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# Comparative development of the four tallest conifer species

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# ABSTRACT

The tallest conifers-Picea sitchensis, Pseudotsuga menziesii, Sequoia sempervirens, Sequoiadendron giganteum-are widely distributed in western North America, forming forests > 90 m tall with aboveground biomass > 2000 Mg ha<sup>-1</sup>. Here we combine intensive measurements of 169 trees with dendrochronology and allometry to examine tree and stand development. The species investing least in bark protection and heartwood defense-P. sitchensis-has more leaves, denser wood, larger appendages, and produces more aboveground biomass during its relatively brief lifespan than other conifers at equivalent ages. The species investing most in bark protection and heartwood defense-S. giganteum-has the least dense wood, largest appendages, and greatest longevity. Evidence for senescence diminishes with longevity; only P. sitchensis exhibits a post-maturity decline in tree productivity after accounting for leaf mass. Growth efficiency declines with age in all species, falling most rapidly in P. sitchensis followed by P. menziesii, S. sempervirens, and S. giganteum in the same sequence as longevity. Centuries-long time series of age, size, and growth increments identify years when trees first reach a given height as well as biomass and growth rates at that height, providing snapshots of performance useful for simulating development. Stands dominated by P. sitchensis and P. menziesii gain height at similar rates, but P. sitchensis accumulates biomass more rapidly until senescence curtails tree productivity, which takes centuries longer in P. menziesii. Whereas S. sempervirens in primary forest grows more slowly than P. sitchensis and P. menziesii until ~70 m tall, S. sempervirens in secondary forest outpaces other conifers with biomass increments approaching global maxima within a few centuries. Beyond ~70 m, S. giganteum gains height more slowly than other conifers, but it sustains relatively high biomass increments for millennia. Both within and beyond their native ranges, the four tallest conifers have unrealized potential to provide ecosystem services.

# 1. Introduction

Tall forests are treasured for their grandeur, yet an emphasis on timber value promotes forests at odds with this aesthetic. Dense plantations of small, rapidly developing trees harvested on short rotations can accumulate  $> 30 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  of aboveground biomass (Ryan et al., 2010; Jones and O'Hara, 2012), far more than the fastest-growing primary forests (5–19 Mg ha<sup>-1</sup> yr<sup>-1</sup>; Sillett et al., 2020). Less well-understood is tree development beyond rotation age in forests managed for non-timber values. In the absence of repeated measurements spanning lives of individual trees, developmental studies have relied on space-for-time substitutions using fixed-area plots established in forests of different ages (e.g., Van Pelt and Sillett, 2008) or aggregate analysis of individual trees measured over short intervals (e.g., Stephenson et al., 2014). The former approach—chronosequence

analysis—assumes equivalent edaphic conditions and histories across plots (Johnson and Miyanishi, 2008), while the latter shows growth rates increasing continuously with tree size even if biomass increments peak well before old age and then decline during senescence (Sheil et al., 2017). A third approach—intensive measurements of standing individuals combined with dendrochronology—can reveal annual increments of tree size, permitting long-term developmental analysis.

The tallest species are uniquely important for understanding tree development and the ecological significance of forests beyond typical rotation ages. Five of the six highest-biomass forests known are dominated by tree species capable of exceeding 95 m tall—four conifers (*Picea sitchensis, Pseudotsuga menziesii, Sequoia sempervirens, Sequoia-dendron giganteum*) and one angiosperm (*Eucalyptus regnans*; Sillett et al., 2020). The sixth is dominated by *Agathis australis*, the largest conifer in the Southern Hemisphere, which reaches < 60 m tall (Silvester and

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Fig. 1. Native geographic ranges of four tallest extant conifers. (a) Two species of Pinaceae overlap in coastal forests from British Columbia to California with interior form of *P. menziesii* (subspecies glauca) extending into Rocky Mountains. (b) Two species of Cupressaceae occur in coastal forests of Oregon and California (*Sequoia*) or in isolated groves of Sierra Nevada (*Sequoiadendron*). Note ranges of *Picea*, *Pseudotsuga*, and *Sequoia* overlap in Oregon and California.

#### Table 1

Organization of article into sections showing locations of figures and tables in Introduction, Methods, with respect to three main research questions, and Conclusions. Text components are indicated by numbers with decimals indicating subheadings.

Section	Figures	Tables	Text
Introduction	1, 2, 3, 4	2, 3	1
Methods	5, 6	4, 5	2
Question 1	7, 8		2.2, 2.3, 2.4, 3.1, 4.1
Question 2	9, 10, 11	6	2.5, 2.6, 2.7, 3.2, 3.3, 4.2
Question 3	12, 13, 14	7	2.8, 2.9, 3.4, 3.5, 4.3, 4.4
Conclusions	15	8	4.5

*Notes*: The three questions are as follows: (1) Does the species investing most in leaves and least in bark protection and heartwood defense—*Picea* —produce larger appendages during its lifespan than the other conifers at equivalent ages? (2) Is evidence for a negative effect of old age on tree growth weaker in long-lived species such that relatively short-lived Pinaceae exhibit senescence and long-lived Cupressaceae do not? (3) In tall forests, how does long-term development of the four species compare in terms of the time necessary for trees to reach a given size and their aboveground productivity at that size?

Orchard, 1999). Only one other tree species—*Shorea faguetiana*—is known to exceed 95 m in height (Shenkin et al., 2019). This tropical angiosperm does not reliably produce wood in annual rings that can be crossdated, similar to the situation in *E. regnans* (Brookhouse, 2006; Sillett et al., 2010). Whereas tree age in the tallest angiosperms cannot be ascertained without prior knowledge of stand history, core-sampling the tallest conifers allows determination of tree age and reliable

#### Table 2

Maximum age and size of four species in forests > 90 m tall. Longevity, height, biomass, and leaf values indicate oldest, tallest, heaviest, and leafiest trees measured since 2001 (Kramer et al., 2018; Sillett et al., 2018b, 2019b, 2020; M. Taylor, pers. comm.). Tree height is measured vertical distance from highest leaf to midpoint ground level around trunk perimeter such that tallest *Sequoia* was 116.07 m (high point of ground = 113.87, low point of ground = 118.27 m) in 2019.

	Maximum (21st century)								
Species	Longevity (yr)	Height (m)	Biomass (Mg)	Leaves (kg)	Leaves (millions)				
Picea sitchensis	<500	96.86	155	1262	299				
Pseudotsuga menziesii	<1000	98.39	117	712	216				
Sequoia sempervirens	>2000	116.07	394	1958	1417				
Sequoiadendron giganteum	>3000	96.50	564	1827	1932				

measurement of radial growth in annual rings. Stem analysis merging ring width and trunk diameter data can be used to reconstruct annual increments of tree height, wood volume, and other quantities depending on availability of allometric equations. Trees spanning the maximum size range have recently been climbed and measured intensively to make allometric equations necessary for accurate quantification of aboveground biomass in the four tallest conifer species (Kramer et al., 2018; Sillett et al., 2018b, 2019a, 2019b, 2020). After reviewing the natural history, geographic distribution (Fig. 1), and physical attributes

#### Table 3

Leaf sampling of four species in primary forests. Number of trees and samples is shown separately for morphology (mass, area, LMA = leaf-mass-to-area ratio) and isotope composition ( $\delta^{13}$ C, numbers in parentheses). Values for mass, area, LMA, and  $\delta^{13}$ C are sample means with coefficients of variation (standard deviation  $\div$  mean) in parentheses. Data come from different sources for *Picea* (Chin et al., 2017; Kramer et al., 2018), *Pseudotsuga* (Sillett et al., 2018); Chin and Sillett, 2019), *Sequoia* (Koch et al., 2004; Oldham et al., 2010; Sillett et al., 2015b), and *Sequoiadendron* (Chin and Sillett, 2016; Sillett et al., 2015b).

Leaf sampling	Picea	Pseudotsuga	Sequoia	Sequoiadendron
Trees	10 (5)	15 (5)	48 (7)	34 (6)
Samples	71 (43)	87 (47)	427 (84)	264 (55)
Single leaf mass (mg)	4.04 (41)	3.27 (19)	2.22 (40)	1.11 (31)
Single leaf area (mm <sup>2</sup> )	18.4 (32)	19.0 (19)	15.0 (61)	4.27 (28)
LMA (g $m^{-2}$ )	215 (17)	174 (12)	170 (27)	258 (11)
Leaf $\delta^{13}$ C (‰)	-28.7 (7)	-27.4 (4)	-26.9 (7)	-24.7 (6)

(Tables 2 and 3, Figs. 2–4) of the four species, we reconsider the trees used to create these allometric equations in a new set of comparative analyses designed to answer three main questions (Table 1).

How quickly trees gain size within an ecosystem reflects ecological strategy, response to disturbances, and investment in defense, while species longevity ultimately limits maximum biomass. Even in species not exhibiting senescence (defined here as a post-maturity decline in tree productivity), inevitable disturbances lead to accumulating injuries and decay that eventually cause mortality (Lanner and Connor, 2001; Thomas, 2013). Whereas one tall conifer—*P. menziesii*—exhibits senescence after accounting for variation in tree size and aboveground vigor (Sillett et al., 2018b), evidence for senescence is lacking or equivocal in

two others—*S. sempervirens* and *S. giganteum* (collectively redwoods) with much longer lifespans (Sillett et al., 2015b). The combined ability to survive fire and resist fungal decay enables redwoods to live for millennia, achieve individual-tree biomass increments up to 1000 kg yr<sup>-1</sup>, and dominate the only forests with aboveground biomass > 2500 Mg ha<sup>-1</sup> (Sillett et al., 2019b, 2020). Limited by shorter tree lifespans and weaker defense against fire and fungal decay, forests dominated by *P. menziesii* accumulate less biomass than redwood forests, though individual trees can gain height more rapidly (Sillett et al., 2018b). The fourth tall conifer—*P. sitchensis*—outpaces *P. menziesii* in biomass accumulation by virtue of maximum investment in leaves and minimal investment in defense (Kramer et al., 2018), but evidence for senescence has yet to be examined.

Crown development of tall conifers, regardless of species, occurs in stages at variable rates depending on both an individual's neighborhood and disturbance history. Original branches arise from rapidly ascending trunks of young, undamaged trees in dense stands, forming excurrent crowns that deepen with age until shaded lower branches die, thereby lifting crown bases. Height growth slows as trees approach maximum height, and if no top damage occurs for many years, the population of original branches is supplemented by epicormic branches arising from trunks, and crowns deepen following mortality of neighboring trees that allows more light to penetrate the canopy (Ishii and McDowell, 2002; Franklin et al., 2002; Bond et al., 2007). Damage to the treetop and appendages initiates the process of trunk reiteration in which new trunks arise epicormically (sprout) from the main trunk at or below the break or from broken branch segments that become transformed into what we refer to henceforth as limbs (Van Pelt and Sillett, 2008). By supporting trunks that each have their own set of branches, limbs gain



**Fig. 2.** Leaf characteristics of four species in relation to height above ground. Single leaf mass and area values are averages based on samples containing 30–300 leaves removed from dissected shoots for scanning, oven-drying, and weighing. LMA is ratio of leaf dry mass to fresh projected area (silhouette). Leaf  $\delta^{13}$ C is carbon isotope composition (‰). Color lines show best linear or nonlinear fits per species with corresponding  $R^2$ . See Table 3 caption for sampling details and data sources.



**Fig. 3.** Trunk wood and bark distributions along gradients of relative height (measurement height  $\div$  tree height) and tree age in four species. Numbers of trees in parentheses correspond to young and old age classes per species (age ranges in upper right). Wood radius is computed as half of measured trunk diameter minus bark. Bark thickness is measured radial distance from diameter tape to cambium based on replicate core samples extracted from 146, 71, 95, and 103 heights on trunks of *Picea, Pseudotsuga, Sequoia,* and *Sequoiadendron,* respectively. Values are means of all measurements per relative height quartile with horizontal bars indicating 1 *S<sub>E</sub>*. In each panel, note that bark thickness axis (right of 0) is expanded 10 × compared to wood radius axis (left of 0). Data come from different sources for *Picea* (Kramer et al., 2018), *Pseudotsuga* (Sillett et al., 2018), *Sequoia* (Sillett et al., 2020), and *Sequoiadendron* (Sillett et al., 2019b).



**Fig. 4.** Variation in tissue densities (dry-mass-tofresh-volume ratios) of four species. Values are means of all trunk bark, trunk sapwood, trunk heartwood, and branch samples with replication varying by species (*Picea* = 42, 33, 33, 115; *Pseudotsuga* = 6, 94, 94, 25; *Sequoia* = 11, 415, 416, 913; and *Sequoiadendron* = 6, 92, 91, and 271, respectively). Branch densities are for pieces 4–40 cm diameter, including bark, sapwood, and heartwood (if any). Brackets within bars indicate how much denser (kg m<sup>-3</sup>) heartwood is than sapwood, on average, per species. Vertical bars indicate 1 *S<sub>E</sub>*. Data come from different sources for *Picea* (Kramer et al., 2018), *Pseudotsuga* (Sillett et al., 2018b), *Sequoia* (Sillett et al., 2015b, 2020), and *Sequoiadendron* (Sillett et al., 2015b, 2019b).

diameter more rapidly than branches and become important habitat elements in primary forest canopies (Sillett and Van Pelt, 2007; Sillett et al., 2018a). Complex, multi-segmented appendages eventually emerge in tall conifers with maximum size depending on stand density (trees ha<sup>-1</sup>). Whereas crowded neighborhoods produce narrow-crowned trees with relatively small appendages, emergent trees with few codominant neighbors develop massive crowns with larger appendages (Kramer et al., 2019). In addition to stimulating trunk reiteration and limb formation, injuries expose trunks and appendages to wood-decay fungi. Old trees thus accumulate structural complexity, wood decay, and arboreal biodiversity until crown collapse and mortality (Van Pelt and Sillett, 2008; Sillett et al., 2018b, 2020).

