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Changes in biomass and production over 53 years in a coastal *Picea sitchensis* – *Tsuga heterophylla* forest approaching maturity

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Using periodic remeasurements of tagged trees in nine 0.4-ha sample plots in a *Picea sitchensis* (Bong.) Carr. – *Tsuga heterophylla* (Raf.) Sarg. forest at Cascade Hand Experimental Forest, Oregon, we calculated that biomass of bolewood increased from 570 Mg·ha^{-1} at age 85 years to 760 Mg·ha^{-1} at age 138 years. Net primary production of bolewood declined from 11 to about 6 Mg·ha^{-1}·year^{-1}, and mortality loss increased from 2 to about 6 Mg·ha^{-1}·year^{-1}. Values for 37-year-old plots in the same area were 210–360 Mg·ha^{-1}·year^{-1} bole biomass, 7–20 Mg·ha^{-1}·year^{-1} bolewood production, and 0–2 Mg·ha^{-1}·year^{-1} mortality loss. Indications are that bolewood production and biomass were lower in the older plots when they were 37 years old. In the older plots, biomass did not increase between ages 120 and 138. Of the photosynthate potentially available for bolewood production, some replaces biomass lost via mortality and some is allocated to maintenance (respiration plus allocation to fine roots). We estimate that one-quarter to one-half of the production is lost by mortality, and that mortality loss may thus be an important factor limiting forest biomass accumulation.

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À l'aide des résultats du remesurage périodique d'arbres marqués, dans neufs places échantillons de 0,4 ha établies dans une forêt de *Picea sitchensis* (Bong.) Carr. – *Tsuga heterophylla* (Raf.) Sarg. située dans la forêt expérimentale de Cascade Head en Orégon, nous avons calculé que la biomasse du bois de fût était passée de 570 à 760 Mg·ha^{-1} de l'âge de 85 à 138 ans. La production primaire nette de bois de fût a diminué de 11 à environ 6 Mg·ha^{-1}·an^{-1} et les pertes dues à la mortalité ont augmenté de 2 à environ 6 Mg·ha^{-1}·an^{-1}. Les valeurs pour les places échantillons vieilles de 37 ans dans la même région variaient de 210 à 360 Mg·ha^{-1}·an^{-1} pour la biomasse du bois de fût, de 7 à 20 Mg·ha^{-1}·an^{-1} pour la production de bois de fût et de 0 à 2 Mg·ha^{-1}·an^{-1} pour les pertes dues à la mortalité. Tout indique que la production de bois de fût et la biomasse du bois de fût étaient plus faibles dans les places échantillons plus vieilles lorsqu'elles avaient 37 ans. Dans les places plus vieilles, la biomasse n'a pas augmenté entre 120 et 138 ans. Une partie des produits de la photosynthèse potentiellement disponibles pour la production de bois sert à remplacer la biomasse perdue par la mortalité et une autre partie est affectée à la subsistance via la respiration et l'allocation vers les racines fines. On estime qu'un quart à un demi de la production est perdue à cause de la mortalité et que les pertes dues à la mortalité pourraient être un facteur important qui limite l'accumulation de biomasse forestière.

[Traduit par la revue]

Long-term variation in forest aboveground biomass accumulation is of interest to ecologists and foresters, as it can potentially reveal much about both ecosystem- and population-level controls of ecosystem function. Fluctuations or asymptotic declines in biomass following an initial peak, for example, might reveal important controls related to population dynamics (mortality and recruitment) or to ecosystem processes (e.g., respiration or nutrient immobilization; see Peet 1981; Sprugel 1985, and examples therein). In addition, an understanding of carbon storage patterns in ecosystems is crucial to understanding the role of the biosphere in the global carbon cycle and its response to global climate change (Woodwell et al. 1978; Emanuel et al. 1984; Goudriaan and Ketner 1984).

Kira and Shidei (1967) suggested that biomass increases in a logistic fashion during succession. They argued that biomass should increase rapidly early in succession when net production is highest, and then increase more slowly to an asymptote as respiratory loss increases with increasing biomass. This pattern is supported by several studies (e.g., MacLean and Wein 1976; Forcella and Weaver 1977; Holt and Woodwell (in Whittaker 1975); Peet 1981; T. Spies and J.F. Franklin, unpublished data), including simulations of species-rich subtropical forests (Doyle 1981).

