Journal of Vegetation Science **26** (2015) 722–732

Testing predictions of forest succession using long-term measurements: 100 yrs of observations in the Oregon Cascades

Mark E. Harmon & Robert J. Pabst

Keywords
In-growth; Live forest biomass; Mortality; Permanent plots; Successional theory; Time series

Nomenclature
USDA Plants Database (http://plants.usda.gov/java/; accessed on 1 July 2014)

Received 12 August 2014
Accepted 23 December 2014
Co-ordinating Editor: Otto Wildi

Harmon, M.E. (corresponding author, mark.harmon@oregonstate.edu),
Pabst, R.J. (rob.pabst@oregonstate.edu)

Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

Abstract

Question: Many predictions about forest succession have been based on chronosequences. Are these predictions – at the population, community and ecosystem level – consistent with long-term measurements in permanent plots?

Location: *Pseudotsuga menziesii* (Mirb.) Franco dominated forest in western Oregon, US.

Methods: Over a 100-yr period, measurements every 5–10 yrs of the growth, mortality and regeneration of individually tagged trees in three 0.4-ha forest plots dominated by *P. menziesii* were used to test predictions derived from chronosequence studies.

Results: Population- and community-level predictions generally matched observations: the initial cohort of pioneer species declined exponentially, with the shorter-lived *Prunus emarginata* (Douglas ex Hook.) Eaton and *Arbutus menziesii* Pursh disappearing altogether, and long-lived species such as *P. menziesii* persisting; tree size distribution shifted from a log-normal to a normal distribution, although the establishment of mid- to late-seral species created a bimodal distribution that may represent a transitional phase not usually elaborated in prior work; and mortality shifted from largely density-dependent to increasing amounts of density-independent causes. The observed biomass composition of these forests, even after 154 yrs, was still largely dominated by *P. menziesii*, which was consistent with the prediction from chronosequence studies. The slowing of biomass accumulation as stands aged predicted from ecosystem theory was not consistent with the observation that live biomass accumulated at a relatively constant rate for the 100-yr period.

Conclusion: Predictions from chronosequences at the population and community level were consistent with long-term observations in permanent plots, whereas those at the ecosystem level were not. At the spatial scale (<2 ha) examined with these plots, the high heterogeneity of tree mortality may lead to a multi-modal pattern of net live biomass accumulation with long periods of constant gain interrupted by sudden losses of live biomass.

Introduction

Globally, forests are an important ecosystem: they provide sources of building material, energy, habitat and clean water, and they store a large share of terrestrial carbon. How forests fulfill these functions is dependent on how they develop over time, and although there have been many studies of this process in forests, most of these studies have not involved direct observations over long periods of time. Indeed, much of what has been learned about forest succession involved substitution of differences in space for those in time (Pickett 1989; Bakker et al. 1996). This is logical, given that forests may take centuries to develop, but substituting space for time also has its limitations (Walker et al. 2010) because of, e.g. differences in disturbance history and productivity from site to site. This raises the question whether or not the temporal patterns hypothesized from chronosequences occur in individual forests or if they

Doi: 10.1111/jvs.12273

are artifacts of the chronosequence approach (Pickett 1989; Bakker et al. 1996).

Over 100 yrs ago, in April of 1910, Thornton T. Munger, a pioneer in forest research in the Pacific Northwest, established three 1-acre plots in well-stocked *Pseudotsuga menziesii* (Mirb.) Franco forests that had established 54 yrs previously, most likely after a wildfire (Munger 1946). Individual trees in the plots were tagged so that their growth and fate could be observed. Of particular interest was the rate of tree mortality and whether capturing it via harvest was a potential path toward increasing the net yield of these forests (Worthington 1957).

Observations have continued in these forest plots for 100 yrs, and although the original questions regarding timber yield have been largely addressed (McArdle et al. 1949; Staebler 1955; Williamson 1963), the length of these observations is extremely valuable in answering other questions, particularly those related to long-term successional trends in forests (Sollins 1982; Acker et al. 1998). Given the very long length of time it takes for forests to develop, direct observations of the relevant time scale are extremely rare, and while 100 yrs is short compared to the potential length of succession in *P. menziesii*-dominated forests (Franklin et al. 2002), it represents a substantial period and offers an unparalleled opportunity to directly test hypotheses about forest succession at the population, community and ecosystem levels of ecology. For example, at the population level, several related trends have been implied: (1) the number of individuals of pioneer tree species should decline as mortality occurs without replacement; and (2) the number of individuals of mid- to late-seral species should increase (e.g. Clements 1928; West et al. 1981). This should lead to an overall U-shaped pattern of tree density (stems per area) over time (Fig. 1a, for derivation see supplemental online material). The first two trends should also contribute to related changes in the size class structure of the aging forest, with a log-normal distribution of pioneer species diameters eventually giving way to normal distribution, and that giving way to a reverse J-shaped size structure as mid- to late-seral species enter the stand (Fig. 1b; e.g. Leek 1964; Mohler et al. 1978; Peet & Christensen 1987; Coomes & Allen 2007). Mortality as a proportion of live trees has been predicted to decline over time, from largely density-dependent mortality early in succession to largely density-independent mortality late in succession (Franklin et al. 1987). At the community level, classic successional theory predicts that species that thrive in situations where competition for resources is low should be replaced by those that tolerate competition for limited resources (e.g. Pianka 1970; Grime 1979). In closed, temperate forests, since much of the competition is for light, shade-tolerant species should replace those that are shade intolerant; the timing of this change depends on the dominant species in a particular region. In the case of *P. menziesii*-dominated forests, shade-intolerant species would include *P. menziesii*, *Alnus rubra* Bong. and *Prunus emarginata* (Dougl. ex Hook.) Eaton; whereas shade-tolerant species would include *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn ex D. Don, *Acer macrophyllum* Pursh and *Taxus brevifolia* Nutt. (Fig. 1c; Franklin & Hemstrom1981). The transition from a majority of shade-intolerant *P. menziesii* to a majority of shade-tolerant *T. heterophylla* after a major disturbance would be expected after 200–350 yrs in terms of stems and after 500–800 yrs in terms of biomass (Franklin et al. 2002). Finally, at the ecosystem level, classic successional theory predicts that after a period of increase associated with stand establishment, the net rate of biomass accumulation or periodic increment should decline as mortality claims an ever larger share of net primary production (NPP; Fig. 1c, d). This declining rate of net increase leads to a convex-shaped biomass accumulation curve, which could either approach an asymptote or decline, depending on the degree to which mortality continues to increase and regeneration can replace it (e.g. Peet 1981).