The four tallest conifers, representing two families (Pinaceae and Cupressaceae), are variously distributed across western North America

(Fig. 1). Picea sitchensis (hereafter Picea) inhabits low-elevation rainforests from Alaska to California (59–40° latitude), extending far inland up river valleys in mountains north of Oregon. Pseudotsuga menziesii (hereafter Pseudotsuga) partly overlaps Picea from British Columbia to California (51–37° latitude), occurring farther inland and at higher elevations (up to 1800 m), not including a more widely distributed interior subspecies (glauca). Sequoia sempervirens (hereafter Sequoia) occurs in coastal forests < 1000 m elevation from southwestern Oregon through California (42–36° latitude), overlapping the southern ranges of Picea and Pseudotsuga. Sequoiadendron giganteum (hereafter Sequoiadendron) is restricted to 150 km<sup>2</sup> of scattered groves at mid-elevations (1400–2400 m) in California's Sierra Nevada (39–36° latitude), overlapping Pseudotsuga in the northernmost grove. Aside from their capacity for reaching extreme tree height, partially overlapping ranges,

#### Table 4

Summary of 169 trees and 27 locations used for developmental analysis of four species. All trees were completely mapped except 9 *Sequoia* in secondary forests. Numbers in parentheses indicate trees completely re-mapped after 3–9 yr. Values show minimum and maximum age, height, *f*-DBH (functional diameter at breast height), DTB (diameter at top of buttress), crown volume, aboveground biomass, leaf mass, aboveground biomass increment, and years of reconstructed growth history among measured trees per species or forest type. Rainfall values reflect long-term annual averages (Parameter-elevations Regressions on Independent Slopes Model, LT-81 at 800-m resolution; PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu).

			Sequoia sempervirens		
Attribute	Picea sitchensis	Pseudotsuga menziesii	(primary forest)	(secondary forest)	Sequoiadendron giganteum
Trees	42 (0)	15 (0)	47 (33)	33 (24)	32 (21)
Age (yr)	94–389	81–624	120-1900	93–173	39–3298
Height (m)	49.8–93.7	53.1-91.6	47.0-115.9	59.4-87.0	24.2-96.5
f-DBH (cm)	71–395	92–429	91–680	95–193	39-814
DTB (cm)	71–248	82–282	74–385	93–175	39–525
Crown volume (m <sup>3</sup> )	398-13,712	306-9432	978–19,251	832–7938	84-21,127
Biomass (Mg)	3.8-86.6	6.3–117.5	3.2-250.5	5.5-26.7	0.3-551.4
Leaf mass (kg)	85-1074	54–712	32-1178	73–794	17-1827
Increment (kg yr <sup>-1</sup> )	36-465	23–286	5–738	101-440	5–647
History (yr)	63-302	65–558	9–918	62–126	15–1078
Locations	5	4	7	6	5
Latitude (°N)	42–48	47–48	38–42	37–42	36–38
Elevation (m)	54-400	100-240	47–327	35–299	1480-2150
Rainfall (cm $yr^{-1}$ )	195–428	297-337	88–201	112–224	88–122

and similar crown development, these species have divergent characteristics controlling tree longevity and rates of aboveground biomass accumulation.

Among extant trees, maximum longevity and size increase from Picea, Pseudotsuga, Sequoia, to Sequoiadendron in the same sequence as their northern latitude range limits, but these are not necessarily the oldest, tallest, or heaviest individuals ever recorded (Table 2). Picea is the shortest-lived with the heaviest living tree reaching 76 m tall, 155 Mg biomass, and 480 yr (Kramer et al., 2018), which is 21 m shorter than the tallest living tree (Chin and Sillett, 2017). The heaviest recorded Pseudotsuga tree died during the 20th century after reaching ~900 yr, > 200 Mg biomass, and nearly 120 m tall—greater than any living tree (Carder, 1995; Van Pelt, 2001; Sillett et al., 2018b). Sequoia is currently the tallest and second heaviest with living trees up to 116 m tall, nearly 400 Mg biomass, and > 2000 yr (Sillett et al., 2020). Sequoiadendron is the heaviest and longest-lived with extant trees exceeding 96 m tall, 500 Mg biomass, and 3000 yr (Sillett et al., 2019b). Emphasizing the family-level difference in longevity is the fact that since the year 2000 (Van Pelt, 2001), most of the 20 largest known Pinaceae (5 of 10 Picea, 6 of 10 Pseudotsuga) have died, whereas all of the 20 largest known Cupressaceae are alive in 2020. Greater longevity allows Sequoia and Sequoiadendron to grow heavier and to develop larger crowns with more leaves.

Evergreen leaves of the four conifers vary in ways affecting productivity and reflecting different strategies for coping with water stress at great height. Branch dissections associated with allometric work and other studies provide sufficient samples per species to compare leaf characteristics (Table 3, Fig. 2). Branch allometry reveals that average 10- and 20-cm-diameter Picea branches carry more leaf mass (3.2 and 10.4 kg) and projected leaf area (15.0 and 51.0 m<sup>2</sup>) than equivalentdiameter branches of Pseudotsuga (2.6 and 8.2 kg, 14.7 and 47.4 m<sup>2</sup>), Sequoia (2.2 and 7.5 kg, 12.8 and 40.7 m<sup>2</sup>), and Sequoiadendron (2.5 and 8.8 kg, 9.0 and 35.4 m<sup>2</sup>; Sillett et al., 2015b, 2018b; Kramer et al., 2018). Picea has the heaviest individual leaves, which become considerably wider with height, and is the only species whose leaf anatomy is controlled primarily by light availability (Chin and Sillett, 2017). Pseudotsuga leaves exhibit the least phenotypic plasticity, remaining relatively long, thin, and low-density (as indexed by leaf-mass-to-area ratio, LMA) despite pronounced within-crown gradients in light availability and water stress (Chin and Sillett, 2019). Sequoia leaves have the most height-associated phenotypic plasticity among the four species (Oldham et al., 2010). Shaded leaves in the lower crown are larger (in silhouette area) than Picea leaves but lower density and thus lighter, whereas treetop leaves are much smaller, denser, and fused with succulent shoots whose stored water helps to sustain both photosynthesis and height growth (Ishii et al., 2014). Sequoiadendron has the smallest and densest leaves, which exhibit strong variation in response to water-stress gradients within tall crowns, including greatly expanded transfusion tissue that may have a heat-sink function promoting stomatal openness (Chin and Sillett, 2016). Such plasticity allows upper crown leaves of Sequoiadendron to function routinely at xylem pressures low enough (<-2 MPa) to damage leaves of Sequoia (Koch et al., 2004; Williams et al., 2017) and sustain global maximum water use rates during summer (Ambrose et al., 2016). While stomatal regulation of gas exchange is a universal feature of tall trees, as shown by height-related changes in leaf carbon isotope composition ( $\delta^{13}$ C,  $^{13}$ C to  $^{12}$ C ratio), Sequoiadendron leaves are the most enriched in <sup>13</sup>C (followed by Sequoia, Pseudotsuga, and Picea), reflecting the fact that Sequoiadendron inhabits forests with a relatively short growing season that become progressively hotter, drier, and prone to lightning-ignited fires (Sillett et al., 2019b).

Fire frequency correlates positively with longevity in the four conifers. On one extreme is short-lived Picea, whose coastal rainforests may not burn for centuries (Gavin et al., 2003a,b), and on the other extreme is long-lived Sequoiadendron, whose montane forests-prior to Euro-American settlement-burned several times per century (Swetnam, 1993). Relative adaptation to fire is reflected by the investment each species makes in bark protecting the trunk (Pausas, 2015; Fig. 3). Bark of all species thickens with tree age, but Picea bark is by far the thinnest and least variable along the height gradient. Pseudotsuga bark is moderately thick, accumulating roughly in proportion to one-tenth the wood radius along the height gradient. Bark of lower trunks is thicker on Sequoia than on Pseudotsuga, but Sequoia bark becomes thinner in proportion to wood radius with increasing height in older trees. Sequoiadendron bark is thickest of all species on the lower trunk, but higher above the ground, bark of Sequoiadendron is thinner than Pseudotsuga and Sequoia in proportion to wood radius. Heavy investments in fibrous, resin-free bark on lower trunks allow Sequoia and Sequoiadendron to survive repeated low to moderate intensity burns scorched but virtually unscathed, whereas young Pseudotsuga and Picea of any age are far more vulnerable to these disturbances. Reaching old age in tall trees, however, requires far more than fire-protective bark.

Resistance to wood decay is a key determinant of longevity in the four conifers. Heartwood durability is correlated with the amount, type, and micro-distribution of extractive compounds toxic to fungi deposited in sapwood during its conversion to heartwood (Taylor et al., 2002). Longevity of the four species increases monotonically with amount of toxins deposited during heartwood formation, adding 27, 37, 42, and 73 kg m<sup>-3</sup>, on average, to sapwood densities in *Picea, Pseudotsuga, Sequoia*,

## Table 5

6

Allometric equations for estimating aboveground tree biomass and biomass increment of four species. Separate equations are provided for *Sequoia* in primary vs. secondary forests. Predictors (V1–V3) are listed from left to right in descending order of importance (MWV = main trunk wood volume, MWVI = main trunk wood volume increment, TVI < 10 = trunk volume increment below 10 m, CrV = crown volume) followed by regression coefficients (*a*-*c*), sample size (*N*), goodness of fit (*R*<sup>2</sup>), root mean square error (RMSE), average of dependent variable (mean), coefficient of variation (CV) computed as RMSE  $\div$  mean, and form of equation. Blank cells indicate where fewer coefficients were needed in these equations. MWVI and TVI < 10 are mean annual increments computed from most recent 5 yr. Data source for each equation is shown, indicating new equations derived from completely mapped trees in this study (Table 4).

Species	Dependent variable	V1	V2	V3	а	b	с	Ν	$R^2$	RMSE	Mean	CV	Form	Source
Picea sitchensis	Biomass (Mg)	MWV (m <sup>3</sup> )			4.16E-01	1.04E+00		42	0.989	2.27E+00	3.47E+01	7%	$aV1^b$	Kramer et al.
Pseudotsuga menziesii	Biomass (Mg)	MWV (m <sup>3</sup> )			4.89E-01	1.01E+00		15	0.996	1.89E+00	3.75E+01	5%	$aV1^b$	Sillett et al.
Sequoia sempervirens (primary forest)	Biomass (Mg)	MWV (m <sup>3</sup> )			4.99E-01	9.75E-01		47	0.995	5.11E+00	7.73E+01	7%	$aV1^b$	Sillett et al. 2020, this study
	Biomass increment	MWVI (m <sup>3</sup> yr <sup>-1</sup> )			5.38E+02			39	0.902	6.04E+01	2.45E+02	25%	aV1	Sillett et al. 2020
	(kg yr <sup>-1</sup> ) Biomass increment (kg yr <sup>-1</sup> )	MWVI ( $m^3 yr^{-1}$ )	$\begin{array}{l} \text{TVI} < 10 \\ \text{(dm}^3  \text{yr}^{-1} \text{)} \end{array}$	CrV (m <sup>3</sup> )	6.27E+02	-5.50E-01	7.56E-03	39	0.938	5.08E+01	2.65E+02	19%	aV1 + bV2 + cV3	Sillett et al. 2020
Sequoia sempervirens	Biomass (Mg)	MWV (m <sup>3</sup> )			3.96E-01	1.02E+00		44	0.987	7.74E-01	8.45E+00	9%	$aV1^b$	Sillett et al. 2019a
(secondary forest)	Biomass increment $(kg vr^{-1})$	MWVI (m <sup>3</sup> yr <sup>-1</sup> )			4.31E+02			24	0.938	2.22E+01	1.91E+02	12%	aV1	Sillett et al. 2019a
Sequoiadendron giganteum	Biomass (Mg)	MWV (m <sup>3</sup> )			3.12E-01	1.05E+00		32	0.975	2.12E+01	1.16E+02	18%	$aV1^b$	Sillett et al.
	Biomass increment	MWVI ( $dm^3 yr^{-1}$ )			2.61E-01	1.14E+00		21	0.949	3.61E+01	2.35E+02	15%	aV1 <sup>b</sup>	Sillett et al. 2019b
	(kg yr <sup>-1</sup> ) Biomass increment (kg yr <sup>-1</sup> )	MWVI (dm <sup>3</sup> yr <sup>-1</sup> )	CrV (m <sup>3</sup> )		2.21E-01	1.14E+00	5.44E-03	21	0.960	3.19E+01	2.35E+02	14%	$aV1^b + cV2$	Sillett et al. 2019b



**Fig. 5.** Logarithmic relationship between age and aboveground biomass for 169 trees of four species. Color lines show best fits per species or forest type ( $R^2 = 0.56$ , 0.77, 0.67, 0.42, and 0.78 for 42 *Picea*, 15 *Pseudotsuga*, 47 *Sequoia* in primary forest, 33 *Sequoia* in secondary forest, and 32 *Sequoiadendron*, respectively).

and Sequoiadendron, respectively (Fig. 4). The reddish extractives may make Cupressaceae heartwood more expensive to produce (i.e., costlier use of photosynthate; Loehle, 1988) than Pinaceae heartwood, contributing to observed differences in growth rates between species (Kramer et al., 2018). Unlike the trend in heartwood investments, longevity of the four species decreases monotonically with increasing tissue densities. The degree to which differences in tissue density contribute to growth variation remains unclear. Picea accumulates crown mass and large-diameter branches much faster than Pseudotsuga (Kramer et al., 2019), whose branches are 81% as dense, while Pseudotsuga deposits 10 kg m<sup>-3</sup> more toxins in heartwood than Picea. Compared to Sequoia, heartwood production is initially delayed in Sequoiadendron, presumably to enable rapid early growth and maintain sufficient sapwood to meet high transpirational demands (Sillett et al., 2015b; Chin and Sillett, 2016). Once deposition begins, however, Sequoiadendron deposits 31 kg m<sup>-3</sup> more toxins in heartwood than Sequoia, explaining why the negative effect of heartwood area on sapwood production of branches is much larger in Sequoiadendron than Sequoia (Kramer et al., 2014).