A biomass peak late in succession, followed by a decline to a steady-state value was proposed by Loucks (1970). The peak occurs when individuals in an even-aged forest area reach maturity more or less simultaneously. The decline in biomass could be due to synchronous senescence and mortality, or it could be due to asynchronous (patchy) mortality. In the latter case, the decline occurs on some plots, but not on others, the net result being a decline in average biomass. Eventually, if the area is large enough to contain patches in all stages of recovery, a steady-state biomass, representing the average over these patches, is reached (Bormann and Likens 1979; Shugart and West 1981). A decline in biomass

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may also be a result of replacement of a large seral dominant by one lesser stature (Shugart and West 1981).

Peet (1981) identified two additional possible long-term patterns of biomass change following an initial phase of logistic increase: damped or sustained oscillations following the initial maximum. He suggested, by analogy with population models, that oscillations may be due to lags in regeneration or in release of limiting nutrients. Furthermore, any of four patterns could be generated depending on the degree of synchrony in mortality and the amount of lag in regeneration response.

Aboveground biomass increases only so long as net primary production of bolewood exceeds biomass loss via tree mortality. Hence the patterns of production and mortality are of interest for the interpretation of biomass dynamics. Net production reaches a maximum around the time of canopy closure (Waring and Schlesinger 1985) and subsequently declines because of increased respiration or reduced nutrient availability (Sprugel 1985, and references therein). Such a decline in productivity has been inferred from stand tables constructed for *Tsuga* forests in the northwestern United States (Meyer 1952), as well as for other systems (Zavitkovski and Stevens 1972; O'Neill and DeAngelis 1981; Waring and Schlesinger 1985; Pearson et al. 1987).

Biomass loss by canopy tree mortality should be low when trees are small and vigorous. At some point, thinning commences or stands begin to break up because of disturbance or natural senescence of canopy trees (Bormann and Likens 1979; Peet 1981; Shugart and West 1981). Biomass loss due to tree mortality should then reach a maximum. Following that, mortality loss might remain constant, fluctuate, or decline, depending on the temporal and spatial scale of disturbance patterns relative to the size of the sample, the pattern of thinning mortality, the longevity of the component species, and the synchrony of canopy tree death.

Patterns of production and biomass change are mostly inferred from chronosequences and thus are subject to confounding of temporal and spatial variability. Time-series data would circumvent this problem, but such data are scarce. A limitation of time-series data is that they are often limited to measurements of diameter at breast height (dbh) and individual height. Information on other components, especially crowns and roots, from chronosequence studies (e.g., Grier et al. 1981; Keyes and Grier 1981) can help provide a context for interpretation of bolewood production, loss of bolewood via mortality, and the resultant net change in aboveground bolewood biomass. Here we report on changes in production rates, mortality rates, and consequent biomass accumulation using a 53-year time series in a forested area dominated by *Tsuga heterophylla* (Raf.) Sarg. and *Picea sitchensis* (Bong.) Carr. on the coast of Oregon. The forest cover originated after a large fire in about 1845; long-term remeasurement was begun in 1935, at stand age 85 years. As succession proceeds, the more massive species (*Picea*) might eventually be replaced by the more shade-tolerant species (*Tsuga*). Hence, we predicted that biomass, net production, and mortality loss would reach peaks and decline, especially as canopy tree mortality was substantial in some plots.

Study site

The study was done at the Cascade Head Experimental Forest near Otis, Lincoln County, Oregon (45°03′N, 123°55′W). The environment of the area was described by Grier (1978) and Greene (1982), from which much of the following is abstracted. The forest is situated on a ridge system that juts out as one of the characteristic headlands of the Pacific Northwest coast. A cool and wet climate prevails; annual precipitation is 3420 mm, coming mostly in the winter; mean January temperature is 4.6°C, and July temperature is 15.7°C. Actual evapotranspiration is 525 mm (Mather 1974). The ridge system reaches 400 m elevation. Marine tuffaceous siltstone of the Tyee formation overlies a volcanic substrate (Baldwin 1964; Snavely and Wagner 1964). Soils are residual silt loams to silty clay loams, moderately well drained, strongly acidic (surface pH about 4.0), and high in nitrogen (0.5%) and organic matter (28%) in the A1 horizon.

Forest cover is predominantly *Tsuga heterophylla* and *Picea sitchensis* (SAF cover types 223, 224, and 225 (Eyre 1984); spruce–cedar–hemlock of Kuchler (1964); *Picea sitchensis* Zone of Franklin and Dyrness (1973)). Most of the trees germinated after a widespread catastrophic fire, the Nestucca burn of the mid-19th century (Morris 1934; Munger 1944), though a few older trees apparently survived the fire (Greene 1982; Quaye 1982). In 1989, average tree height was about 45 m. Density ranged from 230 to 540 stems/ha (>5cm dbh); basal area was 90–120 $m^2 \cdot ha^{-1}$. Important understory shrubs include *Menziesia ferruginea* Smith, *Vaccinium ovalifolium* Smith, and *Oplopanax horridum* (J.E. Smith) Miq. The herb layer consists of ferns, especially *Polystichum munitum* (Kaulf.) Presl. and *Blechnum spicant* (L.) With., and herbs, especially *Tiarella trifoliata* L. and *Oxalis oregana* Nutt. ex T & G.

