.0117	0.0002	0.0426
	Var	43	< 1	31	
SVI	Est	-0.8967	1.6386	-0.0014	1.1895
	$S_E$	1.0588	0.4866	0.0013	0.2793
	Var	< 1	37	35	
GE	Est	-0.0605	-0.0261	-0.0008	0.8187
	$S_E$	0.1454	0.0546	0.0004	0.1238
	Var	7	4	48	

#### 3.3. Long-term growth trends

The relationship between WVI and tree age in recent years (2010-2014) indicated that wood volume production in Olympic forests diminished over time after accounting for variation in tree size. We used a size-detrended metric-residual wood volume increment (RWVI)-to quantify the magnitude of changes in wood production over 265 years (1750-2010) for eight Olympic trees (5, 6, 7, 9, 11, 12, 13, 15). RWVI expressed each main trunk's measured WVI as a proportion of growth expected if its cambium expanded at the mean annual rate. RWVI of P. menziesii was significantly higher than expected most years in the first half and significantly lower than expected most years in the second half of the time series with a negative linear trend explaining 79% of RWVI variation (Fig. 5). Main trunk wood production of these trees averaged 48% higher than expected in the second half of the 18th century, 16% higher than expected in the 19th century, 16% lower than expected in the 20th century, and 28% lower than expected so far in the 21st century.

# 3.4. Evaluating allometric equations

The 15 Olympic trees were combined with the 15 California trees to develop equations for *P. menziesii* in coastal forests, and separate equations were developed for *P. menziesii* in montane forests using the 30 Cascade trees. We applied each set of equations to the other set of trees to quantify prediction bias. The 30-tree coastal equations underestimated aboveground biomass and leaf mass of Cascade trees by 16 and 9%, respectively, whereas the 30-tree Cascade equations overestimated biomass of coastal trees by 8% and underestimated leaf mass of coastal trees by 6%, respectively (Fig. 6a and c). Bias was small enough to justify considering coastal and montane trees as one population in 60-tree equations with less systematic error (Fig. 6b and d). Ultimately, we developed allometric equations for 16 rigorously measured aboveground quantities that explained 84–97% of the variation using predictors measurable from the ground or with ladders (Table 6) as well as other equations for various tree components (Appendix A).

The plethora of allometric equations for *P. menziesii* produced over the past 40 years prompted comparisons with those developed here. All equations relied on DBH to predict aboveground biomass, except those recently published for the species in forests dominated by *S. sempervirens* that also used DTB and crown volume as predictors. We considered five primary equation sources (Gholz et al., 1979; Jenkins et al., 2003; Harrison et al., 2009; Chojnacky et al., 2014; Van Pelt et al., 2016) as well as new DBH-only equations developed here (N = 60; Appendix A). For one study (Gholz et al., 1979), aboveground biomass was computed as the sum of five DBH-predicted masses (i.e., foliage, live branches, dead branches, stem wood, stem bark). Each equation was applied to measured ground-level predictors of the 60 trees, using *f*-DBH in all cases to be conservative. The two largest trees (9, 14) were excluded



**Fig. 5.** Times series of main trunk residual wood volume increment (RWVI) for eight *P. menziesii* trees (5, 6, 7, 9, 11, 12, 13, 15; Fig. 3; Appendix D) spanning 265 years. Red line represents mean observed RWVI with 95% confidence intervals in gray. Dotted line represents growth expected under null hypothesis of uniform growing conditions through time, where cambium expands at mean annual rate and WVI is proportional to cambium. RWVI is calculated as percentage difference between observed and expected growth (Sillett et al., 2015a). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

from calculation of prediction bias of previously published equations, because these individuals—393 and 429 cm *f*-DBH—far exceeded size of the largest trees considered in those studies. The DBH-only equation from this study and the Van Pelt et al. (2016) equation had the least prediction bias, underestimating and overestimating biomass by 2 and 9%, respectively (Fig. 7a and b). The Harrison et al. (2009) equation, which was based on dissection of 31 trees in a 47-year-old plantation, underestimated biomass by 28% (Fig. 7c). The other three equations, all of which include old trees from the Oregon Cascades sampled in the 1970 s using pioneering methods, overestimated biomass by 84, 55, and 54%, respectively, and grossly overestimated biomass of trees 9 and 14 (Fig. 7d–f). In contrast, the Harrison et al. (2009) equation yielded



reasonable biomass predictions for trees 9 and 14 despite these individuals being > 550 years older than those used to develop the equations (Fig. 7c).

#### 3.5. Olympic and Cascade forest structure

Fixed area plots provided tagged populations of live trees, surveys of dead trees, and complete inventories of understory vegetation that—after applying allometric equations—yielded aboveground quantities of all living vascular plants in nine locations. Biomass was computed separately for wood, bark, and leaves along with carbon mass and leaf area (Table 7). Dead tree masses were computed separately for snags

**Fig. 6.** Measured versus predicted aboveground biomass (a and b) and leaf mass (c and d) of 60 *P. menziesii* trees. On left, each set of 30 trees—Coast (15 Olympic + 15 California) or Cascade—is predicted using independent equations derived from other set of 30 trees (Appendix A). Linear relationships and  $R^2$  are shown with black (Coast) or gray (Cascade) dotted lines. On right, each tree is predicted using final equations (N = 60 trees, Table 6), and gray diagonal lines show 1:1 relationships.

Allometric equations to predict aboveground quantities of *P. menziesii* trees using ground-based measurements. Predictors (V1, V2, V3) are listed from left to right in descending order of importance (*f*-DBH = functional diameter at breast height, cm; DTB = diameter at top of buttress, cm; CV = crown volume,  $m^3$ ; SABH = sapwood cross-sectional area at breast height, cm<sup>2</sup>) followed by regression coefficients (*a*–*f*), sample size (*N*), goodness of fit (*R*<sup>2</sup>), root mean square error (RMSE), and form of equation. Two equations are given for leaf quantities (with and without SABH—the better predictor but more difficult to measure). Blank cells indicate unnecessary values, as fewer coefficients were needed in these equations. Two outliers with unusually large reiterated trunks (trees 11, 21) were excluded from equation for crown mass.

Dependent variable	V1	V2	V3	а	b	с	d	е	f	Ν	$R^2$	RMSE	Form
Total mass (Mg)	<i>f</i> -DBH	DTB	CV	1.885E-03	1.701E + 00	4.738E-05	2.447E+00	8.239E-04		60	0.971	3.77E+00	$aV1^b + cV2^d + eV3$
Crown mass (Mg)	<i>f</i> -DBH	DTB	CV	1.980E - 05	2.019E + 00	1.312E - 07	3.045E + 00	2.067E - 04	1.009E + 00	58	0.913	5.86E - 01	$aV1^b + cV2^d + eV3^f$
Bark mass (Mg)	<i>f</i> -DBH	CV		6.683E - 04	1.667E + 00	1.698E - 04				60	0.965	6.87E - 01	$aV1^b + cV2$
Wood mass (Mg)	<i>f</i> -DBH	DTB		1.520E - 03	1.703E + 00	4.134E - 05	2.468E + 00			60	0.965	3.43E + 00	$aV1^b + cV2^d$
Dead mass (Mg)	DTB	CV		2.542E - 09	3.515E + 00	2.981E - 06	1.296E + 00			60	0.843	1.14E - 01	$aV1^b + cV2^d$
Total volume (m <sup>3</sup> )	<i>f</i> -DBH	DTB	CV	5.457E - 03	1.698E + 00	1.206E - 04	2.420E + 00	2.098E - 03		60	0.972	9.48E + 00	$aV1^b + cV2^d + eV3$
Bark volume (m <sup>3</sup> )	<i>f</i> -DBH	CV		2.084E - 03	1.664E + 00	4.745E - 04				60	0.963	2.13E + 00	$aV1^b + cV2$
Sapwood volume (m <sup>3</sup> )	<i>f</i> -DBH	CV		1.540E - 02	1.200E + 00	5.500E - 04				60	0.862	2.19E + 00	$aV1^b + cV2$
Heartwood volume (m <sup>3</sup> )	<i>f</i> -DBH	DTB		2.181E - 03	1.793E + 00	4.064E - 05	2.587E + 00			60	0.970	6.85E + 00	$aV1^b + cV2^d$
Dead volume (m3)	DTB	CV		5.082E - 09	3.514E + 00	5.954E - 06	1.296E + 00			60	0.843	2.27E - 01	$aV1^b + cV2^d$
Bark area (m <sup>2</sup> )	<i>f</i> -DBH	CV		2.201E + 00	1.144E + 00	1.171E - 01				60	0.854	2.67E + 02	$aV1^b + cV2$
Cambium area (m <sup>2</sup> )	<i>f</i> -DBH	CV		1.483E + 00	1.145E + 00	7.263E - 02				60	0.873	1.63E + 02	$aV1^b + cV2$
Heartwood area (m <sup>2</sup> )	<i>f</i> -DBH	DTB	CV	1.444E - 01	1.261E + 00	1.567E - 02	1.715E + 00	5.716E-03		60	0.967	2.27E + 01	$aV1^b + cV2^d + eV3$
Leaf mass (kg)	SABH	CV		4.258E - 02	3.190E - 01	7.016E - 01				60	0.898	4.13E + 01	$aV1 + bV2^{c}$
Leaf mass (kg)	CV	<i>f</i> -DBH		4.107E - 01	7.016E - 01	4.355E - 02	1.457E + 00			60	0.850	5.01E + 01	$aV1^b + cV2^d$
Leaf area (m <sup>2</sup> )	CV	SABH		1.482E + 00	7.629E - 01	2.138E - 01				60	0.885	2.77E + 02	$aV1^b + cV2$
Leaf area (m <sup>2</sup> )	CV	f-DBH		1.819E + 00	7.629E - 01	2.425E - 01	1.427E + 00			60	0.848	3.19E + 02	$aV1^b + cV2^d$
Leaves (millions)	SABH	f-DBH		1.320E - 02	7.303E - 03	1.505E + 00				60	0.900	1.18E + 01	$aV1 + bV2^{c}$
Leaves (millions)	f-DBH	CV		1.402E - 02	1.505E + 00	5.445E - 03				60	0.850	1.44E + 01	$aV1^b + cV2$