Our purpose in this study of the four tallest conifers is to reconsider replicated sets of aged and structurally mapped trees in two types of developmental comparisons. First, current sizes and recent growth rates are regressed against tree age to infer rates of development and examine evidence for senescence. Second, each tree's trunk wood volume is reconstructed via dendrochronology in annual increments and combined with allometric equations to produce centuries-long time series of tree size and growth increments. We have three main questions: (1) Does the species investing most in leaves and least in bark protection and heartwood defense-Picea-produce larger appendages during its lifespan than the other conifers at equivalent ages? (2) Is evidence for a negative effect of old age on tree growth weaker in longer-lived species such that relatively short-lived Pinaceae exhibit senescence and longlived Cupressaceae do not? (3) In tall forests, how does long-term development of the four species compare in terms of the time necessary for trees to reach a given size and their aboveground productivity at that size? For Sequoia, we consider primary and mature secondary



**Fig. 6.** Reconstructed growth histories for tallest completely mapped individuals of four species. Once tree age at measurement in 2015 or 2016 is estimated, years are assigned to annual increments by subtraction as far back in time as permitted by dendrochronology (**a**). Each line represents a tree, whose height is reconstructed via trunk measurements and dendrochronology (**b**), aboveground biomass is computed as function of main trunk wood volume (MWV) decremented in annual increments (**c**), and biomass increment is computed as function of main trunk wood volume increment (MWVI or MWV<sub>2</sub> – MWV<sub>1</sub>) via specific equations (**d**, Table 5). Biomass increment. Profile illustrations of four trees (**b**) by Robert Van Pelt are based on photographs combined with orthographic projections of AutoCAD (Autodesk Inc.) models depicting main trunk and all appendages (Sillett et al., 2015b, 2018b; Kramer et al., 2018).

forests separately to compare trees of similar height in different management contexts (i.e., old-growth silvatic mosaic vs. post-logging regeneration).

# 2. Methods

Because this study is an unusual blend, combining extensive results of previous work with unpublished data to compare species development, we generated Table 1 to clarify its organization into figures, tables, and text with linkages to the three main questions. Here we provide an inventory of sampled trees and locations (Table 4), a brief review of standard methods with references to articles containing more detail per species, a summary of biomass allometry (Table 5), illustrated examples of reconstructed growth histories (Fig. 6), and descriptions of new methods.

# 2.1. Tree selection

Among 338 individuals recently used to create allometric equations, we selected for developmental analysis 160 trees receiving a complete set of measurements—trunk footprint analysis from ground to top of buttress (TB), measurements of trunk diameter from TB to treetop at <5-m height intervals, size measurements of all appendages, and coresampling main trunks at regular height intervals-as well as nine partially mapped Sequoia in secondary forest (Table 4). The partially mapped trees, whose appendages were not measured, were 80.3-87.0 m tall and included to increase sample size for developmental comparisons. Excluded from completely mapped Sequoia were five trees from an extreme southern forest < 80 m tall (8, 10, 11, 12, 19 in Sillett et al., 2015b) and two trees (6 and 36 in Sillett et al., 2015b) whose rings could not be crossdated beyond the most recent decade. The 169 trees chosen for intensive study occurred in 27 locations-Olympic rainforests of Washington (36 Picea and 15 Pseudotsuga), coastal forests of California (6 Picea and 80 Sequoia), Sierran forests of California (32 Sequoiadendron)—spanning > 3000 yr age and > 500 Mg biomass (Table 4, Fig. 5). A subset of these trees—33 Sequoia in primary forest, 24 Sequoia in secondary forest, and 21 Sequoiadendron-were completely re-mapped after 3-9 yr for calculation of biomass increments as the annualized increase in aboveground biomass (Sillett et al., 2018a, 2019b, 2020). Most of the Sequoia in secondary forest originated as vegetative sprouts from stumps of trees felled between the mid-19th and early 20th centuries (see Fig. 9 in Sillett et al., 2019a). Primary and secondary Sequoia forests overlapped broadly in terms of latitude, elevation, and annual rainfall (Table 4), and all occurred on productive sites capable of supporting extremely tall trees.

# 2.2. Trunk measurements

Core-sampling trunks allowed direct measurements of bark, sapwood, and heartwood radii (radial distances to outer edge from pith), subsamples for quantifying wood density, and tree-ring samples for dendrochronology. Sampling the 169 trees involved collecting 3071 cores containing > 580 thousand annual rings (13% *Picea*, 8% *Pseudotsuga*, 33% *Sequoia* in primary forest, 6% *Sequoia* in secondary forest, 40% *Sequoiadendron*). After mounting, polishing, scanning, and crossdating wood cores, annual ring widths were measured to the nearest micron as previously described (Carroll et al., 2014). Volumes, areas, and masses of trunk bark, cambium, sapwood, heartwood, and dead components were added to those of appendages, including leaves, to obtain total aboveground quantities per tree. All measurements and size calculations were previously described in detail per species (Kramer et al., 2018; Sillett et al., 2015b, 2018b, 2019b, 2020).

#### 2.3. Appendage measurements

Branches, limbs, and reiterated trunks, including segments (partitioned sections of abnormal appendages; Kramer et al., 2018), were measured for basal and distal diameters as well as height above ground, direction, horizontal distance from trunk, and dead proportions (missing cambium). If > 75% of cambium was missing, appendages were classified as dead. Allometric equations for branches of Pseudotsuga and Sequoiadendron required counting foliar units (repeating units of foliage with 4-cm and 7-cm basal diameters, respectively), and three species (all but Picea) required measurements of linear path length along branches, including forks, to estimate branch quantities. Appendage inventories of the 160 completely mapped trees involved > 55 thousand tape measurements of diameter (24% Picea, 8% Pseudotsuga, 31% Sequoia in primary forest, 11% Sequoia in secondary forest, 26% Sequoiadendron). Small, unbroken branches and reiterated trunks each required a single basal measurement of diameter, whereas broken or forked branch, limb, and trunk segments each required basal and distal measurements, and complex appendages such as large limbs bearing reiterated trunks each required dozens of measurements, including each trunk's branches. All diameter measurements were made at the bark (or wood) surface beneath any epiphytes. In rainforest trees, this often necessitated use of a curved metal bar to lift epiphytic material, including vascular plant roots, temporarily away from bark for accurate tape measurements.

Diameters of heavily buttressed appendages lacking round cross sections were measured using calipers as averages of vertical and horizontal thickness.

#### 2.4. Age estimates

Tree age was estimated as the *y*-intercept of a linear relationship between trunk age and height at 10-m intervals below 50 m. Trunk age was determined by counting annual rings along wood radii from cambium to pith. When pith was not reached on a large trunk, ring widths in remaining wood radius were predicted via height-, species-, and location-specific power functions of wood radius (Kramer et al., 2018; Sillett et al., 2018a,b, 2019a,b, 2020), and number of predicted annual rings was added to crossdated total to estimate trunk age at a given height.

Appendage age was estimated by considering the complete set of trunk ages revealed by core-sampling, regressing trunk age against measurement height, and developing linear and quadratic equations to estimate trunk age at intervening heights on 160 trees. Quadratic equations accounted for nonlinear relationships between trunk age and height, especially above 50 m. Origin heights of live branches and limb segments arising from trunks of known age were then used to estimate trunk ages at these heights via tree-specific equations. Regressing trunk ages against corresponding basal diameters per tree permitted identification of original appendages-those produced by axillary buds of trunk apical meristems-occupying the upper envelope of each tree's appendage size distribution. Excluded from consideration were slowgrowing appendages as well as all those arising epicormically and, therefore, substantially younger than trunks. The number of original appendages selected per tree (1-7) depended on how widely they were distributed across the trunk age gradient. Some trees had few appendages arising from regions of the trunk with known age, as lower trunks were clear of branches or trunk age within the crown could not be reliably estimated. This screening procedure yielded 600 dominant appendages-185 Picea, 52 Pseudotsuga, 172 Sequoia in primary forest, 72 Sequoia in secondary forest, 119 Sequoiadendron-of known age, including 486 branches and 114 limb segments as old as trunks at their heights of origin.

# 2.5. Biomass allometry

High-resolution data from mapped trees were used to develop allometric equations for predicting biomass and biomass increment from wood volume of the main trunk, including reiterated trunks (if any) replacing a broken treetop (Table 5). We used the conic frustum formula to compute main trunk wood volume (MWV) from measured wood radii and lengths, where wood radius was total radius minus bark radius, and length was distance along pith between measurement heights. Ring widths were interpolated for measurement heights between core samples. Uppermost cores and trunk measurements were used to reconstruct tree heights back through time with pith locations determining years of known height and increments between heights computed in proportion to ring-width-to-wood-radius ratio of nearest core samples. At each measurement height below the lowest cores, ring width was calculated by averaging two quantities: (1) ring width of the lowest cores and (2) ring width: wood radius ratio of the lowest cores multiplied by wood radius at measurement height. By sequentially subtracting ring widths from all wood radii, main trunk wood volume (MWV) was calculated at annual intervals, yielding time series of main trunk wood volume increment (MWVI), the best allometric predictor of biomass increment for Cupressaceae (Sillett et al., 2019a,b, 2020).

# 2.6. Recent growth analysis

After age and biomass of each tree were determined, biomass increment was quantified by direct measurements (54 trees completely



**Fig. 7.** Relationships between age and appendage diameter of 136 completely mapped trees (42 *Picea*, 15 *Pseudotsuga*, 47 *Sequoia* in primary forest, 32 *Sequoia dendron*). Color lines are best linear or nonlinear fits with corresponding  $R^2$ . Data from 24 completely mapped *Sequoia* in secondary forest are shown for comparison but not used to develop fits. Appendages include all live and dead branches, limbs, and reiterated trunks receiving direct basal and distal measurements of diameter. Upper scatterplots show tree age versus total number of diameter measurements (**a**), live branch proportion of measurements (**b**), and maximum diameter (**c**). Lower scatterplots show appendage age versus branch or limb basal diameter (**d**). Solid lines are best fits for limbs with corresponding  $R^2$ , and dotted lines are best fits for branches ( $R^2 = 0.66$ , 0.89, 0.76, and 0.94 for *Picea*, *Pseudotsuga*, *Sequoia*, and *Sequoiadendron*, respectively). In *Sequoiadendron* charts, best fits for other species are shown to scale. Note overlapping *Sequoia* and *Sequoiadendron* lines (**c**).

mapped at 4–9 yr intervals), predicted as functions of MWVI (most recent 5-yr mean) and other metrics (Table 5, Cupressaceae), or computed as one-fifth the predicted biomass change over 5 yr  $(aMWV_5^b - aMVW_0^b)$  via allometric equations (Table 5, Pinaceae). Even though 24 *Sequoia* in secondary forest were completely re-mapped after 3 yr, we used MWVI to predict biomass increments for the most recent 5 yr preceding an experiment involving treetop removal (Sillett et al., 2018a). Prior to computing biomass increments, MWV-predicted biomass was adjusted by each tree's measured-to-predicted biomass ratio to accommodate observed tree-to-tree variation in crown structure, wood density, and tissue proportions (Sillett et al., 2015b). For each species or forest type, tree age and leaf mass were considered as

potential predictors of biomass increment in a likelihood framework. Three models (age, leaves, age × leaves) were compared on the basis of AIC<sub>c</sub> and Akaike weights. If the best model had > 90% of Akaike weight, it alone was used to draw inferences. If model selection was ambiguous, evidence for each parameter was examined by calculating the AIC<sub>c</sub>-weight-averaged model from those necessary to achieve cumulative Akaike weight > 90%. Model averaging was used to produce unconditional standard errors (*S*<sub>E</sub>) incorporating uncertainty in parameter estimation as well as model selection (Burnham and Anderson, 2002). JMP (version 13.2.0, SAS Institute Inc.) was used to compute log likelihood and parameter estimates, whereas Excel (version 16.35, Microsoft Inc.) was used to compute AIC<sub>c</sub>, *w*<sub>i</sub>, and model-averaged parameters.