Methods

Nine 0.4-ha plots were established in 1935 along the ridgetop 1–4.5 km from the Pacific Ocean on moderate south- to southwest-facing slopes in uniform timber. All individuals greater than 5 cm dbh were tagged and measured. Living trees were remeasured in 1940, 1945, 1955, 1968, 1978, 1983, and 1988, and trees dying in each interval were recorded. The fieldwork was done by the Pacific Northwest Research Station, USDA Forest Service; data are archived in the Oregon State University Forest Science Data Bank. Growth and yield data for the period 1935–1968 (ages 85–118) were summarized by Smith et al. (1984). Other aspects of yield and mortality in these plots have been summarized by Grier (1976, 1978), Sollins (1982), and Harcombe (1986). We supplemented these data with measurements from six plots for ages 12–37 collected as part of a hemlock and spruce spacing study also conducted at Cascade Head Experimental Forest (see Hoyer and Swanzy 1986 for details). The trees in the young plots originated by natural regeneration after shelterwood cutting or clear-cutting. We used data from spacings of 1 and 6.5 m (240 – 10 000 individuals/ha). The presumed range in initial density of the older plots was 500 – 10 000 individuals/ha (Harcombe 1986).

Allometric equations for estimating total aboveground biomass exist (Gholz et al. 1979; Standish et al. 1985), but we were concerned about problems of extrapolation beyond the size range and also appropriateness of the equations for the conditions represented by the study site. Trial computations indicated foliage biomass of 30–35 $Mg \cdot ha^{-1}$, even when adjusted for sapwood area. Given leaf litter input of

TABLE 1. Regression coefficients for equations used to calculate tree volume in cubic metres (stump, wood, and bark) and percent sapwood from diameter at breast height in centimetres

(A) Tree volume

Age (years)	B_0	B_1	C	r^2	N
Picea sitchensis					
85	−7.3478	2.151	1.006	0.975	151
90	−7.6585	2.236	1.008	0.967	197
95	−7.7800	2.274	1.010	0.971	143
105	−7.6670	2.254	1.005	0.982	191
118	−8.2626	2.401	1.007	1.007	138
Tsuga heterophylla					
85	−9.1427	2.621	1.009	0.974	265
90	−8.7916	2.533	1.006	0.977	304
105	−8.9792	2.579	1.007	0.978	279
118	−8.8547	2.550	1.005	0.984	268
128	−8.4974	2.467	1.004	0.985	201
Pseudotsuga menziesii					
85	−8.2664	2.378	1.003	0.983	107
90	−8.0887	2.339	1.002	0.988	113
95	−7.7379	2.276	1.001	0.993	35
105	−8.1665	2.361	1.002	0.987	81
118	−8.0256	2.348	1.002	0.989	41

NOTE: Regression equation form was $\ln(Y) = \ln(B_0) + B_1\ln(X)$. To correct for bias, the antilog of $\ln(Y)$ was multiplied by C.

(B) Percent sapwood

	B_0	B_1	B_2	r^2	N
Picea sitchensis	31.53	0.1021	137.43	0.95	17
Tsuga heterophylla	54.38	0.2096	78.79	0.92	8
Pseudotsuga menziesii	21.88	0.0651	135.49	0.97	16

NOTE: Equation form was $Y = B_0 + B_1X + B_2/X$.

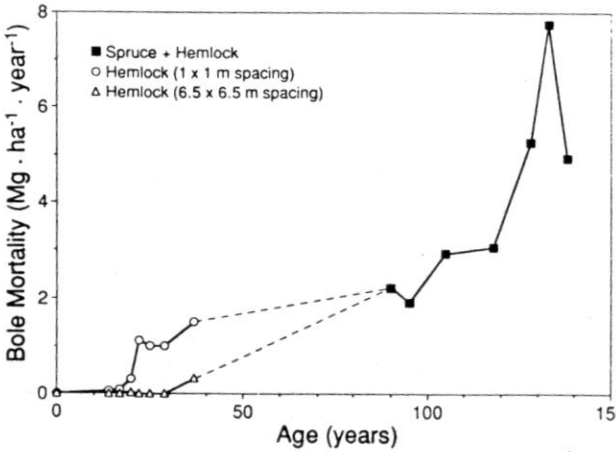

FIG. 1. Biomass loss by tree mortality vs. stand age. Open symbols represent data from 7- to 37-year-old *Tsuga heterophylla* spacing trials initiated in 1952. Closed symbols represent averages of measurements made on nine 0.4-ha plots from ages 85 to 138 years.