Our objective in this paper is to test these predictions against the 100 yrs of observations these plots offer. Although some of these predictions are highly supported by chronosequence studies based on temporary (single measurement) plots (e.g. Spies & Franklin 1991), they have not been directly observed, and hence remain hypothetical until direct observations are made over time (Pickett 1989). We therefore compare observed and predicted temporal trends of population-, community- and ecosystem-level variables to directly test successional theory.

Methods

Study area

The three forest plots analysed in this paper were established in April 1910 in the Willamette National Forest, about 30 miles southeast of Eugene, Oregon (122.62° W, 43.82° N) above what is now Lookout Point Reservoir on the Middle Fork of the Willamette River (Fig. 2). The topography where the plots are located is relatively flat, with slopes of 0–30%, at elevations ranging from 380 to 430 m, and an aspect that is generally north facing (Williamson 1963). Long-term spatial databases of climate (i.e. PRISM Climate Group 2004 http://prism.oregonstate.edu) indicate a mean annual temperature of about 11 °C and mean annual precipitation ranging from 126 to 152 cm. Soils were characterized as deep, well-drained loam (unpubl. report, 1910). The plots are in the *T. heterophylla* vegetation zone. Acker et al. (1998) estimated that the 50-yr site index of *P. menziesii* based on King (1966) ranged between 106 and 120 feet (32–37 m).

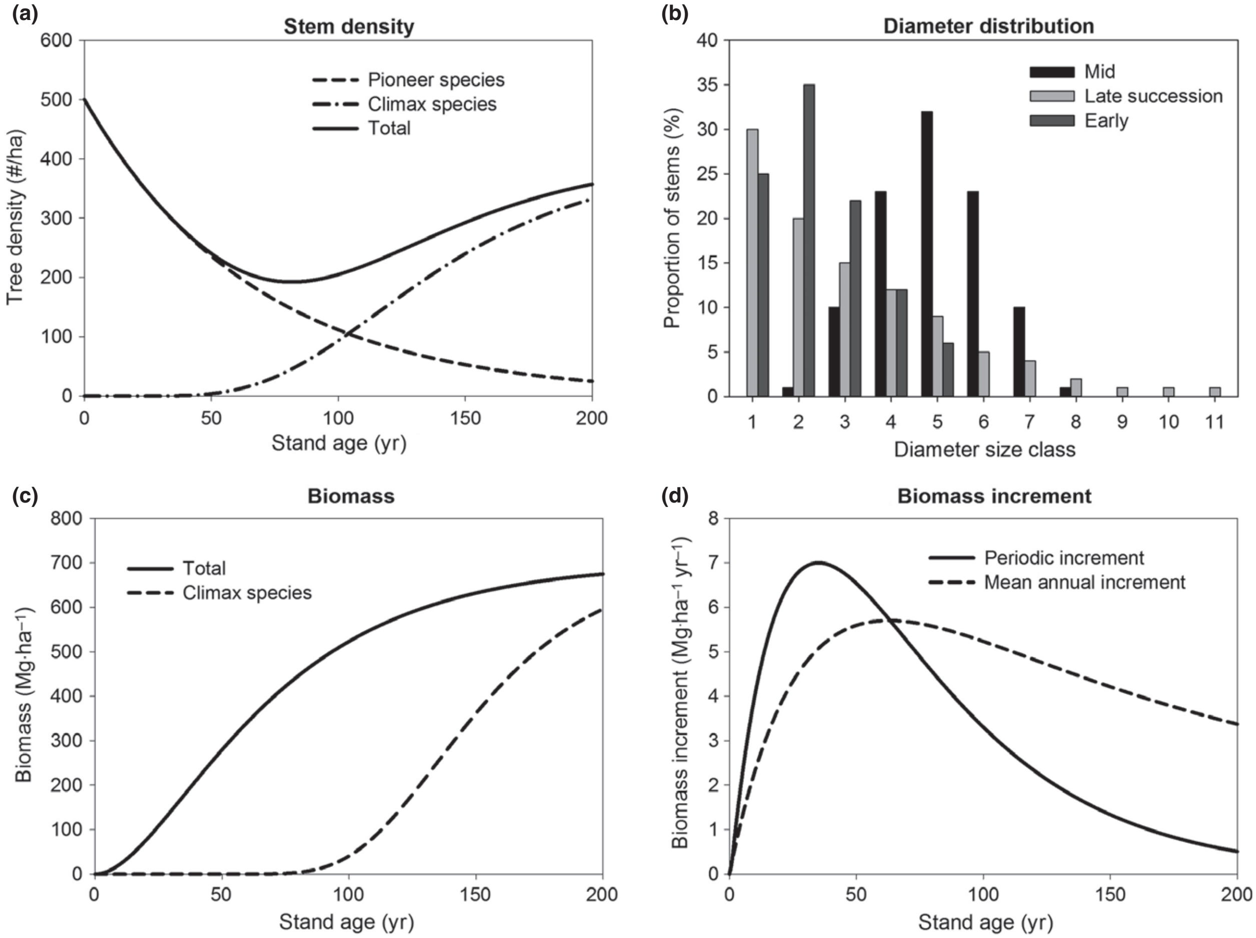

Fig. 1. Hypothetical predictions from forest succession theory at the population, community and ecosystem levels: (**a**) stem density (trees ha^{-1}), (**b**) tree diameter distribution, (**c**) stand biomass (Mg ha^{-1}), and (**d**) increments in biomass (Mg ha^{-1} yr^{-1}). See Supplemental online material for details.