**Fig. 8.** Frequency distributions of appendage diameters along tree age gradient with dead, branch, limb, and trunk appendage types arranged top to bottom within species. Numbers of trees in parentheses correspond to age classes (range in upper right) with Pinaceae divided into three, *Sequoiadendron* divided into four, and *Sequoia* divided into five classes. For *Sequoia*, youngest class is from secondary forest with older classes from primary forest. Within panels, value in upper right is average number of diameter measurements per tree, and rotated number is highest measured diameter (cm).

#### 2.7. Long-term growth analysis

Excluding 8 Sequoiadendron from partially logged Whitaker Forest, 96 trees yielded times series from 2016 or 2015 (Pseudotsuga) to 1901, and 71 trees yielded time series from 1900 to 1800. We also generated 67-yr series (1950-2016) for 23 Sequoia in secondary forest. We considered time series separately to examine long-term growth trends using constant sample size. In addition to computing maximum, average, and minimum biomass increments per species, we converted MWVI to a size-detrended metric of trunk productivity known as the residual wood volume increment (RWVI), which was computed as observed MWVI minus expected MWVI under a null hypothesis of uniform growing conditions, where cambium expands at the mean annual rate and MWVI is proportional to cambium area (Sillett et al., 2015b, 2018b, 2019b). For each series, we combined trees per species and expressed RWVI as % for comparison of growth trends. We also computed RWVI for individual trees as far back in time as possible and then regressed RWVI against tree age to evaluate statistical significance

of age vs. RWVI correlations on an annual basis per species.

#### 2.8. Size threshold analysis

We reconstructed > 45 thousand years of sizes for 169 trees, yielding growth histories up to 126 (*Sequoia* in secondary forest), 302 (*Picea*), 558 (*Pseudotsuga*), 918 (*Sequoia* in primary forest), and 1078 (*Sequoia dendron*) yr per tree (Table 4). For example, the tallest measured individuals of *Picea*, *Pseudotsuga*, *Sequoia*, and *Sequoiadendron* provided growth histories extending back to calendar years 1855, 1669, 1500, and 1318 when these trees were 138, 70, 393, and 643 yr old (Fig. 6a); 76, 44, 100, and 79 m tall (Fig. 6b); 21, 4, 80, and 43 Mg biomass (Fig. 6c); and producing 265, 115, 423, and 187 kg yr<sup>-1</sup> (Fig. 6d), respectively. Such time series supplied the replication per species or forest type (primary or secondary) necessary to compare long-term development as trees enlarge with age.

Time series of age, height, biomass, biomass increment, and height increment were cross-referenced to identify calendar years when trees



**Fig. 9.** Relationships between leaf mass, tree age, and growth increments of 136 completely mapped trees (42 *Picea*, 15 *Pseudotsuga*, 47 *Sequoia* in primary forest, 32 *Sequoiadendron*). Color lines are best fits with corresponding  $R^2$ . Data from 33 *Sequoia* in secondary forest are shown for comparison but not used to develop fits. Upper scatterplots show aboveground biomass increment (most recent 5-yr mean) as linear functions of leaf mass (**a**). Lower scatterplots show leaf mass (**b**) and growth efficiency (**c**) as linear functions of tree age. Growth efficiency is aboveground biomass increment divided by leaf mass. In *Sequoiadendron* charts, best fits for other species are shown to scale. Note *Sequoiadendron* and *Picea* lines overlap *Pseudotsuga* line (**a**).

reached the following size thresholds: 5, 10, 50, 100, 200 Mg biomass; 20, 30, 40, 50, 60, 70, 80, 90, 100, 110 m height. At each biomass threshold, tree age and biomass increment (centered 5-yr mean) were recorded. At each height threshold, tree age, biomass, biomass increment (centered 5-yr mean), and height increment (centered 5-yr mean) were recorded. Height reconstructions were not possible for trees with long-dead or broken upper trunks. For example, the trunk of the oldest *Sequoiadendron* was dead above 62 m where it was 309 cm diameter, so the highest core samples from this tree reached nowhere near the pith. We used average height threshold values per species or forest type to develop equations for predicting tree age, biomass, biomass increment, and height increment as nonlinear functions of tree height. Heartwood proportions of aboveground biomass were also predicted as a power function of tree age per species or forest type.

#### 2.9. Stand simulations

We explored the allometric consequences of species differences by applying equations derived from reconstructed height development to identical tree height distributions. Measured heights of 49 co-dominant trees (67.2–88.5 m tall) in a 1-ha plot of Olympic rainforest with the maximum known *Pseudotsuga* biomass (1289 Mg ha<sup>-1</sup>; Sillett et al. 2018b) were used as the primary basis of species comparison, because trees within this height range were common in all the forests we studied.

Simulated stands of 49 trees were projected 50 yr forward and 50 yr backward in time, changing tree heights by predicted height increments, and using tree height to predict biomass and biomass increments. Tree age was predicted for the initial height distribution, changed in annual increments, and used to predict heartwood proportions of aboveground biomass. Per hectare quantities of biomass, biomass increment, and heartwood increment were computed as 49-tree sums of predicted values per year of simulation.

## 3. Results

# 3.1. Appendage development

When examined against age, diameter measurements exhibited consistent trends with contrasting rates of appendage development across species. The number of diameter measurements increased exponentially with tree age, exhibiting high tree-to-tree variation attributable to trunk reiteration (Fig. 7a). For example, an 850-yr-old *Sequoia* (tree 34 in Sillett et al., 2015b) required nearly 2000 diameter measurements, whereas a 1900-yr-old *Sequoia* (tree 54 in Sillett et al., 2015b) required < 400. The former tree had a highly reiterated crown with 604 trunk and limb segments; the latter was nearly model-conforming with only six. The number of measurements required to map the crown increased with tree age fastest in *Picea*, though

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#### Table 6

Linear models predicting annual growth increments ranked by AIC<sub>c</sub> per species or forest type. Dependent variable is aboveground biomass increment (most recent 5-yr mean). Parameters for tree age (Age) and leaf mass (Leaves) are noted for positive (+) and negative (-) correlations with dependent variable. AIC<sub>c</sub>,  $w_i$ ,  $w_i$  ratio (top-ranked model  $w_i \div$  model  $w_i$ ), goodness of fit, and final (model-averaged) coefficients are listed per model. Coefficient estimates include intercept with 1  $S_E$  in parentheses expressed as %.

Biomass increment (kg yr <sup>-1</sup> )	Model parameters	AIC <sub>c</sub>	Wi	w <sub>i</sub> ratio	$R^2$	Final coefficient	'S
Picea sitchensis (42 trees)	+ Leaves – Age	469	0.9997	1	0.630	Leaves	0.360 (12)
	+ Leaves	485	0.0003	3714	0.419	Age	-0.626 (21)
	– Age	508	0.0000	3.E+08	0.005	Intercept	160 (19)
Pseudotsuga menziesii (15 trees)	+ Leaves – Age	158	0.6360	1	0.736	Leaves	0.339 (24)
	+ Leaves	159	0.3637	2	0.634	Age	–0.0891 (95)
	+ Age	172	0.0004	1771	0.078	Intercept	55.2 (40)
Sequoia sempervirens (47 trees in primary forest)	+ Leaves	567	0.5364	1	0.700	Leaves	0.508 (12)
	+ Leaves – Age	567	0.4636	1	0.713	Age	-0.0346 (131)
	+ Age	612	0.0000	8.E+09	0.208	Intercept	83.3 (33)
Sequoia sempervirens (33 trees in secondary forest)	+ Leaves	269	0.6690	1	0.579	Leaves	0.423 (19)
	+ Leaves + Age	270	0.3309	2	0.604	Age	0.398 (133)
	+ Age	286	0.0001	6.E+03	0.127	Intercept	84.5 (77)
Sequoiadendron giganteum (32 trees)	+ Leaves	376	0.5673	1	0.710	Leaves	0.286 (17)
	+ Leaves – Age	376	0.4327	1	0.728	Age	–0.0220 (127)
	+ Age	402	0.0000	4.E+05	0.347	Intercept	50.9 (48)



**Fig. 10.** Time series (1901–2016 and 1950–2016 upper, 1800–1900 lower) of annual growth increments in four species. Upper *Sequoia* series are shown separately for trees in primary (1901–2016) and secondary (1950–2016) forest. For each series, top panel charts mean biomass increment as black line with maximum and minimum shown as gray lines above and below mean, and bottom panel charts residual wood volume increment (RWVI) of combined trees with faster-than-expected growth highlighted blue and slower-than-expected growth highlighted red. RWVI is expressed as percentage and computed as observed wood volume increment (WVI) minus expected WVI under a null hypothesis of uniform growing conditions, where cambium expands at mean annual rate and WVI is proportional to size. Sample size is constant per series, as indicated by number of trees in upper left. Note different *y*-axis scales between panels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Sequoiadendron < 200 yr often required more than Picea of equivalent age. Two deep-crowned Sequoia in secondary forest required > 500 diameter measurements, far more than any other trees < 200 yr. The proportion of live branch measurements declined with tree age as branches died and were replaced by segmented appendages (Fig. 7b). This decline was steepest in Picea, reaching 60% in 302 yr compared to 742 (Pseudotsuga), 1563 (Sequoia), and 1789 yr (Sequoiadendron). Live branches in the aforementioned highly reiterated, 850-vr-old Sequoia represented only 32% of its appendage diameter measurements, the lowest proportion among 160 completely mapped trees. Maximum appendage diameters increased with tree age, reaching 40 cm centuries sooner in Pinaceae (Picea 350, Pseudotsuga 458 yr) than in Cupressaceae (Sequoia 641, Sequoiadendron 655 yr; Fig. 7c). Whereas Pinaceae had no appendages > 100 cm diameter, Cupressaceae produced 100-cm-diameter appendages in 1600 yr and 200-cm-diameter appendages in 3200 yr (Sequoiadendron only). Among 600 original aged appendages, basal diameter was larger at a given age in limbs than branches, though limb diameter did not exceed branch diameter until the second and third centuries in *Picea* and *Sequoia*, respectively (Fig. 7d). Limbs gained basal diameter much faster in *Picea* than the other species, reaching 60 cm in 375 yr compared to 630 (Pseudotsuga), 702 (Sequoia), and 672 yr (Sequoiadendron).

Diameter distributions varied with tree age similarly for branches, limbs, reiterated trunks, and dead appendages across species (Fig. 8). Small branches (live and dead) dominated appendage populations of Pinaceae < 200 yr and Cupressaceae < 300 yr. Dead appendages > 30cm diameter were rare except on Sequoiadendron > 1000 yr. Live branches > 40 cm diameter were rare regardless of tree age or species. Limbs and reiterated trunks were prevalent within 300 yr on Picea and 400 yr on Pseudotsuga, centuries sooner than on Cupressaceae. Limbs became the largest-diameter appendages on Picea (92 cm), Pseudotsuga (61 cm), and Sequoiadendron (210 cm), but maximum reiterated trunk diameter (142 cm) exceeded maximum limb diameter (107 cm) on Sequoia. Diameter distributions of limbs and reiterated trunks broadened greatly with tree age across species with live branches < 10 cm diameter maintaining prevalence as reiterated trunks produced new sets of branches. Among appendages < 10 cm diameter, limbs were less frequent than trunks, and trunk frequency remained relatively high (>20% of measurements) until tree age exceeded 1000 yr. Even though all Sequoia in secondary forest had intact treetops, within-crown injuries resulted in ~1 subterminal reiterated trunk per tree. These trunks arose directly from the main trunk so were not connected via limbs.

## 3.2. Predicting recent tree growth

Leaf mass was the best individual predictor of aboveground biomass increment across species, explaining 42-71% of recent growth variation (Fig. 9a). The leaf-driven rise in biomass increment was fastest in Sequoia, increasing by 477 (10) g  $yr^{-1}$  per kg leaves compared to 254 (19), 277 (21), and 255 (12) g yr<sup>-1</sup> per kg leaves in *Picea*, *Pseudotsuga*, and Sequoiadendron, respectively (1  $S_E$  in parentheses expressed as %). After accounting for leaf mass, tree age explained additional variation in biomass increment, but the coefficient for age was well-defined only in Picea. Unlike Picea, where the leaf-only model (+Leaves) was 3714 times less likely than the 2-term model (+Leaves - Age), the leaf-only model was just as likely as the 2-term model to explain growth variation of Pseudotsuga, Sequoia, and Sequoiadendron (Table 6). In model-averaged coefficients, the standard error  $(S_E)$  for age was almost as large as (Pseudotsuga) or larger than (Sequoia, Sequoiadendron) its estimate (Table 6). Unlike Picea, biomass increments of Pseudotsuga, Sequoia, and Sequoiadendron increased with tree age, which explained 8-35% of growth variation (Table 6).