**Fig. 7.** Measured versus predicted aboveground biomass of 60 *P. menziesii* trees. Predicted biomass is based on six equations, five of which—this study; Harrison et al. (2009), Gholz et al. (1979), Jenkins et al. (2003); Chojnacky et al. (2014)—use DBH as the sole predictor. The other—Van Pelt et al. (2016)—uses DBH, DTB, and crown volume as predictors. Compare DBH-only prediction here to best prediction using DBH, DTB, and crown volume (Fig. 6b). Gray diagonal lines show 1:1 relationships. Black dotted lines show best linear fits. Blue numbers correspond to trees 9 and 14, which are included in linear fit from this study but excluded from linear fits for five other equations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and logs (Table 8). Stem maps of the Olympic plots revealed not only the size class distribution of conifers by species, but also the areal extent of bark mounds (i.e., accumulations of bark, humus, and vegetation) beneath *P. menziesii*, size and distribution of snags and logs, major woody angiosperms, and regions of seasonal inundation (Fig. 8).

The aerial LiDAR dataset corresponding to these plots highlighted vertical stratification by species and differences in canopy structure (Fig. 9). The youngest forest (2) had a dense upper canopy dominated

Aboveground quantities of live plants in vegetation plots at nine locations (Table 1). Density includes only tagged trees  $\geq 5$  cm DBH. Values are best estimates  $\pm 1 S_E$  unless taxon is absent or non-woody. Total amounts are highlighted in bold. Species of conifers, angiosperms, and ferns are listed in Appendix E.

Location	Taxon	Density (trees ha <sup>-1</sup> )	Total mass (Mg ha <sup><math>-1</math></sup> )	Wood mass (Mg $ha^{-1}$ )	Bark mass (Mg ha <sup>-1</sup> )	Leaf mass (Mg ha <sup>-1</sup> )	Carbon mass (Mg ha <sup>-1</sup> )	Leaf area $(ha ha^{-1})$
2	Pseudotsuga menziesii	135	$1135.76 \pm 42.64$	885.89 ± 30.41	$214.65 \pm 5.79$	$10.98~\pm~0.42$	$549.55 \pm 20.20$	$6.66~\pm~0.27$
	Tsuga heterophylla	106	57.60 ± 6.49	$56.05 \pm 5.77$	8.57 ± 0.69	$1.55~\pm~0.18$	$32.16~\pm~3.32$	$0.88~\pm~0.11$
	Thuja plicata	0	0	0	0	0	0	0
	Other conifers	0	0	0	0	0	0	0
	Angiosperms	127	$4.54 \pm 0.13$	$1.44 \pm 0.07$	$0.23 \pm 0.02$	$1.59 \pm 0.06$	$1.56 \pm 0.07$	$2.75 \pm 0.27$
	Ferns	0	$1.39 \pm 0.40$	0	0	$1.39 \pm 0.40$	$0.67 \pm 0.20$	$2.00 \pm 0.44$
	Total	368	$1199.29 \pm 49.65$	$943.38 \pm 36.25$	$\textbf{223.45}~\pm~\textbf{6.50}$	$15.50~\pm~1.06$	$583.94 \pm 23.79$	$12.30~\pm~1.08$
3	Pseudotsuga menziesii	50	$1288.99 \pm 34.04$	$1014.81 \pm 21.46$	$214.30 \pm 5.91$	$10.21 \pm 0.34$	$611.87 \pm 16.05$	$6.38~\pm~0.24$
	Tsuga heterophylla	32	$125.32 \pm 9.93$	$119.51 \pm 7.58$	17.62 ± 1.46	$3.27~\pm~0.33$	$68.25 \pm 4.76$	$1.38~\pm~0.16$
	Thuja plicata	1	$27.98 \pm 3.69$	$24.30 \pm 2.57$	$3.41 \pm 0.47$	$0.27 \pm 0.04$	$14.09 \pm 1.57$	$0.22 \pm 0.04$
	Other conifers	10	$1.28 \pm 0.17$	$0.88 \pm 0.09$	$0.40 \pm 0.06$	$0.05~\pm~0.01$	$0.66 \pm 0.08$	$0.15 \pm 0.03$
	Angiosperms	179	$5.15 \pm 0.20$	$3.25 \pm 0.21$	$0.57 \pm 0.03$	$0.53~\pm~0.05$	$2.12 \pm 0.15$	$2.82~\pm~0.28$
	Ferns	0	$0.78 \pm 0.13$	0	0	$0.78~\pm~0.13$	$0.38 \pm 0.06$	$1.04~\pm~0.16$
	Total	272	$1449.50 \pm 48.16$	$1162.75 \pm 31.92$	$236.31 \pm 7.92$	$15.12 \pm 0.90$	$697.36 \pm 22.68$	$12.00 \pm 0.91$
4	Pseudotsuga menziesii	23	$1146.15 \pm 32.47$	$943.92 \pm 25.83$	$175.80 \pm 4.70$	$6.55~\pm~0.20$	555.35 ± 17.24	$4.02~\pm~0.16$
	Tsuga heterophylla	347	$247.99 \pm 21.08$	233.88 ± 19.20	34.97 ± 2.81	$6.87~\pm~0.65$	134.04 ± 11.41	$3.43~\pm~0.42$
	Thuja plicata	1	$60.30 \pm 8.54$	$52.67 \pm 7.21$	$7.26 \pm 0.97$	$0.38~\pm~0.06$	$30.37 \pm 4.19$	$0.31~\pm~0.06$
	Other conifers	0	0	0	0	0	0	0
	Angiosperms	47	$2.1c2 \pm 0.04$	$0.42 \pm 0.02$	$0.29 \pm 0.02$	$0.14 \pm 0.01$	$0.42 \pm 0.03$	$0.51 \pm 0.03$
	Ferns	0	$0.37 \pm 0.12$	0	0	$0.37 \pm 0.12$	$0.18 \pm 0.06$	$0.45 \pm 0.14$
	Total	418	$1456.93 \pm 62.24$	$1230.89 \pm 52.26$	$218.32 \pm 8.49$	$14.32 \pm 1.04$	$720.36 \pm 32.93$	$8.71 \pm 0.81$
6	Pseudotsuga menziesii	434	817.30 ± 50.18	632.43 ± 43.31	$181.02 \pm 4.11$	$10.91~\pm~0.42$	408.37 ± 25.11	6.33 ± 0.24
	Tsuga heterophylla	5	$0.97~\pm~0.18$	$0.75 \pm 0.15$	$0.15 \pm 0.01$	$0.05 \pm 0.01$	$0.46~\pm~0.08$	$0.03 \pm 0.00$
	Thuja plicata	0	0	0	0	0	0	0
	Other conifers	3	$0.02 \pm 0.01$	$0.01 \pm 0.00$	$0.00 \pm 0.00$	$0.01 \pm 0.00$	$0.01 \pm 0.00$	$0.04 \pm 0.01$
	Angiosperms	7	$5.45 \pm 1.67$	$4.20 \pm 1.44$	$1.10 \pm 0.13$	$0.15 \pm 0.03$	$2.67 \pm 0.79$	$1.79 \pm 0.34$
	Ferns	0	$0.05 \pm 0.02$	0	0	$0.05 \pm 0.02$	$0.03 \pm 0.01$	$0.12 \pm 0.02$
	Total	450	$823.79 \pm 52.05$	$637.39 \pm 44.91$	$182.28 \pm 4.24$	$11.17 \pm 0.48$	$411.54 \pm 26.00$	$8.31 \pm 0.61$
7	Pseudotsuga menziesii	291	761.48 ± 44.23	629.35 ± 37.37	163.16 ± 5.16	$6.85 \pm 0.23$	395.43 ± 22.58	$3.78 \pm 0.19$
	Tsuga heterophylla	10	4.69 ± 0.82	3.90 ± 0.69	0.58 ± 0.06	0.17 ± 0.02	2.26 ± 0.38	0.11 ± 0.02
	Thuja plicata	3	$2.98 \pm 0.87$	$2.53 \pm 0.75$	$0.37 \pm 0.06$	$0.08 \pm 0.01$	$1.50 \pm 0.42$	$0.07 \pm 0.02$
	Other conifers	4	$1.46 \pm 0.42$	$0.97 \pm 0.29$	$0.39 \pm 0.06$	$0.09 \pm 0.02$	$0.72 \pm 0.18$	$0.07 \pm 0.02$
	Angiosperms	109	$11.18 \pm 3.25$	8.44 ± 2.51	$2.38 \pm 0.38$	$0.35 \pm 0.06$	$5.47 \pm 1.47$	$2.87 \pm 0.71$
	Ferns	0	$0.06 \pm 0.02$	U 645 10 ± 41 61	U 166 90 + E 70	$0.06 \pm 0.00$	$0.03 \pm 0.01$	$0.20 \pm 0.05$
8	Pseudotsuga	101	753.44 ± 26.73	$609.08 \pm 21.16$	$100.89 \pm 3.72$ 144.15 ± 3.72	$7.01 \pm 0.34$ $6.43 \pm 0.21$	$403.41 \pm 23.04$ 375.46 ± 13.82	$3.79 \pm 0.14$
	menziesii Tsuga	204	187.97 ± 20.00	$183.75 \pm 19.15$	27.48 ± 2.13	$5.81~\pm~0.58$	$105.52 \pm 10.92$	$2.81~\pm~0.32$
	heterophylla	_						
	Thuja plicata	10	$10.07 \pm 1.79$	$8.55 \pm 1.48$	$1.26 \pm 0.16$	$0.26 \pm 0.04$	$5.07 \pm 0.86$	$0.21 \pm 0.04$
	Angiognorma	19	$10.13 \pm 1.70$	$0.22 \pm 1.05$	$2.50 \pm 0.32$	$1.54 \pm 0.29$	$5.05 \pm 0.84$	$0.25 \pm 0.04$
	Forms	0	$0.04 \pm 0.00$	3.02 ± 0.20	0.82 ± 0.04	$0.70 \pm 0.08$	$2.30 \pm 0.17$	$1.34 \pm 0.17$ 0.14 ± 0.02
	Total	331	966 78 + 50 51	811 22 + 43 04	176 21 + 6 37	1477 + 120	493 62 + 26 61	$873 \pm 0.02$
9	Pseudotsuga	17	472.06 ± 11.63	$378.09 \pm 7.05$	77.94 ± 2.48	$3.35 \pm 0.11$	$226.74 \pm 5.64$	$2.10 \pm 0.08$
	menziesii Tsuga hatawah 11	211	374.11 ± 27.65	343.72 ± 19.22	50.81 ± 4.85	$10.32 \pm 1.00$	196.81 ± 12.80	4.59 ± 0.53
	neteropnylla Thuia plicate	00	176.00 + 01.60	152 20 + 14 19	21 = 0 + 2.44	0.01 <b>-</b> ⊢ 0.06	00 40 + 0.15	
	1 nuja plicata	23 12	$1/0.00 \pm 21.08$ 12.78 $\pm$ 1.54	$152.20 \pm 14.18$ 11.56 + 1.07	$21.59 \pm 3.44$	$2.21 \pm 0.36$ 1.50 ± 0.20	$88.02 \pm 9.15$	$1.84 \pm 0.35$ 0.22 + 0.04
	Angiosperme	13	$12.70 \pm 1.30$ 0.61 + 0.07	0.29 + 0.03	$2.93 \pm 0.40$ 0.07 + 0.01	$1.30 \pm 0.20$ 0.27 + 0.05	$7.03 \pm 0.92$ 0.30 + 0.04	$0.22 \pm 0.04$ 0.90 + 0.10
	Ferns	0	$0.36 \pm 0.07$	0.25 - 0.05	0.07 ± 0.01	$0.27 \pm 0.03$ $0.36 \pm 0.04$	$0.30 \pm 0.04$ 0.17 + 0.02	$0.50 \pm 0.19$ $0.58 \pm 0.19$
	Total	266	$1035.92 \pm 62.64$	885.85 ± 41.54	153.33 ± 11.24	$18.01 \pm 1.83$	520.46 ± 28.59	$10.22 \pm 1.32$