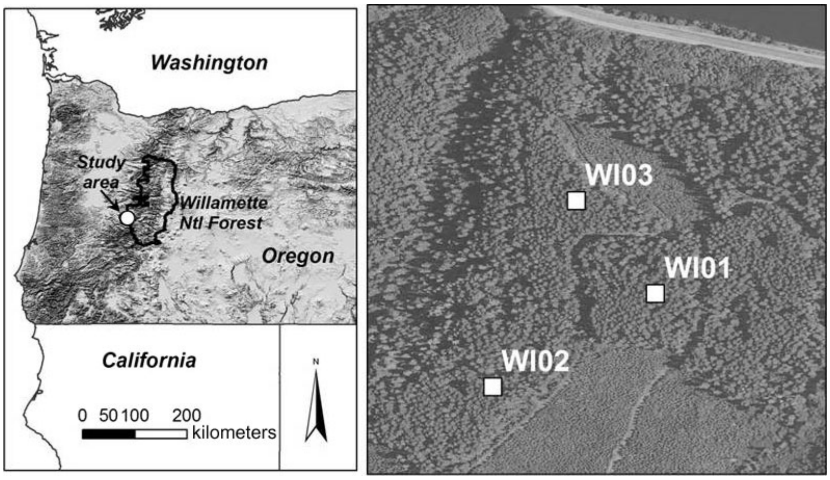

Fig. 2. Location of the permanent plots in western Oregon.

Each plot is a 0.4-ha (1 horizontal acre) square situated in well-stocked stands of *P. menziesii* that likely originated following wildfire in the mid-1850s, a time when forest fires were frequent in Oregon (Weisberg & Swanson 2003). These stands were disturbed by a surface fire in 1895, ice- or snow-related breakage in 1888 (Munger 1946) and 1915–1920, as well as by a bark beetle attack between 1935 and 1945 (Williamson 1963). Unfortunately, due to a lack of awareness about the study plot locations, two trees in Plot 1 were cut in 1970 as a result of road construction. Similarly, nearby clearcut harvests prior to the 1992 measurement removed six trees from Plot 2 and two trees from Plot 3. At the measurement preceding harvest, the cut trees comprised about 2.1% of basal area in Plot 1 (1950), 7.1% in Plot 2 (1970) and 3.5% in Plot 3 (1970).

Measurements

All woody plants, except *Acer circinatum* Pursh, exceeding the minimum diameter of 5 cm in the plots (hereafter referred to as trees) were marked at breast height (1.37 m) with individually numbered aluminium tags nailed into the stems. The DBH was initially determined using calipers and diameter tapes, but eventually only diameter tapes were used. The plots have been measured 15 times over the 100-yr period, at mostly 5-yr intervals from 1910 to 1955, in 1970 and again at 5-yr intervals starting in 1992, except for the last measurement in 2010. At the time of census all trees were visited, their status determined (live, dead or missing) and their DBH measured if they were alive. Dead trees were assigned the DBH from the previous measurement, since it was unknown when in the intervening years the trees died. In most cases this approach would slightly underestimate the DBH of trees at the time of death. Notes were taken on conditions and potential causes of tree death. Trees that surpassed the 5 cm minimum DBH since the previous measurement were tagged as in-growth and included in future measurements. Trees that were cut from the plots (two each in Plots 1 and 3, six in Plot 2) were removed from the data set prior to analysis.

Biomass

Above-ground biomass was estimated using species-specific equations (Appendix S5). For *P. menziesii*, *T. heterophylla*, *T. plicata*, *Chrysolepis chrysophylla* (Douglas ex Hook.) Hjelmqvist and *A. rubra*, we used allometric equations from Biopak (Means et al. 1994) to estimate the biomass of different tree components (bole, bark, branches, foliage), which were then summed to estimate total above-ground biomass. The equations for *A. rubra* were used for *Cornus nuttallii* Audubon ex Torr. & A. Gray, *P. emarginata* and *Frangula purshiana* (DC) A. Gray, which have a similar growth form as *A. rubra* but a limited suite of equations. Similarly, *A. macrophyllum* and *Arbutus menziesii* Pursh do not have a full set of component equations, so we used equations for above-ground volume and converted that to biomass by multiplying volume by specific gravity of the wood (USDA Forest Service 1999). Tree height in the volume equations was estimated with asymptotic height–diameter equations (Garman et al. 1995). The biomass of trees dying over each observation interval was estimated in similar fashion as live trees, and the cumulative mortality of trees was calculated by summing all the tree biomass that had died since the inception of the plots. It therefore does not include losses from decomposition and therefore cannot be used directly to estimate a carbon balance, but does provide a good approximation of how much live woody biomass has been produced above ground. For the sake of comparison, component and summed biomass were also estimated with standard national-level equations (Jenkins et al. 2003). These values were 2–8% less than those reported here, but the resulting trends were the same (results not shown).

Mortality

Mortality rates were estimated as the annualized percentage (Sheil et al. 1995) of trees that died in each observation period, calculated separately for the initial cohort of trees and for all trees (i.e. initial cohort plus in-growth). Mortality rates of all trees were also expressed as a percentage of basal area lost. We broadly categorized mortality of individuals as density-dependent or density-independent, based on tree condition at the time mortality was documented; unless otherwise noted, trees that died standing were assumed to have succumbed to competition, whereas broken or downed trees, plus those noted as having evidence of attack by bark beetles (*Dendroctonus pseudotsugae* Hopkins) or pathogens, were assumed to have died from density-independent agents.

Diameter distributions

Stem diameter distributions were derived for each species at each measurement by determining the number of live stems per ha in 10-cm DBH classes. The relative abundance of tree species was expressed as a function of both stem number and live above-ground biomass.

Results

Stem density

The temporal trend in total stems per area (i.e. density) over the 100 yrs of observations (Fig. 3) was consistent with the ‘open’ U-shaped curve implied by replacement of species during succession (Fig. 1a). The average initial density of live trees was 530 trees ha^{-1} (TPH), declined to 290 TPH at age 95 yrs, and slightly increased to 300 TPH at the end of the observation period. The cumulative density of trees that have died (vs the number at any one time), rapidly increased from 0 to 300 stems ha^{-1} at age 114 yrs, and steadily increased another 75 stems ha^{-1} by age 154. At the last measurement, the cumulative number of dead trees exceeded the number of live trees by about 15%.

Mortality

The annualized rate of stem mortality of the initial cohort of trees averaged 0.997% over the 100-yr time frame; the periodic rate (i.e. for specific periods) has generally declined over time, from 2.1% to 3.2% per year at age 59–64, to 0.3% per year at age 154 (Table 1, Appendix S1). There were two exceptions to this decreasing trend in mortality: at stand age 74 yrs when the mortality rate dropped several-fold, and stand age 146 yrs when there was higher rate of mortality than the years preceding or following this period. When all trees are considered (initial cohort plus in-growth), the mortality rates are slightly higher than for the initial cohort in three of the past four measurement periods, indicating that mortality is also occurring in stems that have in-grown since the measurements started. Mortality rates expressed as the annual percentage of basal area lost are lower than those based on stem density, suggesting that most trees dying tend to have a 20–50% smaller DBH than live trees (Appendix S2). The decline in mortality rates over time coincided with a shift away from density-dependent mortality (i.e. resource limited) to density-independent processes, such as those related to wind, insects and disease, which have comprised about half of the mortality since stand age 136 yrs (Table 1, Appendix S3).