Leaf mass increased with tree age in all species (Fig. 9b) faster than biomass increment such that growth efficiency (GE)—aboveground biomass increment per unit leaf mass—declined significantly with tree age (Fig. 9c; 2-tailed P < 0.0001, 0.005, 0.005, and 0.004 for *Picea*,



**Fig. 11.** Decadal summary of statistically significant correlations between tree age and residual wood volume increment (RWVI) in four species. Values are years per decade with positive and negative correlations (2-tailed P < 0.05 and 0.01). Number of trees diminishes back in time per species. *Sequoia* trees from secondary forest and *Sequoiadendron* trees from partially logged forest are excluded. Final decade is incomplete (5–6 yr).

*Pseudotsuga, Sequoia* in primary forest, and *Sequoiadendron*, respectively). The age-related decline in GE was steepest in *Picea*, decreasing by 1.67 (14) g kg<sup>-1</sup> yr<sup>-1</sup> compared to 0.97 (29), 0.31 (33), and 0.01 (31) g kg<sup>-1</sup> yr<sup>-1</sup> in *Pseudotsuga, Sequoia*, and *Sequoiadendron*, respectively (1 *S<sub>E</sub>* in parentheses expressed as %). Some young trees of each species had GE > 0.8 kg kg<sup>-1</sup> yr<sup>-1</sup>, but *Picea, Pseudotsuga*, and all but one *Sequoiadendron* tree > 300 yr had GE < 0.5 kg kg<sup>-1</sup> yr<sup>-1</sup>. Growth efficiency was highest and most variable in *Sequoia* with trees < 500 yr having GE ranging from 0.2 to 1.5 kg kg<sup>-1</sup> yr<sup>-1</sup> and more than half of trees > 500 yr having GE > 0.6 kg kg<sup>-1</sup> yr<sup>-1</sup>. Within the narrow age range (93–173 yr) of secondary *Sequoia* forest, GE was unrelated to tree age (r = -0.204, 2-tailed P = 0.255).

#### 3.3. Long-term growth

Diameter measurements and core-sampling trunks at regular height intervals allowed us to reconstruct centuries of annual increments, providing long-term context for recent growth analysis (Fig. 10, upper panels). Growth increments of 33 *Picea*, 13 *Pseudotsuga*, 51 *Sequoia*, and 22 *Sequoiadendron* trees since 1901 showed family-level differences.



Fig. 12. Reconstructed aboveground biomass development in four species using growth histories of 169 trees (Table 4). Sequoia in primary and secondary forests are summarized separately. Number of trees per class is indicated in color at top of each panel. Values are average age and biomass increment (centered 5-yr mean) during year each tree surpasses biomass threshold (Mg). Vertical bars indicate 1  $S_E$ .

Whereas biomass increments of Pinaceae exhibited no trends (*Picea* =  $-6 \pm 12$ , *Pseudotsuga* =  $1 \pm 7$  kg yr<sup>-1</sup> century<sup>-1</sup>), biomass increments of Cupressaceae increased substantially (*Sequoia* in primary forest =  $137 \pm 21$ , *Sequoia* in secondary forest =  $177 \pm 16$ , *Sequoiadendron* =  $96 \pm 10$  kg yr<sup>-1</sup> per century;  $\pm 95\%$  confidence interval). For combined trees per species, RWVI decreased for Pinaceae (*Picea* =  $-44 \pm 7$ , *Pseudotsuga* =  $-25 \pm 7\%$  yr<sup>-1</sup> per century) and increased for Cupressaceae (*Sequoia* in primary forest =  $44 \pm 10$ , *Sequoia* in secondary forest =  $18 \pm 13$ , *Sequoiadendron* =  $33 \pm 5\%$  yr<sup>-1</sup> per century;  $\pm 95\%$  confidence interval). In other words, Pinaceae produced substantially less wood than expected for their size in recent decades, whereas Cupressaceae produced substantially more.

A second, older time series (1800–1900) allowed us to determine if growth trends observed since 1901 were consistent during the previous century (Fig. 10, lower panels). Compared to 1901–2016, maximum observed biomass increments during the older time series were similar for *Picea* (511 vs. 526 kg yr<sup>-1</sup>) but substantially lower for *Pseudotsuga* (195 vs. 458 kg yr<sup>-1</sup>), *Sequoia* (631 vs. 997 kg yr<sup>-1</sup>), and *Sequoiadendron* (507 vs. 747 kg yr<sup>-1</sup>). Biomass increments of *Picea* and *Sequoiadendron* increased (29 ± 14 and 82 ± 18 kg yr<sup>-1</sup> per century), whereas biomass increments of *Pseudotsuga* and *Sequoia* exhibited no trends (–8 ± 8 and 9 ± 12 kg yr<sup>-1</sup> per century; ± 95% confidence interval). For combined

trees per species, RWVI decreased for *Picea* and *Pseudotsuga* ( $-77 \pm 7$  and  $-36 \pm 8\%$  yr<sup>-1</sup> per century), exhibited no trend for *Sequoia* ( $-9 \pm 8\%$  yr<sup>-1</sup> per century), and increased for *Sequoiadendron* RWVI ( $22 \pm 7\%$  yr<sup>-1</sup> per century;  $\pm 95\%$  confidence interval). Thus, *Picea* and *Pseudotsuga* exhibited declining RWVI during both time series, and *Sequoiadendron* was the only species with increasing biomass increment and RWVI during both time series.

Analysis of long-term growth revealed species differences and changing relationships between tree age and RWVI (Fig. 11). Age vs. RWVI correlations (*r*) of *Picea* were statistically significant (2-tailed P < 0.05) during 81% of years since 1800, but 1996 was the last such year. All *Picea* correlations were negative—older trees produced less wood than expected for their size. In contrast, the other species had far fewer years with statistically significant correlations (26–29%), and at least some recent decades had positive correlations—older trees produced more wood than expected for their size. Before 1900, however, all correlations were negative. For *Sequoia* in secondary forest (results not shown in Fig. 11), 44% of years since 1901 exhibited statistically significant correlations (66% of years) prior to 1953 being negative, no significant correlations (33% of years) after 1987 being positive.



Fig. 13. Reconstructed height development in four species using growth histories of 169 trees (Table 4). Sequoia in primary and secondary forests are summarized separately. Number of trees per class is indicated in color at top of each panel. Values are average age, aboveground biomass, biomass increment (centered 5-yr mean), and height increment (centered 5-yr mean) during year each tree surpasses height threshold (m). Vertical bars indicate 1  $S_E$ .

## 3.4. Size thresholds

The four species reached aboveground biomass thresholds at different tree ages (Fig. 12). *Picea*, *Pseudotsuga*, and *Sequoia* in secondary forest reached 5 and 10 Mg much faster (84–89 and 114–125 yr) than *Sequoia* in primary forest and *Sequoiadendron* (179–236 and 245–293 yr). *Picea* reached 50 Mg much faster (244 yr) than the others (461–760 yr). Among Pinaceae, zero *Picea* and one *Pseudotsuga* tree reached 100 Mg (558 yr). *Sequoia* reached 100 and 200 Mg much faster (791 and 1085 yr) than *Sequoiadendron* (1000 and 1537 yr). Biomass increment increased monotonically with biomass across species. On average, *Picea* grew more rapidly (276 kg yr<sup>-1</sup>) at 50 Mg than all other trees except the largest size class (200 Mg) of *Sequoia* (374 kg yr<sup>-1</sup>) and *Sequoiadendron* (276 kg yr<sup>-1</sup>).

Like biomass thresholds, height thresholds of the four species were reached at different tree ages (Fig. 13). When young, *Pseudotsuga* gained

height faster than the others, reaching 60 m tall in 96  $\pm$  8 yr and 7.1  $\pm$ 0.9 Mg biomass, followed by Sequoia in secondary forest (106  $\pm$  3 yr and  $8.5\pm0.5$  Mg), Picea (121  $\pm$  7 yr and 11.3  $\pm$  0.9 Mg), Sequoia in primary forest (234  $\pm$  37 yr and 8.8  $\pm$  1.3 Mg), and Sequoiadendron (265  $\pm$  51 yr and 13.7  $\pm$  1.6 Mg; mean  $\pm$  1 S<sub>E</sub>). *Picea* reached 90 m tall faster (247  $\pm$ 30 yr) than Pseudotsuga (304 yr, 1 tree only), Sequoia in primary forest  $(492 \pm 41 \text{ yr})$ , and Sequoiadendron (1018 yr, 1 tree only), though an 87m-tall Sequoia in secondary forest was only 132 yr old with a 51  $\pm$  11 cm  $yr^{-1}$  height increment (most recent 5-yr mean  $\pm 1 S_E$ ). Sequoia  $\ge 100$  m tall and *Sequoiadendron*  $\geq$  80 m tall were the only trees approaching or exceeding 100 Mg biomass, except for the largest Pseudotsuga (2015 biomass = 117 Mg, height = 89.5 m), whose broken upper trunk precluded height reconstruction. Biomass increment increased with tree height in three species, but Picea exhibited a unimodal trend with 70-mtall trees growing fastest (199 kg yr<sup>-1</sup>) and 90-m-tall trees growing at nearly the same rate (112 kg yr<sup>-1</sup>) as 40-m-tall trees (111 kg yr<sup>-1</sup>).

*Pseudotsuga* had the lowest maximum biomass increment (138 kg yr<sup>-1</sup> at 90 m), but trees ≤ 30 m tall grew faster than *Picea*, trees ≤ 50 m tall grew faster than *Sequoia* in primary forest, and trees ≤ 40 m tall grew faster than *Sequoiadendron* of similar heights. Between 60 and 80 m tall, *Sequoia* in secondary forest gained biomass fastest (189–267 kg yr<sup>-1</sup>). Cupressaceae ≥ 80 m tall had higher average biomass increments (>200 kg yr<sup>-1</sup>) than Pinaceae of any height. *Sequoia* ≥ 100 m tall produced more annual biomass, on average, than all other trees (296–369 kg yr<sup>-1</sup>) except a single *Sequoiadendron* tree producing 374 kg yr<sup>-1</sup> at 90 m tall. Height increments declined nonlinearly with increasing tree height across species with *Sequoia* in secondary forest outgrowing all trees ≥ 50 m tall. *Sequoiadendron* ≥ 70 m tall gained height much more slowly than other trees at similar heights.

## 3.5. Simulated development

The 10-m height thresholds provided sufficient replication to model tree age, biomass, biomass increment, and height increment as nonlinear functions of tree height per species or forest type (Table 7). Tree age and aboveground biomass increased as power functions of tree height in all four species. Biomass increments of Pseudotsuga, Sequoia, and Sequoiadendron also increased as power functions of tree height, but a quadratic function was necessary to accommodate the unimodal distribution observed in Picea (Fig. 13). Height increments were best modeled as negative exponential functions of tree height. We modeled aboveground attributes of single-species plots containing the same 49tree height distribution. Predicted tree age (yr) averaged 143 (Sequoia in secondary forest), 207 (Picea), 219 (Pseudotsuga), 436 (Sequoia in primary forest), and 803 (Sequoiadendron; Fig. 14a). Predicted tree biomass (Mg) averaged 19 (Sequoia in secondary forest), 21 (Pseudotsuga), 28 (Picea), 36 (Sequoia in primary forest), and 81 (Sequoia*dendron*; Fig. 14b). Predicted tree biomass increment (kg  $vr^{-1}$ ) averaged 124 (Pseudotsuga), 158 (Picea), 197 (Sequoia in primary forest), 269 (Sequoia in secondary forest), and 271 (Sequoiadendron; Fig. 14c).

# Table 7

Predicted tree height increment (cm yr<sup>-1</sup>) averaged 6 (*Sequoiadendron*), 14 (*Picea*), 16 (*Pseudotsuga*), 17 (*Sequoia* in primary forest), and 34 (*Sequoia* in secondary forest; Fig. 14d).

At the beginning of the simulation (-50 yr), Pinaceae had broader height distributions than Cupressaceae, but the opposite was true 100 yr later (Fig. 14e). Spanning the 100-yr simulation, rapid height growth resulted in the greatest tree height range for Sequoia in secondary forest (60 m), followed by Pseudotsuga (42 m), Picea (40 m), Sequoia in primary forest (39 m), and Sequoiadendron (29 m). High tree biomass increments allowed the Sequoiadendron plot to accumulate the most additional aboveground biomass (1328 Mg ha<sup>-1</sup>) over 100 yr, followed by Sequoia in secondary forest (1310 Mg ha<sup>-1</sup>), Sequoia in primary forest (967 Mg  $ha^{-1}$ ), Picea (768 Mg  $ha^{-1}$ ), and Pseudotsuga (605 Mg  $ha^{-1}$ ; Fig. 14f). Plot biomass increments changed dramatically during the simulation. After 100 yr, Picea lost 1.1 Mg ha<sup>-1</sup> yr<sup>-1</sup>, Pseudotsuga gained 0.6 Mg ha<sup>-1</sup> yr<sup>-1</sup>, Sequoiadendron gained 2.0 Mg ha<sup>-1</sup> yr<sup>-1</sup>, Sequoia in primary forest gained 4.0 Mg  $ha^{-1}$  yr<sup>-1</sup>, and *Sequoia* in secondary forest gained 7.6 Mg ha<sup>-1</sup> yr<sup>-1</sup> (Fig. 14g). Finally, by predicting the heartwood proportion of tree biomass as a power function of tree age per species or forest type (Table 7), we modeled heartwood increments over 100 yr. Whereas the Picea plot heartwood increment peaked early in the simulation (-31 yr) and lost 0.4 Mg ha<sup>-1</sup> yr<sup>-1</sup> by the end (+50 yr), plot heartwood increments increased monotonically in the other plots and were 0.9 (Pseudotsuga), 1.7 (Sequoiadendron), 3.0 (Sequoia in primary forest), and 6.7 (Sequoia in secondary forest) Mg ha<sup>-1</sup> yr<sup>-1</sup> higher after 100 yr (Fig. 14h).