ca 4 $\mathrm{Mg\cdot ha^{-1}}$ (Grier 1976) and leaf retention of 4–5 years (personal observations), foliage biomass should be 16–20 $\mathrm{Mg\cdot ha^{-1}}$ rather than 30–35 $\mathrm{Mg\cdot ha^{-1}}$. Because of this discrepancy, we chose not to compute foliage biomass. It seems unlikely that this will change the shapes of the biomass curves, as leaf and branch mass probably peak early in stand development and remain relatively constant, at least until peak bole biomass is reached. It is recognized that belowground biomass and production are significant fractions of total biomass and production, but neither allometric equations nor data for these components are available for the plots under study here.

Biomass of living and dead trees was calculated by multiplying wood density by individual tree volume. Individual tree volume was estimated using a two-stage procedure. First, volume was determined from optical dendrometer measurements (Grosenbaugh 1963) made on sample trees (52 *Picea*, 121 *Tsuga*, and 215 *Pseudotsuga*), and a tree form factor was calculated according to the following formula:

$$[1] \quad F = (\pi r^2 H)/V$$

where V = volume, r = tree radius at breast height, H = height, and F = form factor. It may be noted that if $F = 3$, then tree boles are cones, and if $F = 2$, then tree boles are paraboloids. Second, volume was calculated for the subsample of trees for which height measurements existed (see Table 1 for sample sizes) according to the above formula, using measured dbh, height, and the calculated form factor. Then, for each measurement period, separate regressions of ln(volume) vs. ln(dbh) were run for *Tsuga, Picea*, and *Pseudotsuga menziesii* (Mirb.) Franco (see Table 1 for regression parameters) to relate volume to dbh. The following regression model was used:

$$[2] \quad \ln(V) = \ln B_0 + B_1 \ln(D)$$

where D = dbh (cm) and B_0 and B_1 are regression constants. Finally, the regression equations were used to calculate volume from dbh for each tree in the data set. Because of the bias introduced in transformation of $\ln(V)$ back to arithmetic units (Baskerville 1972), the arithmetic value of V was adjusted by a correction factor

$$[3] \quad C = \exp(\mathrm{mse}/2)$$

where mse is the mean square error of the ln–ln regression.

To convert volume to biomass, we used wood density values of 0.420 $\mathrm{Mg\cdot m^{-3}}$ for *Tsuga*, 0.369 $\mathrm{Mg\cdot m^{-3}}$ for *Picea*, and 0.449 $\mathrm{Mg\cdot m^{-3}}$ for *Pseudotsuga* (Smith 1970; Maeglin and Wahlgren 1972).

Sapwood mass for the nine 0.4-ha plots was estimated by first generating regressions of percent sapwood (Y) vs. dbh (D) for *Tsuga*, *Picea*, and *Pseudotsuga* from the data of Buchanen and Englerth (1940). The form of the regressions was as follows:

$$[4] \quad Y = B_0 - B_1 D + \mathrm{B}_2/D$$

Percent sapwood volume was then calculated from the dbh of each tree, and this was multiplied by bole mass to get sapwood mass.

Mortality was calculated as the sum of the bole biomass of all trees that died during an interval. Biomass at death was estimated using dbh at the previous measurement. Net primary production of boles (NPPB) was calculated as follows:

$$[5] \quad \mathrm{NPPB} = \mathrm{d}B + M$$

where dB is the difference in standing live bole biomass between one measurement period and the next, and M is the biomass of the trees that died during the interval. This is equivalent to calculating the sum of the biomass increments for all stems that survived a remeasurement interval.

TABLE 2. Annual bole mortality (Mg·ha^{-1}·year^{-1}) by plot in each measurement interval

Plot	Stand age						
	90	95	105	118	128	133	138
1	2.7	1.7	4.5	5.1	3.6	3.8	3.0
3	3.6	1.1	2.3	2.3	2.9	3.2	1.9
4	1.1	0.3	1.1	1.6	1.7	8.7	2.0
5	1.5	1.9	5.2	3.9	3.8	6.8	0.9
7	0.8	2.8	0.9	3.6	3.5	11.2	6.3
8	4.5	2.6	3.7	2.9	5.2	9.6	4.7
10	3.7	0.9	3.3	3.1	2.9	3.8	7.4
12	0.5	4.4	1.2	1.9	7.2	5.4	8.5
13	1.4	1.5	4.0	3.1	16.6	17.1	9.8
Mean	2.2	1.9	2.9	3.1	5.3	7.7	4.9
SE	0.5	0.4	0.5	0.3	1.4	1.4	1.0

NOTE: The study began at stand age 85 in 1935; the final remeasurement was in 1988 at nominal stand age 138. Original plot numbers are retained so as to allow cross-referencing with other studies.