Diameter distributions

The diameter size class distribution generally changed as predicted, starting as a log-normal distribution, gradually tending toward a normal distribution as smaller stems were lost via mortality, and then starting to resemble a reverse-J distribution by stand age 154 yrs as mid- and late-seral species became established (Fig. 4a–f). However, on closer inspection at the end of the observation period, the overall diameter distribution appears to combine two distinct distributions: a normal one for the initial cohort of trees and a reverse-J for the trees that had come in as in-growth. This therefore seems to represent a transitional phase between the two distinct size class distributions often presented in the literature (e.g. Leek 1964; Mohler et al. 1978; Peet & Christensen 1987; Coomes & Allen 2007).

Species composition

The change in species composition, not surprisingly, was dependent on whether one considered stem density or bio-

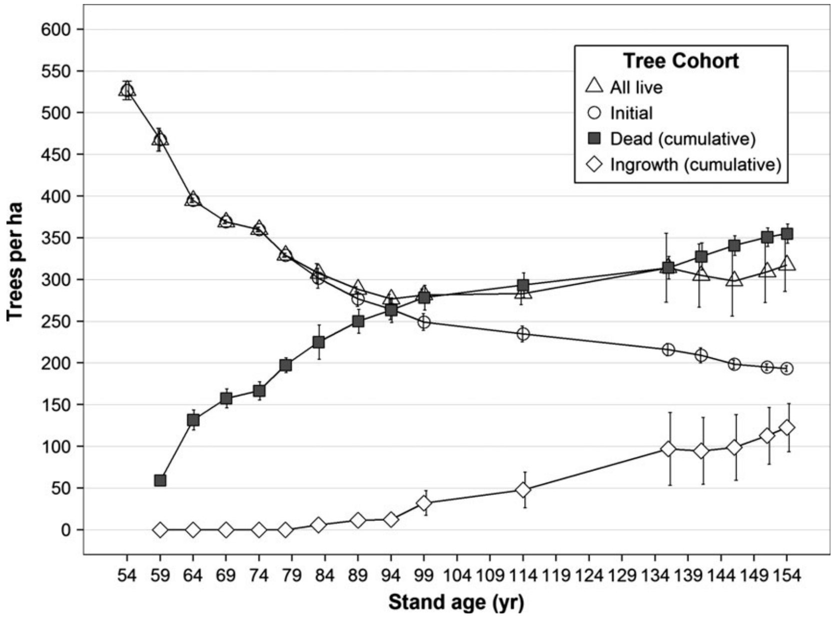

Fig. 3. Mean density (trees ha^{-1}) and SE from three study plots of all live trees (initial cohort plus in-growth), the initial cohort of trees, cumulative density of dead trees and cumulative density of in-growth.

Table 1. Mortality rates, type of mortality and biomass as a function of stand age.

Stand Age (yrs)	Mortality Rate (%): Mean (SE)			Number of Dead Trees by Mortality Type		Above-ground Biomass (Mg ha^{-1}): Mean (SE)	
	Initial Cohort	All Trees	Basal Area Mortality	Density-dependent	Density-independent	Living	Dead (Cumulative)
54	–	–	–	–	–	329.73 (13.66)	–
59	2.363 (0.280)	2.363 (0.280)	0.661 (0.097)	70	1	367.64 (18.16)	7.57 (0.91)
64	3.295 (0.573)	3.295 (0.573)	1.151 (0.195)	70	17	390.36 (12.92)	23.75 (2.27)
69	1.344 (0.041)	1.344 (0.041)	0.355 (0.017)	29	2	418.84 (12.77)	28.52 (2.43)
74	0.502 (0.048)	0.502 (0.048)	0.165 (0.004)	10	1	450.98 (14.62)	31.04 (2.46)
78	2.213 (0.212)	2.213 (0.212)	1.155 (0.360)	30	7	459.62 (9.36)	50.14 (8.52)
83	1.753 (0.900)	1.753 (0.900)	0.964 (0.719)	26	7	473.56 (20.79)	68.97 (20.96)
89	1.419 (0.356)	1.388 (0.339)	0.710 (0.286)	19	11	498.07 (14.35)	86.41 (19.94)
94	0.940 (0.301)	0.950 (0.318)	0.377 (0.146)	6	10	524.28 (15.05)	93.83 (22.50)
99	1.155 (0.191)	1.106 (0.201)	0.565 (0.115)	15	3	537.10 (16.51)	106.56 (25.25)
114	0.389 (0.014)	0.365 (0.010)	0.142 (0.003)	16	2	640.05 (17.13)	115.10 (25.17)
136	0.384 (0.049)	0.352 (0.056)	0.181 (0.040)	14	11	794.00 (24.02)	136.41 (20.37)
141	0.639 (0.185)	0.845 (0.273)	0.413 (0.175)	5	11	819.91 (31.60)	151.36 (14.91)
146	1.031 (0.665)	0.992 (0.587)	0.878 (0.673)	4	12	831.24 (54.63)	183.76 (12.79)
151	0.333 (0.167)	0.679 (0.008)	0.198 (0.088)	7	4	862.88 (55.24)	190.67 (12.78)
154	0.283 (0.142)	0.442 (0.050)	0.109 (0.049)	3	2	880.50 (57.72)	192.63 (13.41)