(continued on next page)

#### Table 7 (continued)

Location	Taxon	Density (trees ha <sup>-1</sup> )	Total mass (Mg ha <sup>-1</sup> )	Wood mass (Mg $ha^{-1}$ )	Bark mass (Mg ha <sup><math>-1</math></sup> )	Leaf mass $(Mg ha^{-1})$	Carbon mass (Mg ha <sup>-1</sup> )	Leaf area (ha ha <sup>-1</sup> )
10	Pseudotsuga menziesii	23	$764.77 \pm 20.92$	$615.04 \pm 14.01$	$121.84 \pm 3.58$	$5.38~\pm~0.17$	$366.23 \pm 10.17$	$3.40~\pm~0.13$
	Tsuga heterophylla	155	177.03 ± 14.53	$173.18 \pm 11.83$	$26.33 \pm 2.32$	5.16 ± 0.49	99.50 ± 7.43	$2.37~\pm~0.26$
	Thuja plicata	32	$332.19 \pm 45.44$	$287.82 \pm 32.77$	$40.63 \pm 5.96$	$3.74 \pm 0.59$	$167.28 \pm 20.02$	$3.10 \pm 0.57$
	Other conifers	9	$3.32 \pm 0.45$	$2.20 \pm 0.25$	$0.91 \pm 0.13$	$0.20 \pm 0.04$	$1.62 \pm 0.22$	$0.39 \pm 0.08$
	Angiosperms	5	$23.32 \pm 2.27$	$18.43 \pm 1.62$	$4.10 \pm 0.47$	$0.78 \pm 0.10$	$11.39 \pm 1.14$	$4.85 \pm 0.83$
	Ferns	0	$0.27 \pm 0.04$	0	0	$0.27 \pm 0.04$	$0.13 \pm 0.02$	$0.55 \pm 0.12$
	Total	224	$1300.89\ \pm\ 83.65$	$1096.67 \pm 60.48$	$193.80 \pm 12.47$	$15.52 \pm 1.43$	$646.15 \pm 38.98$	$14.66 \pm 1.99$
11	Pseudotsuga menziesii	63	$1193.22 \pm 29.04$	$1006.67 \pm 20.14$	$201.20 \pm 4.86$	$6.85 \pm 0.21$	599.32 ± 14.73	3.97 ± 0.15
	Tsuga heterophylla	277	$279.63 \pm 20.42$	$233.68 \pm 14.02$	34.63 ± 2.51	7.33 ± 0.69	$134.00 \pm 8.78$	$4.95~\pm~0.56$
	Thuja plicata	92	$238.21 \pm 28.99$	$204.78 \pm 20.48$	$29.30 \pm 3.54$	$3.61 \pm 0.56$	119.68 ± 12.54	$3.06 \pm 0.57$
	Other conifers	18	$1.71 \pm 0.21$	$1.13 \pm 0.11$	$0.20 \pm 0.02$	$0.17 \pm 0.03$	$0.73 \pm 0.08$	$0.17 \pm 0.03$
	Angiosperms	1	$0.34 \pm 0.04$	$0.17 \pm 0.02$	$0.04 \pm 0.01$	$0.00 \pm 0.00$	$0.11 \pm 0.01$	$0.57 \pm 0.11$
	Ferns	0	$0.10 \pm 0.01$	0	0	$0.10 \pm 0.01$	$0.05 \pm 0.01$	$0.13 \pm 0.02$
	Total	451	$1713.22\ \pm\ 78.72$	$1446.44 \pm 54.78$	$265.37 ~\pm~ 10.94$	$18.07 ~\pm~ 1.50$	$853.89 \pm 36.15$	$12.85~\pm~1.44$

#### Table 8

Above ground biomass and carbon mass of dead trees—logs and snags—in vegetation plots at nine locations (Table 1). Values are best estimates  $\pm 1 S_E$  with percentage of mass in snags indicated. Logs include all mapped pieces  $\geq 30$  cm diameter (Fig. 8) supplemented by line-intercept sampling of smaller pieces. Total masses are computed as products of decay class volumes and densities (Appendix C).