#### 4. Discussion

Forests with trees over 90 m tall are rare not only because few species have the capacity to attain extreme height, but also because the vast majority of tall forests were logged, and even within reserves the tallest trees are restricted to groves with plentiful soil resources plus adequate protection from wind. In tall forests managed for long-term carbon

Allometric equations used to simulate tree performance based on reconstructed height development in four species. Predictors (V) are tree height and age. Samples (*N*) are 10-m-height threshold averages (Fig. 13) from 20 to 110 m (*Sequoia* in primary forest), 20–80 m (*Sequoia* in secondary forest), 20–90 m (other species), or trees (heartwood as % biomass). For each tree-level dependent variable, regression coefficients (a-c), sample size (*N*), goodness of fit ( $R^2$ ), root mean square error (RMSE), sample average (mean), coefficient of variation (CV) computed as RMSE  $\div$  mean, and form of equation are listed. Blank cells indicate where fewer coefficients were needed.

Species	Dependent variable	V	а	b	с	Ν	$R^2$	RMSE	Mean	CV	Form
Picea sitchensis	Age (yr) Biomass (Mg) Biomass increment (kg yr <sup>-1</sup> ) Height increment (cm yr <sup>-1</sup> )	Height (m) Height (m) Height (m) Height (m)	1.24E-01 1.24E-04 -8.11E-02 -5.74E+01	1.69E+00 2.81E+00 1.05E+01 2.66E+02	-1.63E+02	8 8 8 8	0.991 0.991 0.931 0.983	8.14E+00 1.42E+00 1.64E+01 4.20E+00	1.22E+02 1.35E+01 1.28E+02 4.18E+01	7% 10% 13% 10%	$aV^b$ $aV^b$ $aV^2 + bV + c$ aLN(V) + b
Pseudotsuga menziesii	Heartwood (% biomass) Age (yr)	Age (yr) Height (m)	2.52E+01 6.34E-03	1.94E-01 2.38E+00		41 8	0.725 0.980	3.35E+00 1.45E+01	7.23E+01 1.19E+02	5% 12%	$aV^b$ $aV^b$
	Biomass (Mg) Biomass increment (kg yr <sup>-1</sup> ) Height increment (cm yr <sup>-1</sup> ) Heartwood (% biomasc)	Height (m) Height (m) Height (m)	2.49E-06 1.25E+01 -6.20E+01	3.63E+00 5.24E-01 2.87E+02		8 8 8	0.994 0.878 0.984	9.51E-01 1.03E+01 4.39E+00	1.00E+01 9.92E+01 4.52E+01	9% 10% 10%	$aV^b$ $aV^b$ aLN(V) + b $aV^b$
Sequoia sempervirens (primary forest)	Age (yr) Biomass (Mg) Biomass increment (kg yr <sup>-1</sup> ) Height increment (cm yr <sup>-1</sup> )	Height (m) Height (m) Height (m)	1.05E-01 1.59E-07 2.86E-02 -2.40E+01	1.90E+00 4.38E+00 2.02E+00 1.22E+02		10 10 10 10	0.988 0.966 0.991 0.925	3.01E+00 3.01E+01 9.66E+00 1.30E+01 4.02E+00	3.46E+02 3.61E+01 1.54E+02 2.45E+01	9% 27% 8% 16%	$aV^{b}$ $aV^{b}$ $aV^{b}$ aI N(V) + b
	Heartwood (% biomass)	Age (yr)	1.90E+01	2.00E-01		45	0.740	5.19E+00	6.69E+01	8%	$aV^b$
Sequoia sempervirens (secondary torest)	Age (yr) Biomass (Mg) Biomass increment (kg yr <sup>-1</sup> ) Height increment (cm yr <sup>-1</sup> ) Heartwood (% biomass)	Height (m) Height (m) Height (m) Height (m) Age (yr)	6.60E-01 5.59E-05 7.50E-01 -4.58E+01 1.15E+01	1.23E+00 2.90E+00 1.34E+00 2.35E+02 3.12E-01		7 7 7 7 33	0.995 0.999 0.997 0.960 0.276	3.26E+00 2.80E-01 5.12E+00 5.04E+00 4.84E+00	8.19E+01 6.84E+00 1.49E+02 6.01E+01 5.26E+01	4% 4% 3% 8% 9%	$aV^{b}$ $aV^{b}$ aLN(V) + b $aV^{b}$
Sequoiadendron giganteum	Age (yr) Biomass (Mg) Biomass increment (kg yr <sup>-1</sup> ) Height increment (cm yr <sup>-1</sup> )	Height (m) Height (m) Height (m) Height (m)	5.51E-03 1.20E-06 2.77E-02 -3.36E+01	2.71E+00 4.11E+00 2.10E+00 1.53E+02		8 8 8 8	0.943 0.970 0.963 0.923	1.00E+02 8.91E+00 2.44E+01 5.43E+00	4.13E+02 3.60E+01 1.49E+02 2.19E+01	24% 25% 16% 25%	$egin{array}{l} a {f V}^b \ a {f V}^b \ a {f V}^b \ a {f V}^b \ a {f N}({f V}) + b \end{array}$
	Heartwood (% biomass)	Age (yr)	1.97E + 01	1.84E - 01		29	0.893	4.57E+00	6.67E+01	7%	$aV^b$



Fig. 14. Equations derived from reconstructed height development (Table 7) are used to simulate temporal changes in 1-ha plots with identical tree heights (67.2-88.5 m) and stand densities  $(49 \text{ trees ha}^{-1})$  per species or forest type. Height is used to predict age (a), aboveground biomass (b), biomass increment (c), and height increment (d) per tree. Simulations begin (0 yr, vertical gray line) with identical tree height distributions and are projected 50 yr forward and 50 yr backward in time, changing by predicted annual increments with tallest, average, and shortest trees shown as thin (tallest, shortest) or thick (average) lines color-coded by species or forest type (e). Plot biomass is 49-tree sum of predicted aboveground biomass (0 yr) increased (to right) and decreased (to left) by height-predicted biomass increments (f). Plot biomass increments are annual per hectare changes in aboveground biomass (g). Plot heartwood increments are annual per hectare changes in aboveground heartwood mass, where heartwood mass per tree is computed as the product of biomass and the agepredicted heartwood proportion of biomass (h).

sequestration and biodiversity conservation, results from this study of four conifers establish reasonable expectations for developmental rates. Examination of 169 trees 24–116 m tall and 39–3298 yr old provides the basis for two types of comparisons. The first type relies on intensive measurements to quantify aboveground attributes—tree age, crown structure, leaf mass, biomass increment, growth efficiency—for recent growth analysis. The second type utilizes long-term reconstructions of tree size and growth increments, though photosynthetic capacity cannot be reliably reconstructed due to uncertainty regarding temporal changes in crown volume (i.e., strongest allometric predictor of leaf quantities) and the fact that leaf estimates based on the best allometric equations have substantially larger errors (RMSE  $\div$  mean = 17–24%) than those for completely mapped trees (RMSE  $\div$  mean = 4–8%; Kramer et al.,

2018; Sillett et al., 2018b, 2019b, 2020). Small sample size and restricted geographic coverage (i.e., 15 trees from Olympic rainforests) limit inferences pertaining to *Pseudotsuga*, but species comparisons are strengthened by the fact that 36 of 42 *Picea* trees co-occur with *Pseudotsuga* in Olympic rainforests and the remainder co-occur with *Pseudotsuga* and *Sequoia* in California.

# 4.1. Crown ontogeny

The appendage population of a conifer includes young branches arising from the treetop and epicormically throughout the crown as well as original branches—and limbs derived from them via trunk reiteration—that are as old as the trunk at their heights of origin. Thus,



Fig. 15. Epiphytes thrive on large-diameter appendages of four species. (a) This 56-cm-diameter limb of 318-vr-old *Picea* extends 15 m from trunk, supporting lush mat of vascular plants (Polypodium glycyrrhiza, Selaginella oregana) as well as mosses, liverworts, and lichens. (b) This 46-cm-diameter branch of 615-vr-old Pseudotsuga consists of 7 segments giving rise to 13 branches requiring 27 tape measurements of diameter. Extending 11 m from trunk, most of its bark is thickly covered by epiphytes, including S. oregana and several mosses. (c) This 107-cm-diameter limb of 1100-yr-old Sequoia gives rise to multiple reiterated trunks and supports well-developed Polypodium scouleri fern mat interspersed with shrubs (Vaccinium ovatum), mosses, liverworts, and lichens. (d) This 177cm-diameter limb of 2400-yr-old Sequoiadendron, whose farthest branches extend nearly 16 m from trunk, supports two woody species (Pinus lambertiana on right with red arrows, Ribes nevadense on left with yellow asterisk at base) rooted in decaying heartwood. Note two epiphytic pines, one live and one dead (leaning to right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

appendages in a tall, deep-crowned conifer can span an age range nearly as old as the tree itself. The capacity of *Picea* to produce limbs almost 1 m diameter in 300 yr-larger than any observed on Pseudotsuga and as large as any observed on Sequoia twice as old and Sequoiadendron three times as old (Fig. 7)—is made more remarkable by the fact that Picea has the highest tissue densities (Fig. 4). While more expensive to produce, higher wood density makes Picea branches stronger with greater hydraulic safety margins (Gelder et al., 2006), allowing tall crowns to carry more leaves than other conifers at equivalent ages. By investing heavily in construction of high-density wood (Fig. 4), Picea branches can not only support high photosynthetic capacity, but also maintain large surface areas for foliar water uptake (Kerhoulas et al., 2020; Schreel and Steppe, 2020). Unlike the situation in tropical angiosperms (Meinzer et al., 2008), Picea is able to offset the increased carbon and hydraulic costs of denser wood relative to co-occurring conifers by producing deep crowns of sturdy branches displaying massive quantities of leaves. Its ability to develop ecologically significant appendage diameters far more quickly than other conifers gives Picea high conservation value in rainforest canopies, where epiphytes abound (Fig. 15a).

Living up to twice as long in Olympic rainforests, *Pseudotsuga* develops appendages almost as large as those of *Picea* (Figs. 7c,d, 8). Gaining height more quickly than *Picea* when young, the lower density of *Pseudotsuga* wood makes it more vulnerable to injury as indicated by a higher frequency of reiterated trunks and limbs in trees < 200 yr (Fig. 8). Compared to *Picea*, however, greater investment in heartwood defense (Fig. 4) increases structural integrity of damaged *Pseudotsuga* trunks, allowing these trees to maintain vigorous crowns via epicormic renewal of foliage (Ishii and Ford, 2001; Ishii et al., 2002; Van Pelt and Sillett, 2008) long after tops are broken by extratropical cyclones (Mass and Dotson, 2010). Wood decay eventually leads to structural collapse of rainforest giants, but not before their crowns have supported lush epiphyte communities (Fig. 15b), including angiosperms and conifers (Sillett and Neitlich, 1996; Sillett et al., 2018b).

Superior decay resistance, the ability to survive severe fire, and consequently greater longevity allow *Sequoia* and *Sequoiadendron* eventually to produce much larger appendages than Pinaceae. Nearly a millennium is required to grow limbs > 1 m diameter (Fig. 7c,d), and in Sequoia rainforests these often become colonized by the fern Polypodium scouleri (Sillett and Bailey, 2003), whose mats develop arboreal soils containing acidic residues that are extremely resistant to decomposition (Enloe et al., 2006, 2010). Layers of this material up to 1 m deep accumulate on limbs and in crotches between reiterated trunks, storing water and supporting considerable biodiversity (Fig. 15c; Spickler et al., 2006; Sillett and Van Pelt, 2007). Large crowns of both redwoods contain enormous appendages (Sillett et al., 2015b), but substantially higher investment in heartwood defense (Fig. 4) may promote the extreme longevity that enables Sequoiadendron to retain appendages approaching or exceeding 2 m diameter even if all or part of them is dead (Figs. 8, 15d). High water-holding capacity of slowly decaying heartwood (Sillett and Van Pelt, 2007) permits facultative epiphytism in Cupressaceae to reach its ultimate expression-colonization of the forest canopy by sexually reproducing trees and shrubs normally restricted to terrestrial substrates (Ishii et al., 2018; Sillett et al., 2020).