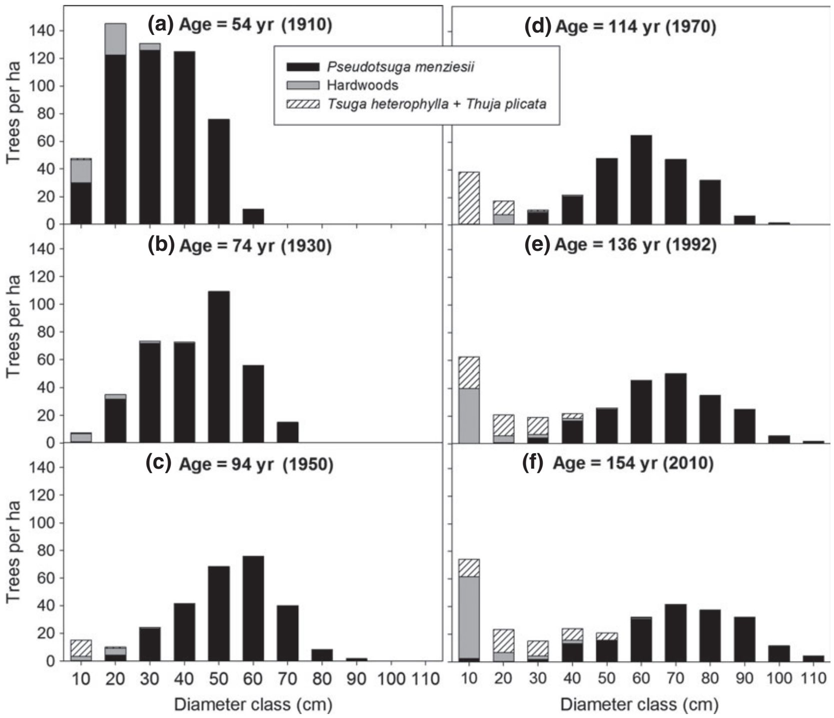

Fig. 4. Diameter distribution in 10-cm classes for trees alive at six points in time (indicated as a to f) from 1910 when the stand was 54 yrs old to 2010 when the stand was 154 yrs old. Hardwood species include *Acer macrophyllum*, *Alnus rubra*, *Arbutus menziesii*, *Chrysolepis chrysophylla*, *Cornus nutallii*, *Frangula purshiana* and *Prunus emarginata*.

mass as the variable of abundance (Table 2). At a stand age of 54 yrs, *P. menziesii* comprised about 90% of the live stems in the plots, whereas shade-tolerant *T. heterophylla* and *T. plicata* were virtually absent (i.e. one *T. heterophylla* in one plot). A mix of hardwood species comprised the remaining 10% of stems at age 54. By age 154, the percentage of *P. menziesii* stems had declined to 60% as shade-tolerant species including *T. heterophylla*, *F. purshiana* and

Table 2. Tree species composition (density in trees ha^{-1}, biomass in Mg ha^{-1}) at the start and end of the 100-yr observation period. Values are means from three study plots, with SE in parentheses.

Species	1910: Age = 54 yrs				2010: Age = 154 yrs			
	Density		Biomass		Density		Biomass	
	Trees ha^{-1}	%	Mg ha^{-1}	%	Trees ha^{-1}	%	Mg ha^{-1}	%
Conifers								
Pseudotsuga menziesii	480.83 (19.60)	91.30	323.81 (15.27)	98.20	191.67 (4.41)	60.37	846.14 (49.50)	96.10
Thuja plicata	0.00 (0.00)	0.00	0.00 (0.00)	0.00	1.67 (1.67)	0.53	0.58 (0.58)	0.07
Tsuga heterophylla	0.83 (0.83)	0.16	0.01 (0.01)	0.00	52.50 (20.05)	16.54	26.94 (14.21)	3.06
Broad-leaf hardwoods								
Acer macrophyllum	5.83 (3.63)	1.11	0.87 (0.72)	0.26	10.83 (3.00)	3.41	5.14 (1.88)	0.58
Arbutus menziesii	5.83 (3.63)	1.11	2.02 (1.01)	0.61	0.00 (0.00)	0.00	0.00 (0.00)	0.00
Chrysolepis chrysophylla	15.00 (3.82)	2.85	1.83 (0.61)	0.56	3.33 (3.33)	1.05	0.03 (0.03)	0.00
Cornus nuttallii	5.00 (1.44)	0.94	0.19 (0.06)	0.06	24.17 (14.24)	7.61	1.01 (0.62)	0.12
Frangula purshiana	0.00 (0.00)	0.00	0.00 (0.00)	0.00	33.33 (12.28)	10.50	0.63 (0.17)	0.07
Prunus emarginata	13.33 (7.26)	2.53	1.01 (0.51)	0.31	0.00 (0.00)	0.00	0.00 (0.00)	0.00

C. nuttallii increased their share. However, in terms of biomass, *P. menziesii* maintained strong dominance, comprising 96% of the biomass at age 154. Thus, although clearly present, mid- to late-successional conifers were not yet important components of the biomass.

Biomass

The observation differing most from the prediction is the accumulation of live biomass. In contrast to the hypothetical convex curve (Fig. 1c), live biomass increased in straight-line fashion from an average of about 330 Mg ha^{-1} at age 54 to about 880 Mg ha^{-1} at age 154 (Table 1, Appendix S4). The same was true for cumulative dead biomass, reaching an average of nearly 200 Mg ha^{-1} by age 154 yrs. Dead biomass comprised ca. 20% of the total biomass production over the 100-yr period of observation. Thus, instead of a decreasing rate of net biomass accumulation as predicted by theory, these plots appeared to experience a constant rate of biomass increase. Examination of the individual plots reveals that two of the plots (Plots 1 and 2) did experience periods when biomass was either constant or decreased (data not shown). Increases in the cumulative dead biomass accompanied these few exceptional periods.

Discussion

Population- and community-level predictions

In terms of population and community aspects of succession, the observations from these plots generally are consistent with the predictions from chronosequences developed in the Pacific Northwest. The initial cohort of pioneer species declined exponentially, with the shorter-lived *P. emarginata* and *A. menziesii* disappearing altogether and the long-lived species such as *P. menziesii* persisting. Shade-tolerant species such as *T. heterophylla* increased in abundance, but since there was ≈50-yr lag in this recruitment relative to peak mortality of the pioneer cohort, there has yet to be a major increase in density that would result in a distinct U-shape. However, the level of shade-tolerant regeneration needed to 'complete' the U-shaped pattern will likely occur in the next 50–200 yrs of stand development, barring major disturbance (Franklin et al. 2002).

Tree size distribution largely followed what would be expected, although it is not entirely clear that a purely normal distribution is present. This is because as the pioneer species developed a normal distribution, the establishment of mid- to late-seral species introduced a negative exponential distribution in the smaller DBH size classes. This created a bimodal distribution that may represent a transitional phase between the two 'classic' distribution shapes described in the literature (Leek 1964; Mohler et al. 1978; Peet & Christensen 1987; Coomes & Allen 2007).