Location	Total mass (Mg ha <sup><math>-1</math></sup> )	Carbon mass (Mg ha <sup><math>-1</math></sup> )	Snag mass (%)
2	133 ± 9	$65 \pm 5$	23
3	$331 \pm 19$	$162 \pm 12$	51
4	$238 \pm 17$	$117 \pm 10$	20
6	$97 \pm 10$	47 ± 6	52
7	$33 \pm 2$	$16 \pm 1$	31
8	$192 \pm 24$	94 ± 13	37
9	$339 \pm 34$	166 ± 19	35
10	$331 \pm 30$	$162 \pm 17$	35
11	$286~\pm~30$	$140 \pm 17$	38

by small-crowned *P. menziesii* (135 trees ha<sup>-1</sup>), a lower canopy dominated by small *T. heretophylla* (106 trees ha<sup>-1</sup>), and an understory dominated by *Frangula purshiana* and *Polystichum munitum* (1.7 and 1.3 Mg ha<sup>-1</sup>, respectively). The intermediate forest (3) had a taller but less dense upper canopy dominated by deep-crowned *P. menziesii* (50 trees ha<sup>-1</sup>), a lower canopy sparsely occupied by *T. heterophylla* (32 trees ha<sup>-1</sup>) with one large *T. plicata* (*f*-DBH = 219 cm), and a well-developed understory dominated by *Acer circinatum* (3.8 Mg ha<sup>-1</sup>). The oldest forest (4) had a sparse upper canopy dominated by large-crowned *P. menziesii* (23 trees ha<sup>-1</sup>), a very dense lower canopy dominated by *T. heterophylla* (347 trees ha<sup>-1</sup>) with one large *T. plicata* (*f*-DBH = 303 cm), and a patchy understory of angiosperms concentrated in areas of open canopy and seasonal inundation with dense recruitment of *T. heterophylla* elsewhere.

Cascade forests resembled Olympic forests in *P. menziesii* dominance of the upper canopy and *T. heterophylla* prevalence in the lower canopy except in the two youngest forests (6, 7), where the quantity of *T. heterophylla* was negligible (Fig. 10). *Thuja plicata* was more abundant



Fig. 8. Stem maps of three Olympic plots depicting trunk cross-sections of *P. menziesii*, *T. heterophylla*, *T. plicata*, and standing dead trees (snags) as well as understory species, logs, seasonal inundation, and *P. menziesii* bark mounds. Logs in plots 2 and 3 are nearly all *P. menziesii*. All but a few of the largest logs in plot 4 are *T. heterophylla*. Trunk cross-sections are drawn to scale of 10-m grid with colors indicating different heights above ground, basal section being darkest.



Fig. 9. LiDAR point clouds associated with three Olympic plots (Fig. 8) isolated by linking stem map to real Earth coordinates. Species separation is done manually using plot measurements to locate tagged individuals within the cloud. Ground returns used to create digital elevation model are shown.

in old-growth Cascade forests, rivalling or exceeding biomass and leaf area of *T. heterophylla* (Fig. 11, Table 7). In both Olympic and Cascade forests, conifers represented 98–100% of live plant biomass and virtually all dead tree mass (Tables 7 and 8, Fig. 11a). High occupancy of upper and lower canopy strata by conifers was associated with sparse understories in all but the oldest forest (10), which had 24 species of angiosperms (Appendix E) and a leaf area index higher than in any other location (Table 7). Even though angiosperms and ferns accounted for only 1–19% of total leaf mass, these understory plants contributed 5–43% of total LAI (Fig. 11b, Table 7).

Dendrochronology determined timing of *P. menziesii* cohort-replacing fires with decadal accuracy, providing an approximate chronosequence of Olympic and Cascade forest development. New *P. menziesii* cohorts established rapidly in the decades following high-intensity fire, diminishing to 500 trees ha<sup>-1</sup> by 100 years, < 100 trees ha<sup>-1</sup> by 300 years, and < 50 trees ha<sup>-1</sup> by 500 years (Fig. 12a). Average biomass of live *P. menziesii* trees increased nonlinearly with time since disturbance, reaching 10 Mg by 300 years and nearly 40 Mg by 600 years with average tree size increasing more rapidly in Olympic than Cascade forests (Fig. 12b). Forest biomass accumulated rapidly, reaching ~ 800 Mg ha<sup>-1</sup> within 100 years and exceeding 1000 Mg ha<sup>-1</sup> within 300 years (Fig. 12c). Leaf area also increased rapidly, exceeding 8 LAI in all but one Cascade forest (7) and reaching a maximum > 14 LAI in the oldest forest (10, Fig. 12e). The proportion of total biomass and leaf area contributed by *P. menziesii* decreased linearly over time with the decrease being more rapid in Cascade forests (Fig. 12d and f).

#### 4. Discussion

Long subjected to scientific scrutiny by virtue of overwhelming economic and ecological importance, a scientific evaluation of *P*.



Fig. 10. Vertical distribution of crown volume by taxon in vegetation plots at nine locations (Table 1). Crown volume of each tagged tree is partitioned into 5-m height bins using geometric shapes and plot measurements. Species of conifers and angiosperms are listed in Appendix E.

*menziesii* has been neglected in unlogged, coastal rainforests. Our aboveground examination of 30 trees in Washington and California, including six > 90 m tall and three > 300 cm DBH, permits accurate quantification of leaves, bark, cambium, sapwood, heartwood, deadwood, biomass, annual growth increments, and age of *P. menziesii* in these forests for the first time. The calculations account for differences in tissue densities among bark, sapwood, and heartwood of trunks and branches as well as variation in wood density along the height gradient, which is often ignored despite being considerable (Wassenberg et al., 2015). After combining the 30-tree dataset with an equal number of trees from Cascade forests, we develop new allometric equations for *P. menziesii* in tall forests, compare these equations with those previously published for the species, and apply them to vegetation plots spanning six centuries of forest development. We thus are able to contrast canopy structure and biomass accumulation in Olympic and Cascade forests.

# 4.1. Crown structure of coastal vs. montane trees

Trees in coastal and Cascade forests progress through similar stages of development, retaining model-conforming crowns until damaged. If damage occurs while trees are young, reiterated trunks arise from the break, replace the leader, and re-assert apical control to maintain mostly model-conforming crowns (e.g., 2, 21; Fig. 3), but if damage occurs later (or repeatedly), not only do reiterated trunks arise to replace the leader, but limbs (i.e., branches giving rise to trunks) also appear lower in the crown (Van Pelt and Sillett, 2008). Over centuries of lifespan, *P. menziesii* crowns can develop complex structure with some individuals (e.g., 11) bearing numerous sizeable reiterations and others developing gnarled, segmented branch systems (e.g., 14). Epicormic branches arise from the trunk to take advantage of light availability during the vertical diversification stage of stand development (Ishii and Ford, 2001; Franklin et al., 2002), allowing trees to develop > 60-m-deep crowns in both coastal and Cascade forests (e.g., 15, 60), though some tall trees maintain high crowns with branch-free trunks for > 40 m (e.g., 6, 29, 54). Sparse-crowned trees with low aboveground vigor occur in Olympic (e.g., 3, 4, 7, 8) and Cascade (e.g., 31, 48, 49, 50) forests where they are surrounded and suppressed by taller neighbors. This is the inevitable situation for P. menziesii in rainforests of California, where the dominant species-S. sempervirens-grows taller and is more shade tolerant, explaining why these trees have consistently low aboveground vigor (Fig. 4). Even though they sometimes rival heights of neighboring S. sempervirens, upper crowns of tall P. menziesii in these forests tend to be narrow, whereas shorter trees develop wider crowns with relatively few, long branches foraging for light in canopy gaps (compare trees < and > 80 m tall, Fig. 3).

# 4.2. Effects of old age on growth increments

Our 60-tree sample includes individuals spanning broad gradients of size and aboveground vigor, but we avoided very low-vigor trees unsafe to climb, and we did not consider very old forests no longer dominated by *P. menziesii* (i.e., advanced pioneer cohort loss stage of stand development; Franklin et al., 2002). Thus, our sample excludes large, suppressed or dying trees that would appear in the lower right of Fig. 4.



**Fig. 11.** Predicted (a) aboveground biomass and (b) leaf area of all live plants in vegetation plots at three Olympic and six Cascade locations (Table 1). Values for *P. menziesii* are derived from equations in Table 6, and values for other species are derived from published equations (Means et al., 1994; Jenkins et al., 2004, Law and Berner, 2015; Sillett et al., 2015a; Van Pelt et al., 2016) applied to plot measurements.

Because ageing is a time-stress response to the cumulative effects of injuries and entropy (Thomas, 2013), and *P. menziesii* is far more vulnerable to decay than two other species recently studied using the same methods (i.e., *S. sempervirens* and *S. giganteum*), age may have more pronounced negative effects on *P. menziesii* productivity after accounting for the effects of size and aboveground vigor.