#### 4.2. Senescence

Minimum investment in heartwood defense combined with maximum investment in leaves and sturdiness may enable Picea to gain biomass more rapidly than other tall conifers in primary forests (Fig. 5). This growth maximization strategy (Buckley and Roberts, 2006)similar to that observed in the tallest angiosperm (Koch et al., 2015)apparently comes at the expense of tree longevity. Among the four tallest conifers, only Picea exhibits strong evidence for an age-related decline in biomass increment after accounting for tree-level variation in leaf mass (Table 6). Growth efficiency (GE)-aboveground biomass increment per unit leaf mass-declines with tree age in all four conifers, and this decline is steepest in Picea followed by Pseudotsuga, Sequoia, and Sequoiadendron in the same sequence as tree longevity (Fig. 9c). In Sequoia and probably Sequoiadendron, the age-related GE decline is attributable to an increasing investment in heartwood defense as trees enlarge with age (Sillett et al., 2020). In Picea and Pseudotsuga, however, declining GE may be more related to increasing respiratory

costs—especially resin production—associated with combating insects and pathogenic fungi as injuries accumulate with age (Franceschi et al., 2005; Sillett et al., 2018b; Vázquez-González et al., 2020). We suspect that biomass increment increases more rapidly with increasing leaf mass (Fig. 9a) and GE is higher as trees enlarge with age (Fig. 9c) in *Sequoia* than other tall conifers because extreme phenotypic plasticity of its foliage (Chin and Sillett, 2019; Fig. 2) augments crown optimization during development (Coomes et al., 2012; Van Pelt et al., 2016). Perhaps more than any other conifer, *Sequoia* foliage acclimates to the local environment by changing traits related to both drought tolerance and photosynthesis (Mullin et al., 2009; Oldham et al., 2010; Ishii et al., 2014).

Long-term trends reinforce results from recent growth analysis pertaining to tree senescence. Whereas both Pinaceae exhibit declining residual wood volume increment (RWVI) across two consecutive centuries, this size-detrended growth metric increases in Cupressaceae across one (Sequoia) or both (Sequoiadendron) centuries (Fig. 10). Negative tree age vs. RWVI correlations signify years when younger trees are growing unusually fast—and gaining height rapidly—as well as vears when older trees are growing unusually slowly-and perhaps recovering from fire (Van Pelt et al., 2016; Sillett et al., 2019b). Consistently negative correlations in Picea, however, are unrelated to fire as it does not survive these rare events in Olympic rainforests (Agee, 1993), and no charcoal or fire scars are evident on any Picea we measured. Unlike other conifers, trunks of older Picea consistently produce less wood than expected for their size (Fig. 11). Whereas adequate sample size makes this a robust result for Picea, it is not the case for Pseudotsuga, whose five decades of predominantly negative tree age vs. RWVI correlations (1850–1900) are attributable to rapid growth of three individuals < 100 yr old in one location (plot 2 in Sillett et al., 2018b). Changing tree age vs. RWVI correlations-negative during 19th century and positive during 20th century-for Sequoia and Sequoiadendron extend results from a previous study using many of the same trees (Sillett et al., 2015b). After more than a century of fire suppression, crowns of older redwoods we studied may be relatively expanded with high photosynthetic capacity and thus growing faster than expected for their trunk size. Unusually high growth increments and positive age vs. RWVI correlations in recent decades until severe drought (2012-2016; Figs. 10, 11) may also reflect older (and larger) trees responding disproportionately to CO<sub>2</sub> fertilization, increasing water use efficiency, or other climate change effects (Soh et al., 2019; Haverd et al., 2020; Kim et al., 2020; Scheiter et al., 2020). More work is needed to understand these possibilities in tall conifers as well as their vulnerability to hotter drought (Allen et al., 2015; Stephenson et al., 2018).

Overall, strength of evidence for senescence diminishes sequentially with lifespan such that Pinaceae > Cupressaceae, and Picea > Pseu*dotsuga* > *Sequoia* > *Sequoiadendron*. Increasing growth increments over centuries (Fig. 10) despite the fact that GE declines with age (Fig. 9c), no evidence for negative effects of age on recent biomass increments (Table 6), and positive tree age vs. RWVI correlations in recent decades (Fig. 11) are all testaments to the incredible rejuvenating capacity of Cupressaceae allowing them to maintain enormous leafy crowns for millennia. But continuously increasing growth is fallacious, because biomass increments fluctuate wildly in response to disturbances during individual lives (Fig. 6d), and all trees eventually senesce if they do not die suddenly (Sheil et al., 2017; Munné-Bosch, 2020). Sequoiadendron is no exception—the oldest individual (3298  $\pm$  53 yr; Quammen and Nichols, 2012) has 153% as much leaf mass yet produces only 83% as much aboveground biomass annually as the tallest individual (Fig. 6), which grows in the same forest and is less than half its age (Sillett et al., 2019b). Despite being inevitable, tree senescence does not preclude sustained high levels of biomass production-primary tropical rainforests and conifer-dominated forests can both accumulate > 10 Mg  $ha^{-1} vr^{-1}$  (Balian and Naiman, 2005; Kho et al., 2013; Sillett et al., 2020).

#### 4.3. Comparative development of tall conifers

In all four species, biomass increment increases with biomass such that the heaviest trees tend to be among the fastest growing (Fig. 12). High-biomass trees in tall forests are often emergent, while smaller trees have crowns shaded by taller neighbors unless standing near canopy gaps. Accordingly, Sequoia in primary forest are much older and slowergrowing than similar-size trees in secondary forest (Figs. 12, 13); they develop with relatively low light availability as crowns rise through a tall canopy. Like Sequoia in secondary forest that regenerate after logging, the Pseudotsuga we measured in Olympic rainforests established after stand-replacing disturbances, in this case high-severity fires (Huff, 1995). Post-fire cohorts of Pseudotsuga in these forests gain height most rapidly-reaching 60 m tall in < 100 yr-with average biomass increments increasing until trees are 50 m tall and then stabilizing at just over 100 kg yr<sup>-1</sup> as trees approach 90 m tall (Fig. 13). In valley bottom rainforests periodically reworked by alluvial processes (Latterell et al., 2006; Van Pelt et al., 2006), young Picea gain height almost as rapidly as *Pseudotsuga*, but average biomass increment peaks at  $\sim 200 \text{ kg yr}^{-1}$ when *Picea* are 70 m tall and < 200 yr old, declining thereafter as trees senesce (Fig. 13). Unlike Pinaceae, biomass increments of Cupressaceae in primary forests increase steadily with tree height such that individuals  $\geq$  90 m tall are faster growing (averaging > 250 kg yr<sup>-1</sup>) than all but the tallest Sequoia in secondary forest (Fig. 13), whose maximum biomass increments can exceed 400 kg yr<sup>-1</sup> (e.g., 3 trees 125–141 yr old and 60-80 m tall from 1999 to 2014; Fig. 10). Since 1800, only 3 Picea (130-241 yr, 67-75 m), 8 Sequoia (649-1900 yr, 86-113 m), and 3 Sequoiadendron (1157-3293 yr, 75-96 m) exhibit biomass increments > 500 kg yr<sup>-1</sup> (Fig. 10). Globally, biomass increments approaching or exceeding 1000 kg  $yr^{-1}$  are known only for three exceptional individuals-Sequoia (790 yr, 98 m; Sillett et al., 2020), Sequoiadendron (1260 yr, 87 m; Sillett et al., 2019b), and E. regnans (480 yr, 79 m; Sillett et al., 2015a). When small, Sequoia and Sequoiadendron in primary forests gain height and biomass at similar rates, but beyond 10 Mg biomass and 60 m height, Sequoiadendron grows much more slowly such that trees are centuries older at equivalent sizes (Figs. 12, 13).

As larger trees gain dominance and occupy increasing growing space during stand development, well-illuminated leaves are distributed among a declining number of tall individuals, some of whose crowns become emergent after co-dominant neighbors die (Van Pelt et al., 2016). Mortality of large trees contributes to declining biomass accumulation in primary forests (Xu et al., 2012), and productivity of these forests is ultimately constrained by a low density of large trees (Ligot et al., 2018). Since large, old trees produce less aboveground biomass per unit leaf mass than small, young trees (i.e., GE declines as trees enlarge with age; Sillett et al., 2020; Fig. 9c), structural differences related to tree size and spacing lead to large growth variation among forests with similar quantities of leaves that is unrelated to species composition. In tagged Sequoia populations of primary rainforest, for example, two 1-ha plots with a similar leaf area index (LAI = 10 vs. 12) have dramatically different biomass increments (9.7 vs. 18.5 Mg  $ha^{-1}$  $yr^{-1}$ ; Sillett et al., 2020). The less productive plot has fewer Sequoia overall (69 vs. 264 trees ha<sup>-1</sup>) but far more emergent trees > 100 Mgbiomass (19 vs. 5 ha<sup>-1</sup>) that contribute 63% of the biomass increment (GE = 0.50), while the latter has far more midsize trees (5–50 Mg biomass, 10 vs. 63  $ha^{-1}$ ) that contribute 70% of the biomass increment (GE = 1.02). The most productive tall forest known is secondary-logged in 1858-with individual Sequoia up to 82 m tall and 28 Mg biomass by 2017 (Sillett et al., 2019a). From 1983 to 1995, biomass increment of this tagged Sequoia population (LAI = 19) averaged 22.9 Mg  $ha^{-1}$  yr<sup>-1</sup> with 40% contributed by trees 5–10 Mg biomass (114 ha<sup>-1</sup>; GE = 0.80) and 52% contributed by trees > 10 Mg biomass (67)  $ha^{-1}$ ; GE = 0.75; Iberle et al., 2020). Regardless of species, biomass increment (Mg ha<sup>-1</sup> yr<sup>-1</sup>)—not standing biomass (Mg ha<sup>-1</sup>)—of tall forests may be greatest in stands with a moderate density of midsize trees and few, if any, giants.

## 4.4. Insights from stand simulations

Reliable estimates of biomass increments are based on repeated measurements of tree populations within fixed-area plots, making it difficult to determine how recent rates compare to those occurring far earlier during stand development, or how rates will change as older trees senesce. By cross-referencing time series of tree age, height, biomass, biomass increment, and height increment, our threshold analysis identifies years when trees first reach a given height as well as biomass and growth rates at that height, providing repeated snapshots of stature and performance spanning decades to centuries per individual. Aggregating these results by species and forest type permits stand development to be simulated across a wide tree size range via applying allometric equations to plot inventories (Table 7). Our simulations evaluate identical sets of tree heights and constant tree densities in single-species stands. Ignoring species interactions, tree mortality, and treetop-damaging disturbances, these simulations do not model real forests but rather explore allometric consequences of divergent growth observed in the reconstructed height development of 169 trees (Table 3, Fig. 13). Extending 50 yr forward and backward in time from initial conditions, simulations reveal tree ages, sizes, and growth increments expected during a century of development in tall, undamaged, stands of moderate density (49 trees  $ha^{-1}$ ) per species.

Initial tree ages for *Picea* and *Pseudotsuga* are similar with *Picea* averaging 12 yr younger, 7 Mg larger, and 34 kg yr<sup>-1</sup> faster growing (Fig. 14a-c). In 1-ha plots with 49 such trees, aboveground biomass, biomass increment, and heartwood increment of the *Picea* simulation are 333 Mg ha<sup>-1</sup>, 1.7 Mg ha<sup>-1</sup> yr<sup>-1</sup>, and 2.1 Mg ha<sup>-1</sup> yr<sup>-1</sup> higher, respectively, than the *Pseudotsuga* simulation (Fig. 14f-h), which has about half as many leaves (LAI = 6 vs. 11, RMSE  $\div$  mean = 55 vs. 52%). Ample growing space is available in both simulations for additional trees. For example, tree height allometry (Table 7) predicts much higher biomass increments (*Picea* = 23.4 ± 3.0, *Pseudotsuga* = 15.0 ± 1.5 Mg ha<sup>-1</sup> yr<sup>-1</sup>) for a 1-ha plot of Olympic rainforest containing 135 trees 37–84 m tall (plot 2 in Sillett et al., 2018b). Unlike *Pseudotsuga*, biomass and heartwood increments decline during the *Picea* simulation, because senescence begins much earlier and affects all trees by the end (+50 yr), when the oldest *Pseudotsuga* (327 yr) is only middle-aged. Even though

heartwood proportions of aboveground biomass increase with tree age across species (Table 7), a relatively high heartwood increment (~6 Mg ha<sup>-1</sup> yr<sup>-1</sup>) becomes increasingly unrealistic by the end of the *Picea* simulation, as heartwood decay is extensive in trunks of rainforest *Picea* > 200 yr old (Kimmey, 1956; Hennon, 1995; Kramer et al., 2018). Mass losses to decay may negate heartwood increments of tall *Picea* as suspected in tall *E. regnans*, whose heartwood is also poorly defended against fungi (Sillett et al., 2015a).