Mortality would be predicted to decline as stands move from largely density-dependent mortality to more small-scale density-independent mortality, which was also consistent with the observations. Between stand ages of 54–64 yrs, there appeared to have been an increase in periodic mortality rates that were mostly from density-dependent causes. This may have reflected a period in which competition between trees increased in association with stand closure, leading to relatively high mortality rates. The proportion of trees dying from density-dependent causes appears to have declined, but this is related to a decrease of density-dependent mortality in absolute terms and not an increase of density-independent mortality in absolute terms. Specifically, density-independent mortality appears to have removed three to ten trees per measurement period during the 100 yrs of observation, whereas density-dependent mortality has generally declined from ≈70 to three to six individual per measurement period (Table 1). The decline in density-dependent mortality in absolute terms may be related to reductions of the pioneer tree density as well as the age at which the maximum crown width is attained (which for *P. menziesii* is age 150–200 yrs; Franklin et al. 2002). As pioneer trees approach the maximum crown width, the death of an overstorey tree may not necessarily free up additional resources to the surviving dominant overstorey trees. This implies that overstorey tree mortality is not competition-driven once the maximum crown width is reached. As the density of climax tree species increases, density-dependent mortality may increase again (He & Duncan 2000).

Although forest succession theory predicts the replacement of shade-intolerant tree species by those tolerating shade, the timing of this transition is controlled by the species dominating in particular regions. In the cases of forests dominated by *P. menziesii*, the extreme longevity of this species (~1000 yrs) means that shade-tolerant species may not assume dominance for many centuries (Franklin et al. 2002). Our observations are consistent with that prediction, as the composition of these forest plots in terms of biomass, even after 154 yrs, is still largely dominated by *P. menziesii*. Based on the current trend in pioneer tree mortality and regeneration of climax species, it may take the plots we examined another 50 yrs before species such as *T. heterophylla* comprise at least 50% of the stems (see supplemental online materials). Using observed rates of mortality, recruitment and approximate growth rates indicates that climax species will still comprise less than 10% of the biomass in 50 yrs. For climax species to comprise > 25% of the biomass in the next 50-yr period, the regeneration and growth rates of climax species would both have to increase six-fold over what has been recently observed. Based on chronosequences in the Pacific Northwest, it may take another 200 yrs before climax species comprise > 25% of the live biomass in these stands (Franklin et al. 2002).

Ecosystem-level predictions

In contrast to those at the population and community level, observations from these study plots are at odds with the predictions from ecosystem chronosequence studies regarding live biomass accumulation patterns (Janisch & Harmon 2002; Hudiburg et al. 2009). To assess the implications of this finding, it is instructive to estimate the biomass that would occur if nothing changed until these plots reached an age of 500 yrs, the approximate age of many old-growth forests that have been inventoried in this region (Smithwick et al. 2002). Based on the average accumulation rate of 5.5 Mg ha^{-1} yr^{-1} in these plots over the past 100 yrs and a biomass of 880 Mg ha^{-1} at age 154 yrs, these plots should reach a live above-ground biomass of ca. 2,783 Mg ha^{-1} after another 346 yrs. However, this seems unlikely, given this level of biomass approaches global record numbers (Keith et al. 2009) and far exceeds what has been observed in old-growth forests in the Pacific Northwest (Smithwick et al. 2002). To reach the above-ground live biomass values typical of forests of this type and productivity by age 500 yrs (i.e. 600–1200 Mg ha^{-1}, as indicated in Harmon et al. (2004)), either the NPP of these forests must decline substantially or the rate of mortality must greatly increase. Major declines in NPP of the order needed seem highly unlikely based on observed values of this variable in old-growth *P. menziesii*-dominated forests (Harmon et al. 2004) and chronosquences in the Pacific Northwest (Hudiburg et al. 2009). This suggests mortality will eventually have to increase substantially in these plots.

What might explain this apparent discrepancy with classical ecosystem succession theory? One possibility is that forests never slow down their rate of live biomass accumulation and continue to accumulate into the future. This might be caused by either mortality never taking a very large share of NPP regardless of forest age, an ever-increasing growth rate of large trees (Stephenson et al. 2014) or some combination of the two. An alternative explanation is that at the scale observed (0.4 ha), plot-level mortality is very heterogeneous and these particular plots have, to date, largely escaped major mortality events in terms of biomass loss. Without these mortality episodes, biomass accumulation should form a straight line, as was observed. When these large mortality events occur there would be a sudden drop in live biomass followed by another period of straight-line accumulation (Fig. 5a). Thus, the net accumulation curve is far more likely to be multi-modal than the continuous trend that classic theory assumes (Fig. 5b). Examining the individual plots hints at this temporal pattern, but there has yet to be a major episode of mortality loss in terms of biomass. According to the most recent (2010) data, only one or two trees of the two largest diameter classes would need to die in a 5-yr period to offset the anticipated net accumulation rate of 27.5 Mg ha^{-1} and cause live biomass accumulation to either level out or decline.

One problem with the classic theory of forest biomass accumulation is that it is scale-independent, viewing NPP and mortality as homogeneous regardless of spatial scale. In reality, NPP is far more homogeneous with respect to spatial scale compared to mortality, a process that is highly heterogeneous at almost any spatial extent and extremely heterogeneous with respect to time (Harmon et al. 1986; Franklin et al. 1987). This suggests that more attention needs to be paid to the effect of spatial scale on the pattern of live biomass accumulation, specifically the degree to