Unlike S. sempervirens and S. giganteum (Sillett et al., 2015a), we find strong evidence for a negative age effect on growth increments of P. menziesii. Main trunks of older trees produce less wood volume annually than younger trees after accounting for size, older trees produce smaller annual rings than younger trees after accounting for aboveground vigor, and older trees have lower growth efficiency (GE) than younger trees (Tables 4 and 5). Despite being > 600 years old, however, the largest tree we studied (14) has the highest biomass increment  $(305 \text{ kg yr}^{-1})$ , similar to the situation in *E. regnans*, which has an even shorter lifespan and is more vulnerable to pathogens than P. menziesii (Sillett et al., 2015b). After reaching great size, trees may go through a protracted period of senescence preceding death during which their growth increments decline (Sheil et al., 2017). The steady decline in size-detrended growth increments (RWVI) of eight Olympic trees since 1750 (Fig. 5), during which average tree age increased from 185 to 450 years, contrasts with observations of S. sempervirens and S. giganteum, which exhibit no such decline over the same period (Sillett et al., 2015a). Even though rates of wood production continue to increase with tree size through old age, GE of older P. menziesii and E. regnans trees declines as the cumulative effects of ageing manifest. If not killed instantaneously by toppling, old trees eventually succumb to decay as portions of crowns fail. That the age-related decline we observe in P. menziesii occurs in otherwise healthy trees with full crowns and does not occur in species with much higher decay resistance suggests a

gradual increase in investments to combat fungi. Mortality of giant trees is more likely to be a consequence of vulnerability to decay than caused by cellular ageing, because *P. menziesii* in low-elevation rainforests can live more than twice as long as the oldest trees we studied (Carder, 1995). The Rocky Mountain variety (*P. menziesii glauca*) sometimes grows nearly beyond the reach of decay fungi at high elevations and can live > 1800 years (Brown, 2018), while another member of the Pinaceae (*Pinus longaeva*) can live over 4000 years without exhibiting senescence (Lanner and Connor, 2001). Comparing trees buffered from decay by virtue of altitude to those in low-elevation rainforests may resolve why *P. menziesii* expresses age-related declines in GE and RWVI.

# 4.3. Evaluating allometric equations

The 60-tree equations we present for *P. menziesii* (Table 6, Appendix A) should work well in any forests capable of growing 90-m-tall trees, but they may be biased for predicting tree sizes in lower productivity forests at higher elevations or on poor soils. Equations based on coastal trees slightly underestimate biomass of Cascade trees, which do not grow as large (Fig. 6a). For young forests, equations derived from a 47-year-old plantation (Harrison et al., 2009) are more appropriate than ours, but for tall forests our 60-tree equations provide less biased predictions of *P. menziesii* quantities (Fig. 7).

Applying allometrics to *P. menziesii* inventories at nine locations reveals that the 60-tree equations are more conservative than nearly all existing equations. The most generous equations we examined (Grier and Logan, 1978; Gholz et al., 1979), which have been most commonly used in studies of old trees, predict *P. menziesii* biomass in the oldest Olympic forest (10) of nearly 2500 Mg ha<sup>-1</sup>—twice as high as the 60-tree equation predicts—even though they are more conservative than ours in the youngest Cascade forests (6, 7; Appendix F). Our density values for *P. menziesii* are generally lower than published values, and they account for variable tissue densities among branches and trunks as well as height-related variation in sapwood and heartwood (Fig. 1). Application of a single published density value to all the volume in a tree may contribute to the mass overestimates of earlier equations.

The proportion of crown mass declines with increasing trunk size, and few *P. menziesii* trees > 60 m tall (e.g., trees 11 and 21) have > 10% of their mass in appendages, which is common in shorter trees (Appendix D), explaining how equations derived from small trees can overestimate crown masses in tall forests. Remarkably, the overestimate of crown mass by plantation-derived equations (Harrison et al., 2009) is enough to compensate for the underestimate of main trunk mass in the two largest Olympic trees (9, 14) and yield reasonably accurate aboveground biomass predictions for these > 600-year-old individuals (Fig. 7c). Most of the equations we examined overestimate leaf quantities of *P. menziesii*, resulting in extravagant LAI estimates for tall forests, though predictions from equations used by Van Pelt et al. (2016) come close to ours (Appendix F).

# 4.4. Canopy structure and biomass accumulation

The wet maritime climate of Olympic rainforests results in fire return intervals centuries longer than found in most Cascade forests (Agee, 1993). Consequently, conditions sufficient for *P. menziesii* cohort establishment rarely occur in these forests. The three Olympic forests we studied represent much of what exists on the western Olympic Peninsula, and they have unusually high *P. menziesii* biomass (1136–1289 Mg ha<sup>-1</sup>; Table 7). Higher biomass of other conifers in oldgrowth Cascade forests (9, 10, 11; Fig. 11a) suggest contrasting post-fire developmental trajectories.

The relatively small size of T. heterophylla trees, which have almost



**Fig. 12.** Aboveground quantities of *P. menziesii* and other vegetation in nine forests established after cohort-replacing fires in Olympic (2, 3, 4) and Cascade (6, 7, 8, 9, 10, 11) locations (Table 1). Black dotted lines show best nonlinear (a, b, c, e) or linear (d, f) fits with corresponding  $R^2$ .

no overlap in trunk diameter distribution with *P. menziesii* in Olympic forests (results not shown), is particularly surprising and implies that *T. heterophylla* establishment was not concurrent with *P. menziesii* establishment despite seemingly abundant local seed sources. The oldest Olympic forest (4) does have a well-developed population of *T. heterophylla* up to 103 cm DBH, yet its diameter distribution is still decoupled from that of *P. menziesii*, whose smallest tree is 145 cm DBH. Suitable nurse logs for *T. heterophylla*, which promote its establishment in these forests (Harmon and Franklin, 1989), may be in short supply for a long time. This may be true in the youngest Olympic forest (2), where small-diameter logs cover a tiny proportion of the ground

(Fig. 8). The intermediate Olympic forest (3) has a comparable mass of dead trees to old-growth Cascade forests (Table 8), but most of this mass is standing as snags and therefore unavailable for much *T. heterophylla* recruitment. Large logs present in this plot are all relatively recent, and even though they have abundant colonization, nearly all establishing *T. heterophylla* and *P. sitchensis* trees are < 3 m tall. Indeed, optimal conditions for *T. heterophylla* regeneration in Olympic forests may not develop until 300 years after fire (Huff, 1995). Aside from a couple of *T. plicata* trees that may have established with initiating cohorts (Figs. 8 and 9), ideal conditions after stand-replacing fire allowed *P. menziesii* to overwhelm other conifers in these forests. Alternatively,



Fig. 13. The rise and fall of P. menziesii in Olympic rainforests. (a) Biomass of P. men*ziesii* reaches a maximum—1289 Mg ha<sup>-1</sup>—in this Olympic location (3, Table 1), where 50 trees up to 90 m tall stand per hectare. (b) The largest P. menziesii tree (14) measured in this study also has the second-highest aboveground vigor (upper right, Fig. 4) and represents the apex of crown size. Illustration by Robert Van Pelt is based on computer model and photographs of tree from different view angle than depicted in Fig. 3. (c) Sporocarps of wood decay fungus Rhodofomes cajanderi (Karst.) B.K. Cui, M.L. Han & Y.C. Dai are prevalent on main trunk of tree 14 just below old break at 80 m. (d) Wood decay by fungus Phaeolus schweinitzii (Fries) Pat. is a common cause of mortality in old P. menziesii, such as this > 4-m-diameter individual in the same forest as tree 14. Note person on left for scale and dark, discolored wood on right where trunk failed. (e) Most giant P. menziesii, such as this individual (largest known in Cascade Mountains; Van Pelt, 2001), fall after acquiring a non-recoverable lean, often in combination with root decay caused by P. schweinitzii. (f) Few P. menziesii > 4 m DBH remain standing, such as this individual, which has been among the largest known since 1940 (Van Pelt, 2001). By 2014 much of its crown had collapsed from bark loss and wood decay, as documented in this illustration by Robert Van Pelt based on ground-level measurements and photographs. Blue arrows (b and f) indicate epiphytic T. heterophylla trees. Just to right of uppermost T. heterophylla is an epiphytic P. sitchensis tree (lighter green, barely visible behind P. menziesii foliage). Tick marks (b and f) indicate two heights relative to ground level-0 and 50 m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

*T. heterophylla* that established early during stand development may have succumbed to wind and pathogens and subsequently disappeared through decay. This species rarely, if ever, reaches great size or age at low elevations even though some of the largest and presumably oldest trees occur > 1000 m in Olympic rainforests (Van Pelt, 2001).