In primary forest, initial tree ages for *Sequoia* are 2–3 centuries older than *Picea* and *Pseudotsuga* with aboveground biomass and biomass increment 0–25 Mg and 151–281 kg yr<sup>-1</sup> higher, respectively, per tree for *Sequoia* (Fig. 14**a-c**). A 1-ha plot with 49 such trees would hold less than half the aboveground biomass (1768 Mg ha<sup>-1</sup>) and leaves (LAI = 9; RMSE  $\div$  mean = 43%) as the global maximum (Sillett et al., 2020), implying that sufficient growing space for at least twice as many trees of similar size may exist under favorable circumstances. If applied to the other height distribution (135 trees 34–84 m tall, plot 2 in Sillett et al., 2018b), tree height allometry (Table 7) predicts a biomass increment (17.7  $\pm$  1.5 Mg ha<sup>-1</sup> yr<sup>-1</sup>) similar to that observed in the most productive known primary *Sequoia* forests (Sillett et al., 2020).

After logging of primary Sequoia forest, absence of shading by taller crowns and perhaps belowground support from root systems of felled trees (Sillett et al., 2019a, 2020) enable Sequoia in secondary forest to outgrow other conifers, reaching the simulated height distribution in 115-161 yr with trees gaining almost as much biomass annually as Sequoiadendron 4-9 centuries older (Fig. 14a,c). Compared to the aforementioned plot in secondary Sequoia forest regenerating after 1858 logging, a 1-ha plot with 49 such trees would hold 56% of the aboveground biomass (927 Mg  $ha^{-1}$ ) and 78% of the leaves (LAI = 12; RMSE  $\div$  mean = 49%). The 16.6 Mg ha<sup>-1</sup> yr<sup>-1</sup> biomass increment of the secondary Sequoia simulation at + 50 yr (Fig. 14g) is reasonable considering that the most productive plot (22.9 Mg  $ha^{-1} yr^{-1}$ ) has higher LAI and 115 trees > 60 m tall (Sillett et al., 2019a; Iberle et al., 2020). If applied to the other height distribution (135 trees 34-84 m tall, plot 2 in Sillett et al., 2018b), height allometry for Sequoia in secondary forest (Table 7) predicts a biomass increment (27.6  $\pm$  1.0 Mg ha<sup>-1</sup> yr<sup>-1</sup>) approaching that of a fully stocked Sequoia plantation (Jones and O'Hara, 2012).

#### Table 8

Tallest trees of four species outside their native ranges. Five locations with tallest known individuals are listed per species with tree height, trunk diameter, age, year planted, latitude (– indicates Southern Hemisphere), elevation, country, significance, and source of information. Trunk diameters are listed with height of measurement (m) in parentheses. Ages are listed ± confidence in year planted with measurements occurring from 2013 to 2020. Abbreviated countries are United Kingdom (UK), New Zealand (NZ), and United States (US). Each tree's significance depends on its height relative to other trees in state, country, or globe. Sources are Monumental Trees (MT, https://www.monumentaltrees.com/en/), Sillett and Van Pelt unpublished measurements (SV), Brett Mifsud (BM, pers. comm.), Mario Vaden (MV, pers. comm.), and New Zealand Tree Register (NZTR, https://register.notabletrees.org.nz/).

Species	Height (m)	Diameter (cm)	Age (yr)	Planted (yr)	Latitude (°)	Elevation (m)	Country	Significance	Source
Picea sitchensis	64.0	242 (1.2)	$163\pm30$	pre-1850	57.5	98	UK	Tallest Picea in Scotland	MT
	62.8	128 (1.3)	$102\pm1$	1916	56.2	83	UK	Tallest Picea grove (several trees > 60 m)	MT
	60.0	88 (1.5)	$119\pm20$	1900	52.3	291	UK	Tallest Picea in Wales	MT
	60.0	191 (1.5)	$143\pm1$	1870	57.2	218	UK	Tallest Picea in Inverness	MT
	55.0	119 (1.5)	$165\pm1$	1849	53.2	91	Ireland	Tallest Picea in Ireland	MT
Pseudotsuga menziesii	69.6	214 (1.4)	$154 \pm 1$	1859	-43.9	281	NZ	Tallest <i>Pseudotsuga</i> grove (several trees > 60 m)	SV
	67.5	99 (1.5)	$95\pm1$	1921	53.1	94	UK	Tallest tree in UK, Wales	MT
	67.1	108 (1.3)	$106 \pm 1$	1913	48.0	490	Germany	Tallest tree in Germany	MT
	66.4	115 (1.5)	$132\pm1$	1882	57.5	87	UK	Tallest tree in Scotland	MT
	63.5	127 (1.3)	$99\pm1$	1920	43.1	560	Spain	Tallest conifer in Spain	MT
Sequoia sempervirens	73.4	158 (1.3)	$116 \pm 1$	1901	-38.2	317	NZ	Tallest Sequoia grove (several trees > 70 m)	MT
	64.8	175 (1.4)	$95\pm10$	1925	-37.7	335	Australia	Tallest conifer in Australia	BM
	63.0	175 (1.5)	$135\pm10$	1885	46.0	441	France	Tallest Sequoia in Europe	MT
	57.3	137 (1.3)	$127\pm30$	1890	40.4	384	Portugal	Tallest conifer in Portugal	MT
	56.8	163 (1.4)	$107 \pm 1$	1912	45.8	348	US	Tallest Sequoia in Washington	SV
Sequoiadendron giganteum	64.6	229 (1.4)	$95\pm10$	1925	42.3	800	US	Tallest Sequoiadendron in Oregon	MV
	58.0	178 (1.5)	$156\pm10$	1860	51.2	203	UK	Tallest Sequoiadendron in UK, England	MT
	57.7	159 (1.3)	$159\pm1$	1856	48.2	515	France	Tallest Sequoiadendron in Europe	MT
	57.4	344 (1.4)	$116\pm2$	1903	-44.2	153	NZ	Tallest Sequoiadendron in NZ	NZTR
	57.3	140 (1.3)	$147 \pm 1$	1872	49.0	438	Germany	Tallest Sequoiadendron in Germany	MT

Initial tree ages for Sequoiadendron are 3-8 centuries older than Pinaceae and 2-5 centuries older than Sequoia with aboveground biomass and biomass increment 22–65 Mg and 49–203 kg yr<sup>-1</sup> higher, respectively, per tree for Sequoiadendron (Fig. 14a-c). A 1-ha plot with 49 such trees would hold more aboveground biomass (3973 Mg  $ha^{-1}$ ) and leaves (LAI = 15; RMSE  $\div$  mean = 45%) than any Sequoiadendron forest vet measured, all species included (Sillett et al., 2019b). Even though such a stand of 49 trees would have little growing space available for other species and may be impossible within the native range of Sequoiadendron, the simulation shows how a high biomass increment  $(12-14 \text{ Mg ha}^{-1} \text{ yr}^{-1})$  can occur in a stand with a moderate density of relatively large and old trees changing very little in height (Fig. 14e). Sequoiadendron has by far the highest initial (-50 yr) heartwood increment (8.7 Mg  $ha^{-1} yr^{-1}$ ), but after only 77 yr of simulation, Sequoiadendron is overtaken by Sequoia in secondary forest, which accumulates heartwood 74% as fast as the global maximum (15.6 Mg  $ha^{-1}$   $yr^{-1}$  in primary Sequoia forest; Sillett et al., 2020) by the end (Fig. 14h). This rapidly increasing heartwood increment occurs because heartwood proportions of biomass rise much faster (averaging 47-60%) for Sequoia in secondary forest over the 100-yr simulation than for Picea (67–74%), Pseudotsuga (58-64%), Sequoia in primary forest (63-66%), and Sequoiadendron (67-68%; Table 7).

## 4.5. Conclusions

The four tallest conifers are each capable of creating forests with aboveground biomass > 2000 Mg ha<sup>-1</sup>, but developmental rate and carbon sequestration vary dramatically by species. After stand-replacing disturbances in Olympic rainforests, Picea-dominated stands gain biomass faster than those dominated by *Pseudotsuga* for  $\sim$ 3 centuries until senescence curtails performance of Picea, which can persist as a late-successional species regenerating on nurse logs (McKee et al., 1982; Van Pelt, 2007). Greater tree longevity allows Pseudotsuga to accumulate more biomass than Picea eventually, but shade intolerance and dependence on mineral soil greatly limit Pseudotsuga regeneration in rainforests, resulting in eventual loss of the pioneer cohort as stands transition to dominance by smaller, shade-tolerant species, especially Tsuga heterophylla (Minore, 1979; Franklin et al., 2002; Van Pelt and Nadkarni, 2004). Picea and Pseudotsuga coexist with Sequoia in rainforests farther south where all three species exceed 90 m tall (Van Pelt, 2001; Chin and Sillett, 2019; Fig. 1). Sequoia may rule these forests by virtue of its ability to survive infrequent, high-severity fires that kill other conifers as well as its high leaf phenotypic plasticity that promotes crown optimization, superior decay resistance, and unique capacity for asexual reproduction via trunk reiteration or sprouting (Lorimer et al., 2009; Van Pelt et al., 2016; O'Hara et al., 2017). After fire and treefall disturbances, Picea and Pseudotsuga take advantage of limited opportunities to gain height faster than regenerating Sequoia, making substantial contributions to both forest productivity (Iberle et al., 2020; Sillett et al., 2020) and biodiversity (Ellyson and Sillett, 2003; Gorman et al., 2019; Fig. 15ab) while maintaining co-dominance long enough to produce seeds before succumbing to fire, wind, or decay. Surviving Sequoia invariably carry scars and charcoal evidence between disturbances bracketing the lifespans of tall Pinaceae. After eventually toppling, heartwood of fallen Sequoia persists for centuries and accounts for the vast majority of carbon storage in dead biomass (Van Pelt et al., 2016). In Sequoiadendron-dominated forests, smaller conifers, especially Abies and Pinus, account for 8-27% of aboveground biomass and 37-60% of leaf mass, but their mortality can overwhelm live biomass increments of Sequoiadendron and dominate aboveground carbon dynamics (Sillett et al., 2019b).

Primary forests are global carbon sinks despite biomass increments substantially lower than those observed in secondary forests and plantations (Luyssaert et al., 2008; Pugh et al., 2019). Occupying only a tiny portion of the landscape (e.g., <500 and 100 km<sup>2</sup> for *Sequoia* and *Sequoiadendron*, respectively; Burns et al., 2018), primary forests of the

four tallest conifers are now largely protected for non-timber values, especially carbon sequestration, biodiversity conservation, and aesthetics (Engbeck, 2018). Our analysis of standing trees establishes reasonable performance expectations for these species in forests  $\geq$  90 m tall with limited applicability to secondary forests and those growing with less access to belowground resources. Allometric simulations reveal how quickly single-species stands can accumulate aboveground biomass under favorable conditions. Restoration management that achieves a moderate density of tall trees can sustain increasingly high biomass increments until establishing cohorts begin to senesce after centuries (Picea, Pseudotsuga) or millennia (Sequoia, Sequoiadendron). Silvicultural prescriptions that maintain adequate growing space for dominant individuals-by removing competing subordinates-and provide opportunity for regeneration-by site preparation and planting-have great potential to maximize long-term carbon sequestration in tall forests. Conservation value can be maximized by designating a subset of dominant individuals to stand near canopy gaps and in low-density neighborhoods. Such trees quickly develop ecologically significant appendage diameters, eventually becoming elite with complex crowns that provide critical arboreal habitats (Sillett and Van Pelt, 2007; Kramer et al., 2019, 2020). Restoration of coastal rainforests can harness the capacity of Picea to become elite centuries sooner than other conifers in forests eventually dominated by Sequoia. Contrasting rates of Sequoia development in primary and secondary forests highlight the remarkable regenerative capacity of this stump-sprouting species as well as its ability to produce durable biomass that is simultaneously resistant to fire and decay. The extent to which rapid growth of Sequoia in secondary forest is attributable to belowground subsidies via root systems of recently felled trees remains to be determined.

Widely planted across temperate latitudes, standing individuals of all four conifers now exceed 60 m tall and are often taller than any native species (Table 8). Geographic distribution of the tallest planted trees implies that Pseudotsuga, Sequoia, and Sequoiadendron can thrive at latitudes far higher than their native ranges. Sequoiadendron is particularly noteworthy in this regard, as the tallest planted individuals occur substantially farther north (and south) than the tallest planted Sequoia, approaching or exceeding 60 m tall centuries faster than Sequoiadendron in primary forest (Fig. 14ae). More work is needed to understand the developmental capacity of other conifers verified > 60 m tall, including species of Abies, Araucaria, Calocedrus, Cedrus, Chamaecyparis, Cryptomeria, Cunninghamia, Cupressus, Pinus, Taiwania, Thuja, and Tsuga. In addition to taking pressure off native forests for supplying timber (Sedjo, 1999), plantations of tall conifers may be especially effective in restoring ecological services and promoting carbon sequestration in the Anthropocene (Paquette and Messier, 2010; Lugo, 2015). The extreme longevity and decay resistance of Cupressaceae make them ideal candidates for intentional forests dedicated to long-term carbon sequestration. With sufficient land allocated to reforestation and management beyond rotation age, tall conifers can play an outsized role in both native and novel ecosystems as part of global adaptation to anthropogenic ecological change (Hobbs et al., 2014; Ellis, 2015).

# **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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