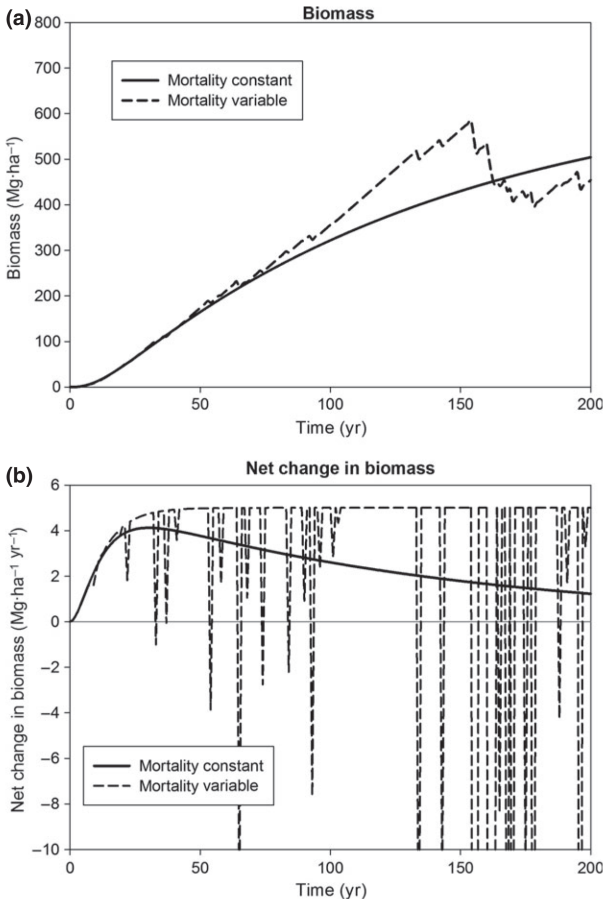

Fig. 5. Suggested alterations in the hypothetical temporal pattern of total (a) and net (b) live biomass accumulation that includes spatial and temporal heterogeneity of tree mortality. See supplemental online material for details.

which heterogeneity of production and mortality vary with scale and how these changes in heterogeneity influence theoretical expectations.

A second related problem with classic theory is that it examines the average trajectory during succession. Within *P. menziesii*-dominated forests, it has become clear that multiple successional trajectories can often lead to very similar end states (Tepley et al. 2013). The particular plots we examined seem to have been on a minimal mortality trajectory. Examination of Fig. 2 indicates that nearby areas of this forest have had large areas of canopy loss, so it seems likely the three plots we examined represent one of the extreme successional trajectories possible in these forests, but others are possible even in the area surrounding the plots examined. Other plots from the same growth and yield series have experienced significant root pathogen and bark beetle mortality that have limited live biomass accumulation (Williamson 1963). Furthermore, other studies of *P. menziesii* stands in this age range in the Pacific Northwest have found that canopy gaps, arising from disease, insects or wind, can occupy more than 20% of the area of a stand (Spies et al. 1990) and range up to more than 30 m across (Bradshaw & Spies 1992) which would roughly equal 20% of the plot area we sampled. This suggests that the average successional trajectory (if there is such a thing) needs to be defined by more stands than is typical practice.

Practical implications

The pattern of biomass accumulation observed from these plots has several practical implications. One biological determinant of whether a forest should be harvested is the timing of the culmination of mean annual increment (MAI); i.e. the age at which the increase in age outstrips the increase in biomass. Typically, chronosequences suggest MAI rises, reaches a distinct peak, and then begins to decline. For *P. menziesii*-dominated forests, the decline in MAI has been thought to occur in stands that are 50–70 yrs old (e.g. table 9 from McArdle et al. 1949). However, as previously noted by Curtis (1992) and Curtis & Marshall (1993) as well as Acker et al. (1998), the decline in MAI in *P. menziesii* forests can be very gradual, making a defined peak hard to identify. In the plots we examined, there has been little to no decline in MAI for a 100-yr period between ages of 54 and 154 yrs. If the stand we sampled is not atypical, then it implies the culmination of MAI for *P. menziesii*-dominated forests could occur in stands as young as 50 yrs old or up to 150 yrs old. Given that the lower end of this 100-yr range typically serves as guide as to when to harvest, it is likely some *P. menziesii* forests have been harvested many decades before their actual culmination of MAI occurred. Our results have implications for carbon storage as well. For example, Lippke et al. (2011) asserted that *P. menziesii* forests reach their maximum live biomass around age 100 yrs; however, this is not consistent with what was observed. Our results suggest some *P. menziesii* forests can accumulate live carbon at least 50 yrs past the 100-yr age, a trend which is more in line with the 200-yr age to reach maximum live biomass revealed by chronosequences derived from regional forest inventories (Hudiburg et al. 2009). While we suspect that live biomass accumulation will eventually slow down and perhaps cease, this is likely to occur many decades in the future, barring a major disturbance in these plots. This implies substantially more live carbon can be accumulated in this type of forest if harvest rotations are extended past the 50- to 100-yr age.

Conclusions

While our observations fit some of the predictions about forest succession over a 100-yr period, those related to biomass accumulation did not. Thus, testing hypotheses developed from chronosequences and other reconstructions with long-running temporal observations as from this study is a necessary step. To that end, longer measurement periods (i.e. >200 yrs) will be required to directly observe some of the changes predicted from chronosequences in forests dominated by long-lived species such as *P. menziesii*. The fact that biomass accumulation did not conform to classical predictions indicates that some of the assumptions upon which the theory is based are not true at all spatial scales. We believe the most likely explanation is that mortality is not homogenous with respect to spatial and temporal scales. This suggests that the net biomass accumulation trend at least for small areas (<2 ha) is multimodal and not continuous. The dependence of heterogeneity in the spatial and temporal extents of tree mortality needs to be examined in other forests to more fully explain live biomass accumulation trends during succession.

Acknowledgements

This study was supported by the Pacific Northwest Research Station and the National Science Foundation's Long-term Ecological Research Program (DEB-0218088, DEB-0823380). The authors thank all those who helped collect the data that made this work possible. Drs Steve Acker, Jerry Franklin and Thomas Spies provided helpful suggestions for manuscript improvements.

References

Acker, S.A., Sabin, T.E., Ganio, L.M. & McKee, W.A. 1998. Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. *Forest Ecology and Management* 104: 265–280.

Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science* 7: 147–156.

Bradshaw, G.A. & Spies, T.A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *Journal of Ecology* 80: 205–215.

Clements, F.E. 1928. *Plant succession and indicators*. H. W. Wilson, New York, NY, US.

Coomes, D.A. & Allen, R.B. 2007. Mortality and tree-size distributions in natural mixed-age forests. *Journal of Ecology* 95: 27–40.

Curtis, R.O. 1992. A new look at an old question – Douglas-fir culmination age. *Western Journal of Applied Forestry* 7: 97–99.

Curtis, R.O. & Marshall, D.D. 1993. Douglas-fir rotations – time for reappraisal. *Western Journal of Applied Forestry* 8: 81–85.

Franklin, J.F. & Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.) *Forest succession: concepts and application*, pp. 212–229. Springer, New York, NY, US.