While angiosperms and ferns represent only a tiny proportion of aboveground biomass in both Olympic and Cascade forests, they account for a substantial proportion of leaf area—non-conifer LAI > 1—in seven of nine locations (Fig. 11) and account for the majority of tagged tree populations in the smallest size classes of three forests (2, 3, 7). The two forests with depauperate understories both have lower canopies crowded by *T. heterophylla* and/or *T. plicata*. In the Olympic forest (4), angiosperms concentrate in a swamp mostly devoid of these shade-tolerant conifers (Figs. 8 and 9), whereas crowns of both

species practically fill the canopy of the Oregon Cascade forest (11) beneath *P. menziesii* (Fig. 10). Unlike the Washington forests, this Cascade location experienced at least one low-intensity fire after establishment of *P. menziesii* that allowed *T. heterophylla* and *T. plicata* to establish relatively early in stand development (i.e., type 2 episodic non-stand-replacing model of Tepley et al., 2013). Indeed, by virtue of having the second highest total mass of *P. menziesii*, *T. heterophylla*, and *T. plicata* among the nine locations, this Cascade forest (11) has the highest aboveground biomass (1999 Mg ha<sup>-1</sup>) and carbon mass (994 Mg ha<sup>-1</sup>), even though it has only the second highest leaf area (Fig. 11, Table 7). The oldest Cascade forest (10), which has the highest total LAI (14.7), highest angiosperm LAI (4.8), and highest species richness (34), also has the lowest conifer density (210 trees ha<sup>-1</sup>) and tallest trees (up to 85 m) among the Cascade forests (Table 7). This

forest canopy is also the only one with a nearly monotonic increase in crown volumes from top to ground level (Fig. 10). It thus exemplifies the recently described phenomenon of emergent facilitation, whereby widely-spaced, deep-crowned, emergent trees (in this case *P. menziesii*) allow light penetration of the canopy and promote light-use complementarity among shorter species, including a well-developed understory (Ishii et al., 2013; Van Pelt et al., 2016).

The post-fire time series we reconstruct using nine forests established after high-intensity fires summarizes the similarities and differences between Olympic and Cascade stand development (Fig. 12). Forests in both regions experience a rapid depletion of the initiating *P*. menziesii cohort, first through density-dependent and then density-independent mortality (Franklin et al., 2002). Biomass and leaf area accumulate rapidly even though the P. menziesii proportion of these quantities steadily declines. In Olympic forests, P. menziesii gains size more rapidly, becomes larger, and maintains a greater proportion of plot-level biomass over time compared to Cascade forests. Higher annual rainfall and a more equitable temperature regime at lower elevations closer to the ocean likely contribute to greater maximum tree sizes in Olympic forests (Larjavaara, 2014). While density-dependent mortality and early stages of stand development may occur more quickly in Olympic than Cascade forests by virtue of higher productivity (Larson et al., 2008), subsequent changes in forest structure seem to be strongly influenced by region. For example, the two forests with the fullest upper canopy containing trees of similar size (late maturation stage of Franklin et al., 2002) are 2 and 6, but the Olympic forest (2) is twice as old as the Cascade forest (6), and thus has a more developed shadetolerant component (Fig. 10, Table 1). The upper canopy of the intermediate Olympic forest (3) is also full, but significant gaps are beginning to appear, and the size range between dominant trees is increasing (early vertical diversification stage of Franklin et al., 2002). This situation is similar to two Cascade forests (7, 8) that are much younger. Higher productivity may promote earlier dominance and greater maximum size of P. menziesii in Olympic forests, prolonging later stages of stand development.

The extreme rarity of trees > 90 m tall-even in protected areas-demonstrates the pernicious and cumulative effects of storms and pathogens leading to disappearance of P. menziesii without high-intensity fire. So far during the 21st century, half of the ten largest known trees (Van Pelt, 2001) died, and many tall trees in the Olympic and Cascades forests we studied (4, 9) have fallen from the combined effects of wind and fungi. The lightning-caused, stand-replacing Paradise Fire burned for six months in 2015 through a patch of Olympic National Park recently discovered via LiDAR to support dozens of P. menziesii trees > 90 m tall, including two individuals confirmed > 95 m tall, both of which were killed (R.D. Kramer, personal observation). Located at the foot of Mount Olympus in the upper Queets drainage, this is the wettest place with a P. menziesii-dominated forest known. Prior to the fire, this Olympic rainforest probably held more aboveground biomass than any P. menziesii-dominated ecosystem ever measured, though now the species will be able to re-establish.

# 4.5. Conclusions

Plentiful precipitation and moderate temperatures allow *P. menziesii* to achieve maximum size in coastal rainforests. The species currently reaches its apex of structural potential on the Olympic Peninsula, as both a forest (Fig. 13a) and a tree (Fig. 13b). Larger individuals than tree 14 are known, and their aboveground attributes can be predicted using equations presented here (Table 6, Appendix A). For example, direct measurements of the largest *P. menziesii* ever recorded (Fig. 1a)

predict a biomass of 212 Mg, which is similar to the largest living E. regnans (Sillett et al., 2015b), half that of the largest living S. sempervirens (Sillett et al., 2015a), and almost twice as high as tree 14. Wood decay fungi observed in tree 14 (Fig. 13c) suggest that crown or basal failure is not far away. Many giant P. menziesii nearby and in other old forests have recently fallen victim to the ubiquitous and persistent fungus, Phaeolus schweinitzii (Fig. 13d and e). Another standing Olympic individual has a much larger base than tree 14 (533 vs. 429 cm f-DBH) but is heavily damaged and has continued to decline since its discovery (Fig. 13f). Prior to crown failure, allometric equations predict an aboveground biomass of 174 Mg. After accounting for the proportion of crown remaining, missing bark and cambium on the main trunk, and the likely volume of decayed, lower-density wood both below the broken top (6.8 m<sup>3</sup>) and within the lower trunk (65.9 m<sup>3</sup>), we estimate a 2014 aboveground biomass of 113 Mg (i.e., a 35% loss). Such fragmented trees may have negative biomass increments caused by crown failure and wood decay, but they maintain other values (e.g., habitat for epiphytes; Fig. 13f) making them an important consideration (Lindenmayer and Franklin, 2002; Carey, 2007).

Coastal rainforests dominated by *P. menziesii* accumulate enormous biomass with the dominant species maintaining 80% or more of this material for at least 600 years following stand-replacing fire. Only forests dominated by *S. sempervirens* (> 2500 Mg Cha<sup>-1</sup>; Van Pelt et al., 2016), *S. giganteum* (> 1500 Mg ha<sup>-1</sup>; R. Van Pelt and S.C. Sillett, *unpublished data*), and *E. regnans* (> 1000 Mg ha<sup>-1</sup>; Keith et al., 2014, but see Sillett et al., 2015) are known to exceed the carbon densities reported here (Tables 7 and 8). Despite a maximum height that surpasses all other species (Carder, 1995), by the time *P. menziesii* trees reach giant size, few individuals remain per hectare, and the pioneer cohort gives way to species of lesser stature (Franklin et al., 2002; Van Pelt and Nadkarni, 2004). Vulnerability to wood decay and dependence on fire for stand dominance set an upper limit for mass density of *P. menziesii* forests near 1000 Mg Cha<sup>-1</sup>.

Understanding the allometry and performance characteristics of tree species over their lifespans helps to establish realistic management goals. For example, Olympic rainforests dominated by P. menziesii (Fig. 14a) can be expected to accumulate  $1200 \text{ Mg ha}^{-1}$  of above ground biomass in 200 years and  $1400 \text{ Mg ha}^{-1}$  in 600 years (Fig. 12c). Because tree- and plot-level biomass can now be accurately predicted via ground-based measurements (Fig. 14b, Table 6, Appendix A; Harrison et al., 2009), productivity and carbon density of regenerating forests can be readily evaluated. Prior to logging or after variable-retention silvicultural prescriptions (see Franklin et al., 2018), dominant and subordinate trees can be expected to accumulate biomass at rates similar to fast- and slow-growing trees in undisturbed forests, respectively (Fig. 14c). More research is needed on long-lived species capable of regeneration without fire in rainforests. Thuja plicata is of particular interest from a carbon sequestration perspective. Like S. sempervirens, heartwood of T. plicata has extremely high decay resistance, and individuals can both live longer and reach greater size than P. menziesii (Van Pelt, 2001; Daniels, 2003; Antos et al. 2016). Thus, forests dominated by T. plicata might have more carbon sequestration potential than those studied here. The best equations available for T. plicata (Appendix B) are provisional, because trees spanning the full size and age range have yet to be measured sufficiently. Robust allometric equations for T. plicata would complement those now available for P. menziesii, P. sitchensis, S. sempervirens, S. giganteum, and other species (Sillett et al., 2015a; Van Pelt et al., 2016; Kramer et al., 2018) and permit accurate quantification of forest biomass and tree performance across vast areas of western North America.



**Fig. 14.** (a) Olympic rainforest dominated by *P. menziesii* shown from treetop view near Lake Quinault. (b) Size of *P. menziesii* varies predictably with trunk diameter (DTB) such that 100-cm-diameter trees weigh 3–11 Mg and 200-cm-diameter trees weigh 36–57 Mg. (c) Rates of biomass accumulation vary dramatically with age such that 100-year-olds weigh 2–12 Mg, 300-year-olds weigh 11–37 Mg, and 600-year-olds weigh 53–112 Mg. Each line represents an individual, whose aboveground biomass is predicted as a function of measured main trunk wood volume ( $R^2 = 0.996$ , Appendix A), DTB is predicted as function of measured wood radius at TB ( $R^2 = 0.996$ , Appendix A), and age is calculated by subtraction from year of measurement (trees 1–15, Appendix D).

# Acknowledgments

Funding for this research was generously provided by Kenneth L. Fisher, who also assisted with fieldwork. Additional support came from the Save the Redwoods League and the National Science Foundation (IOB-0445277). Marie Antoine, Wendell Bedell, Ethan Coonen, Sean Jeronimo, and Kalia Scarla helped with fieldwork. Bill Kruse processed LiDAR datasets and facilitated tree selection. We are grateful to personnel at Olympic National Park, Olympic National Forest, Washington Department of Natural Resources, and California State Parks, especially Pete Erben, Jerry Freilich, Catherine Copass, Louise Johnson, Roger Hoffman, and Jay Harris, for logistical support and permission to conduct research in these locations. The manuscript benefitted from comments of Jerry Franklin, Marie Antoine, Ken Fisher, and an anonymous reviewer. We are indebted to Jerry Franklin for inspiring our *P. menziesii* research and particularly for his insistence that we visit Jackson Creek Research Natural Area.

# Appendix A

Allometric equations for various plot-, tree-, trunk-, branch-, and leaf-level quantities of *P. menziesii*. All dependent variables are for aboveground portions of trees. SLA is specific leaf area. Predictors (V1–3) listed from left to right in descending order of importance. Dependent variables (DBH = tape diameter at breast height, *f*-DBH = functional DBH, BA 5 = basal area of trees  $\geq 5 \text{ cm}$  DBH, BA 25 = basal area of trees  $\geq 25 \text{ cm}$  DBH, DTB = diameter at top of buttress, CV = crown volume, SABH = sapwood cross-sectional area at BH, height = tree height, max height = height of tallest tree in plot, total radius = half the diameter, PC1 and PC2 = relativized scores along first two principal components) followed by regression coefficients (*a*–*e*), sample size (*N*), goodness of fit ( $R^2$ ), and form of equation. If best prediction is the mean, 1 *S*<sub>E</sub> is listed instead of *R*<sup>2</sup>. Blank cells indicate unnecessary values, as fewer coefficients are needed in these equations.

#### Appendix B

Calculation template for *Thuja plicata* using published equations. Columns B to M contain measured values for 297 individuals measured in seven locations, including predictors used in allometric equations. Columns O–T contain predicted values for *T. heterophylla* trees of equivalent size. Columns V–AB contain predicted values for *S. giganteum* trees of equivalent size. Columns AD–AJ contain all calculations for *T. plicata* trees. Allometric equations for all three species are in columns AL–BJ.

#### Appendix C

Density of dead wood categories in kg m<sup>-3</sup>. Values are means  $\pm 1$  SE. Note that we use multi-study means (highlighted bold) for *P. menziesii* and *T. plicata* based on published values from different locations. For *A. circinatum*, we use values for *A. pensylvanicum* for all but Decay I, where we use density from Van Pelt et al. (2016).

#### Appendix D

Aboveground structural attributes of 60 *P. menziesii* trees ranked by height within region (Fig. 3). Values are best estimates  $\pm 1 S_E$ . Tree ages are estimated using trunk cores from multiple heights. Confirmed age is expressed as percentage of annual rings counted compared to estimated tree age. Year of sampling is listed along with height and four ground-based predictors (*f*-DBH, DTB, crown volume, SABH) used to develop allometric equations (Table 6). Missing values are left blank.

# Appendix E

Vascular plant species in vegetation plots at nine locations (Table 1). Numbers of conifer, angiosperm, and fern species as well as total species richness are highlighted in bold.

# Appendix F

Comparison of six allometric equations for predicting (a) aboveground biomass and (b) leaf area index (LAI) of all *P. menziesii* trees in vegetation plots at nine locations (Table 1) using ground-based measurements of DBH only (Grier and Logan, 1978; Gholz et al., 1979; Jenkins et al., 2003; Harrison et al., 2009) or DBH, DTB, and crown volume (Van Pelt et al., 2016; this study). Hatched areas (a) indicate the proportion of aboveground biomass in appendages (i.e., crown mass). Leaf area was calculated as a multiple of leaf mass using plot-level data from eight locations (Appendix A).

#### Appendix G. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.006.

#### References

- Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, D.C., pp. 493.
- Antos, J.A., Filipescu, C.N., Negrave, R.W., 2016. Ecology of western redcedar (*Thuja plicata*): implications for management of a high-value multiple-use resource. For. Ecol. Manage. 375, 211–222.
- Ares, A., Terry, T.A., Piatek, K.B., Harrison, R.B., Miller, R.E., Flaming, B.L., Licata, C.W., Strahm, B.D., Harrington, C.A., Meade, R., Anderson, H.W., Brodie, L.C., Kraft, J.M., 2007. The Fall River long-term site productivity study in coastal Washington: site characteristics, methods, and biomass and carbon and nitrogen stores before and after harvest. USDA Forest Service PNW-GTR-691, pp. 85.
- Beach, E.W., Halpern, C.B., 2001. Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate, and vegetation. Can. J. For. Res. 31, 471–482.
- Bible, K.J., 2001. Long-Term Patterns of Douglas-fir and Western Hemlock Mortality in the Western Cascade Mountains of Washington and Oregon. PhD dissertation.

University of Washington, Seattle, pp. 85.