Franklin, J.F., Shugart, H.H. & Harmon, M.E. 1987. Tree death as an ecological process. *BioScience* 37: 550–556.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A., Thornburgh, D., Berg, D.R., Lindenmayer, D., Harmon, M.E., Keeton, W. & Shaw, D.C. 2002. Disturbances and the structural development of natural forest ecosystems with some implications for silviculture. *Forest Ecology and Management* 155: 399–423.

Garman, S.L., Acker, S.A., Ohmann, J.L. & Spies, T.A. 1995. *Asymptotic height–diameter equations for twenty-four tree species in western Oregon*. Forest Research Laboratory Research Publication 10, Oregon State University, Corvallis, OR, US.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, New York, NY, US.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Lattin, J.D., Anderson, N.H., Gregory, S.V., Cline, S.P., Aumen, N.G., (. . .) & Cummins, K.W. 1986. The ecology of coarse woody debris in temperate ecosystems. *Recent Advances in Ecological Research* 15: 133–302.

Harmon, M.E., Bible, K., Ryan, M.J., Shaw, D., Chen, H., Klopatek, J. & Li, X. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga/Tsuga* forest ecosystem. *Ecosystems* 7: 498–512.

He, F. & Duncan, R.P. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology* 88: 676–688.

Hudiburg, T., Law, B., Turner, D.P., Campbell, J., Donato, D. & Duane, M. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. *Ecological Applications* 19: 163–180.

Janisch, J.E. & Harmon, M.E. 2002. Successional changes in live and dead wood stores: implications for Net Ecosystem Productivity. *Tree Physiology* 22: 77–89.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S. & Birdsey, R.A. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49: 12–35.

Keith, H., Mackey, B.G. & Lindenmayer, D.B. 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences of the United States of America* 106: 11635–11640.

King, J.E. 1966. *Site index curves for Douglas-fir in the Pacific Northwest* [Weyerhaeuser Forestry Paper Number 8]. Weyerhaeuser Forestry research Center, Centralia, WA, US.

Leek, W.B. 1964. An expression of diameter distribution for unbalanced, uneven-aged stands and forests. *Forest Science* 10: 39–50.

Lippke, B., Oneil, E., Harrison, R., Skog, K., Gustavsson, L. & Sathre, R. 2011. Life cycle impacts of forest management and wood utilization on carbon mitigation: knowns and unknowns. *Carbon Management* 2: 303–333.

McArdle, R.E., Meyer, W.H. & Bruce, D. 1949. *The yield of Douglas-fir in the Pacific Northwest*. USDA Agricultural Technical Bulletin [report number 201 (revised)], Washington, DC, US.

Means, J.H., Hansen, H.A., Koerper, G.J., Alaback, P.B. & Klopsch, M.W. 1994. *Software for computing plant biomass 'BioPak Users' guide*. USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR-340, Portland, OR, US.

Mohler, C.L., Marks, P.L. & Sprugel, D.G. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology* 66: 599–614.

Munger, T.T. 1946. Watching a Douglas-fir forest for 35 years. *Journal of Forestry* 44: 705–708.

Peet, R.K. 1981. Changes in biomass and production during secondary forest succession. In: West, D.C., Shugart, H.H. & Botkin, D.B. (eds.) *Forest succession: concepts and application*, pp. 324–338. Springer, New York, NY, US.

Peet, R.K. & Christensen, N.L. 1987. Competition and tree death. *BioScience* 37: 586–595.

Pianka, E.R. 1970. On r and K selection. *American Naturalist* 104: 592–597.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-term studies in ecology*, pp. 110–135. Springer, New York, NY, US.

Sheil, D., Burslem, D.F. & Alder, D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83: 331–333.

Smithwick, E.A.H., Harmon, M.E., Remillard, S.M., Acker, S.A. & Franklin, J.F. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. *Ecological Applications* 12: 1303–1317.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. *Canadian Journal of Forest Research* 12: 18–28.

Spies, T.A. & Franklin, J.F. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B. & Huff, M.H. (eds), *Wildlife and vegetation of unmanaged Douglas-fir forests*, pp. 91–110. USDA Forest Service General Technical Report PNW-GTR-285, Portland, OR, US.

Spies, T.A., Franklin, J.F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Canadian Journal of Forest Research* 20: 649–658.

Staebler, G.R. 1955. *Gross yield and mortality tables for fully stocked stands of Douglas-fir*. USDA Forest Service Pacific Northwest Research Station Research Paper 14, Portland, OR, US.

Stephenson, N.L., Das, A., Condit, J.R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, (…) & Zavala, M.A. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507: 90–93.

Tepley, A.J., Swanson, F.J. & Spies, T.A. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. *Ecology* 94: 1729–1743.

USDA Forest Service. 1999. *Wood handbook – wood as an engineering material*. General Technical Report FPL-GTR-113. Forest Products Laboratory, Madison, WI, US.

Walker, L.R., Wardle, D.A., Bardgett, R.D. & Clarkson, B.D. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98: 725–736.

Weisberg, P.J. & Swanson, F.J. 2003. Regional synchroneity in fire regimes of western Oregon and Washington, USA. *Forest Ecology and Management* 172: 17–28.

West, D.C., Shugart, H.H. & Botkin, D.B. 1981. *Forest succession: concepts and application*. Springer, New York, NY, US.

Williamson, R.L. 1963. *Growth and yield records from well stocked stands of Douglas-fir*. USDA Forest Service Pacific Northwest Forest and Range Experiment Station Research Paper PNW-4, Portland, OR, US.

Worthington, N.P. 1957. *Some economic considerations in thinning Douglas-fir*. Pacific Northwest Forest and Range Experiment Station Research Note 137. Portland, OR, US.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Average annual mortality rate of all trees and the initial cohort based on percent of stems, and mortality rate of all trees based on percent of basal area.

Appendix S2. Average diameter at breast height (DBH) of trees alive and dead at each plot measurement.

Appendix S3. Total number of trees in three study plots assessed as dying from density-dependent causes (suppression/competition) and density-independent agents such as wind, insects and pathogens.

Appendix S4. Aboveground biomass (Mg per ha) of live trees at each plot measurement and the accumulated biomass dead trees since plot inception.

Appendix S5. Equations from BIOPAK used to calculate biomass or volume from tree diameter and height.