- Brown, J.K., 1974. Handbook for Inventorying Downed Woody Material. USDA Forest Service INT-GTR-16, Utah, pp. 24.
- Brown, P.M., 2018. Rocky Mountain Tree-Ring Research. < http://www.rmtrr.org/ OLDLIST.htm > (accessed 2018.04.01).
- Brown, P.M., Swetnam, T.W., 1994. A cross-dated fire history from coast redwood near Redwood National Park, California. Can. J. For. Res. 24, 21–31.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodal Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York.
- Carder, A.C., 1995. Forest Giants of the World Past and Present. Fitzhenry and Whiteside, Markham, pp. 208.
- Carey, A.B., 2007. Aiming for Healthy Forests: Active, Intentional Management for Multiple Values. USDA Forest Service PNW-GTR-721, pp. 447.
- Carroll, A.L., Sillett, S.C., Kramer, R.D., 2014. Millenium-scale crossdating and inter-annual climate sensitivities of standing California redwoods. PLoS ONE 9, 1–18.
- Chojnacky, D.C., Heath, L.S., Jenkins, J.C., 2014. Updated generalized biomass equations for North American tree species. Forestry 87, 129–151.
- Daniels, L.D., 2003. Western redcedar population dynamics in old-growth forests: contrasting ecological paradigms using tree rings. For. Chron. 79, 517–530.
- Franklin, J.F., Dyrness, C.T., 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, pp. 468.
- Franklin, J.F., Cromack Jr., K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., Juday, G., 1981. Ecological Characteristics of Old-Growth Douglas-Fir Forests. USDA Forest Service, PNW-GTR-118, pp. 48.
- Franklin, J.F., Johnson, K.N., Johnson, D.L., 2018. Silvicultural principles for ecological forestry. In: Franklin, J.F., Johnson, K.N., Johnson, D.L. (Eds.), Ecological Forest Management. Waveland Press Inc., Long Grove, pp. 90–115.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.
- Freund, J.A., Franklin, J.F., Larson, A.J., Lutz, J.A., 2014. Multi-decadal establishment for single-cohort Douglas-fir forests. Can. J. For. Res. 44, 1068–1078.
- Freund, J.A., Franklin, J.F., Lutz, J.A., 2015. Structural development of early old-growth Douglas-fir forests of western Washington and Oregon. For. Ecol. Manage. 335, 11–25.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for Estimating Biomass and Leaf Area of Plants in the Pacific Northwest. Research Paper 41. Forest Research Laboratory, Oregon State University, Corvallis, pp. 43.
- Grier, C.C., Logan, R.S., 1978. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47, 373–400.
- Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70, 48–59.
- Harris, L.D., 1984. The Fragmented Forest. University of Chicago Press, Chicago, pp. 230. Harrison, R.B., Terry, T.A., Licata, C.W., Flaming, B.L., Meade, R., Guerrini, I.A., Xue, D., Lolley, R., Sidell, A.R., Wagoner, G.L., Briggs, D., Turnblom, E.C., 2009. Biomass and stand characteristics of a highly productive mixed Douglas-fir and western hemlock plantation in coastal Washington. West. J. Appl. For. 24, 180–186.
- Hemstrom, M.A., Franklin, J.F., 1982. Fire and other disturbances of the forests of Mount Rainier National Park. Quat. Res. 18, 32–51.
- Henderson, J.A., Peter, D.H., Lesher, R.D., Shaw, D.C., 1989. Forested Plant Associations of the Olympic National Forest. USDA Forest Service, R6–ECOL–TP 001–88, Portland.
- Hermann, R.K., Lavender, D.P., 1990. Pseudotsuga menziesii (Mirb.) Franco. In: Conifers. Agricultural Handbook 654, vol. 1. USDA Forest Service, Washington D.C., pp. 527–540.
- Huff, M.H., Agee, J.K., 1980. Characteristics of large lightning fires in the Olympic Mountains, Washington. In: Martin, R.E., Edmonds, R.L., Faulkner, D.A., Harrington, J.B., Fuquay, D.M., Stocks, B.J., Barr, S. (Eds.), Proceedings: Sixth Conference on Fire and Forest Meteorology. Society of American Foresters, Washington D.C., pp. 117–123.
- Huff, M.H., 1995. Forest age structure and development following wildfires in the western Olympic Mountains, Washington. Ecol. Appl. 5, 471–483.
- Ishii, H.R., Ford, E.D., 2001. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* trees. Can. J. Bot. 79, 251–264.
- Ishii, H.R., Ford, E.D., Dinnie, C.E., 2002. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* trees II. Basal reiteration from older branch axes. Can. J. Bot. 80, 916–926.
- Ishii, H.R., Azuma, W., Nabeshima, E., 2013. The need for a canopy perspective to understand the importance of phenotypic plasticity for promoting species coexistence and light-use complementarity in forest ecosystems. Ecol. Res. 28, 191–198.
- Ishii, H.R., Sillett, S.C., Carroll, A.L., 2017. Crown dynamics and wood production of Douglas-fir trees in an old-growth forest. Forest Ecol. Manage. 384, 157–168.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimation for United States tree species. Forest Sci. 49, 12–35.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2004. A comprehensive database of diameter-based biomass regressions for North American tree species. USDA Forest Service GTR-NE-319, pp. 45.
- Keith, H., Lindenmayer, D., Mackey, B., Blair, D., Carter, L., McBurney, L., Okada, S., Konishi-Nagano, T., 2014. Managing temperate forests for carbon storage: impacts of logging versus protection on carbon stocks. Ecosphere 5, 1–34.
- Kramer, R.D., Sillett, S.C., Van Pelt, R., 2018. A generalized guide for quantifying aboveground tree tissues using *Picea sitchensis* and *Eucalyptus globulus* as examples. For. Ecol. Manage (submitted for publication).
- Lanner, R.M., Connor, K.F., 2001. Does bristlecone pine senesce? Exp. Gerontol. 36,

#### S.C. Sillett et al.

675-685.

Larjavaara, M., 2014. The world's tallest trees grow in thermally similar climates. New Phytol. 202, 344–349.

- Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F., Hietpas, F.F., 2008. Potential site productivity influences the rate of forest structural development. Ecol. Appl. 18, 899–910.
- Law, B.E., Berner, L.T., 2015. NACP-TERRA-PNW: Forest Plant Traits, NPP, Biomass, and Soil Properties, 1999–014. ORNL DAAC, Oak Ridge.
- Lindenmayer, D., Franklin, J.F., 2002. Sustaining Forest Biodiversity: A Comprehensive, Multi-scaled Approach. Island Press, Washington, D.C, pp. 352.

McArdle, R.E., Meyer, W.H., 1930. The yield of Douglas fir in the Pacific Northwest. USDA Technical Bulletin 201, pp. 65.

- McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data, version 6. MjM Software, Gleneden Beach.
- Means, J.E., Hansen, H.A., Koerper, G.J., Alaback, P.B., Klopsch, M.W., 1994. Software for Computing Plant Biomass—Biopak Users Guide. USDA Forest Service PNW-GTR-340, pp. 184.

Pike, L.H., Rydell, R.A., Denison, W.C., 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. Can. J. For. Res. 7, 680–699.

- Sheil, D., Eastaugh, C.S., Vlam, M., Zuidema, P.A., Groenendijk, P., van der Sleen, P., Jay, A., Vanclay, J., 2017. Does biomass growth increase in the largest trees? Flaws, fallacies and alternative analyses. Funct. Ecol. 31, 568–581.
- Silen, R.R., Olson, D.L., 1992. A Pioneer Exotic Tree Search for the Douglas-Fir Region. USDA Forest Service PNW-GTR-298, pp. 44 p.

Sillett, S.C., Van Pelt, R., Koch, G.W., Ambrose, A.R., Carroll, A.L., Antoine, M.E., Mifsud, B.M., 2010. Increasing growth through old age in tall trees. For. Ecol. Manage. 259, 976–994.

- Sillett, S.C., Van Pelt, R., Carroll, A.L., Kramer, R.D., Ambrose, A.R., Trask, D., 2015a. How do tree structure and old age affect growth potential of California redwoods? Ecol. Monogr. 85, 181–212.
- Sillett, S.C., Van Pelt, R., Kramer, R.D., Carroll, A.L., Koch, G.W., 2015b. Biomass and growth potential of *Eucalyptus regnans* up to 100 m tall. For. Ecol. Manage. 348, 78–91.
- Sillett, S.C., Antoine, M.E., Campbell-Spickler, J., Carroll, A.L., Coonen, E.J., Kramer, R.D., Scarla, K.H., 2018. Manipulating tree crown structure to promote old-growth characteristics in second-growth redwood forest canopies. For. Ecol. Manage. 417, 77–89.
- Spies, T.A., Franklin, J.F., 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.),

Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service PNW-GTR-285, pp. 91–110.

- Stolnack, S.A., Naiman, R.J., 2010. Patterns of conifer establishment and vigor on montane river floodplains in Olympic National Park, Washington, USA. Can. J. For. Res. 40, 410–422.
- Stoltmann, R., 1993. Guide to the Record Trees of British Columbia. Western Canada Wilderness Committee, Vancouver, pp. 58.
- Tepley, A.J., Swanson, F.J., Spies, T.A., 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. Ecology 94, 1729–1743.
- Thomas, H., 2013. Senescence, ageing and death of the whole plant. New Phytol. 197, 696–711.

Tng, D.Y.P., Williamson, G.J., Jordan, G.J., Bowman, D.M.J.S., 2012. Giant eu-

- calypts—globally unique fire-adapted rainforest trees? New Phytol. 196, 1001–1014. Triska, E.J., Cromack Jr., K., 1980. The roles of wood debris in forests and streams. In: Waring, R.H. (Ed.), Forests: Fresh Perspectives from Ecosystem Analysis. Proceedings 40th Biology Colloquium (1979). Oregon State University Press, Corvallis, pp. 171–190.
- Van Pelt, R., 2001. Forest Giants of the Pacific Coast. Global Forest Society and University of Washington Press, Seattle, pp. 200.
- Van Pelt, R., 2007. Identifying Mature and Old Forests in Western Washington. Washington State Department of Natural Resources, Olympia, pp. 104.
- Van Pelt, R., Franklin, J.F., 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Can. J. For. Res. 30, 1231–1245.
- Van Pelt, R., Sillett, S.C., 2008. Crown development of coastal *Pseudotsuga menziesii*, including a conceptual model for tall conifers. Ecol. Monogr. 78, 283–311.
- Van Pelt, R., Nadkarni, N.M., 2004. Development of canopy structure in *Pseudotsuga* menziesii forests in the southern Washington Cascades. Forest Science 50, 326–341.
- Van Pelt, R., Sillett, S.C., Nadkarni, N.M., 2004. Quantifying and visualizing canopy structure in tall forests: methods and a case study. In: Lowman, M., Rinker, B. (Eds.), Forest Canopies, second ed. Elsevier Academic Press, New York, pp. 49–72.
- Van Pelt, R., Sillett, S.C., Kruse, W.A., Freund, J.A., Kramer, R.D., 2016. Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. For. Ecol. Manage. 375, 279–308.
- Wassenberg, M., Chiu, H.-S., Guo, W., Spiecker, H., 2015. Analysis of wood density profiles of tree stems: incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. Trees 29, 551–561.
- Zenner, E.K., 2005. Development of tree size distributions in Douglas-fir forests under different disturbance regimes. Ecol. Appl. 15, 701–714.