Results

Mortality

Biomass loss due to stem mortality for the last 20-year period in the plots averaged 5.8 Mg·ha^{-1}·year^{-1}, an annual loss rate of about 0.75% of the standing crop biomass. This is higher than the average for mature productive conifer forests (3.2 Mg·ha^{-1}·year^{-1}; Harmon et al. 1986). Fine litter (needles and branches) input in similar ecosystems is 3.5–6.2 Mg·ha^{-1}·year^{-1} (Grier 1976; Cole and Rapp 1981). Branch input associated with stem mortality would be about 0.8 Mg·ha^{-1}·year^{-1} (assuming that it is 12% of total dead tree mass; Sollins 1982). Hence, a rough estimate of total aboveground detritus input would be 10.1–12.8 Mg·ha^{-1}·year^{-1}, of which 45–57% is coarse woody debris. This percentage is also high (Harmon et al. 1986), but it may be typical of conifer forests in the Pacific Northwest.

Although Sollins (1982) found no clear temporal pattern in coarse woody debris production in comparing this forest with others of different ages, we found a significant increase between ages 85 and 138 (Fig. 1, Table 2; the second-order term in a polynomial regression of cumulative mortality loss with time was significant; $p < 0.05$).

Concentrated blowdown at age 122 (1972) resulted in major loss of biomass in plot 13, but its effect was dampened by the values from other plots not affected by blowdown and also by the fact that the blowdown was not instantaneous; the gap continued to grow, resulting in biomass loss over a 20+ year period. The strong peak in mortality at 133 years (the 1978–1983 interval) is a consequence of a windstorm in 1981 that caused considerable local damage (Harcombe 1986). It is interesting to note that the 1981 storm, which blew down scattered trees over a large area, caused greater overall mortality loss than did the storm in 1972 which caused a 0.25-ha gap in plot 13, and initiated continued loss of biomass from that plot. While the concentrated blowdown in plot 13 was more obvious in the field, the diffuse effects of the 1981 storm were more important to overall mortality loss.

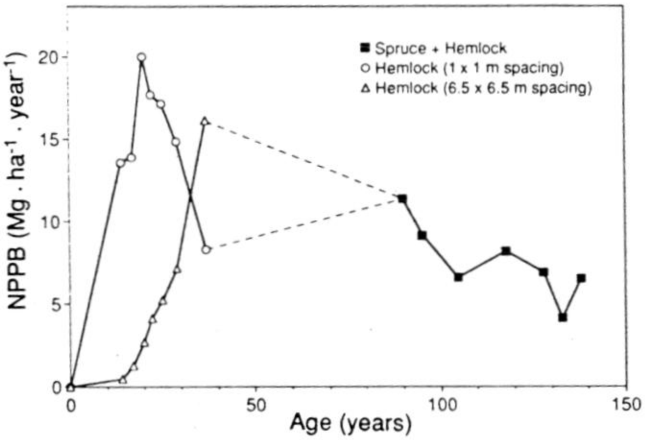

FIG. 2. Net primary production of bolewood (NPPB) vs. stand age.

TABLE 3. Net primary production of bolewood (Mg·ha^{-1}·year^{-1}) by plot and measurement interval (stand age in years)

Plot	Stand age						
	90	95	105	118	128	133	138
1	10.7	7.9	5.0	7.0	7.4	3.6	6.0
3	10.3	10.3	6.7	8.3	7.0	3.5	6.4
4	12.3	10.7	7.7	9.0	8.6	2.0	6.2
5	13.2	11.4	7.7	9.5	7.5	0.6	6.8
7	10.2	7.1	6.1	7.4	8.0	5.1	4.9
8	11.1	8.0	5.1	7.4	8.3	2.6	6.4
10	13.5	11.9	7.1	10.0	4.4	9.2	8.3
12	10.6	8.0	7.3	8.0	5.8	6.4	5.0
13	10.1	6.9	6.6	7.1	5.5	2.7	8.4
Mean	11.3	9.1	6.6	8.2	6.9	4.0	6.5
SE	0.4	0.6	0.3	0.3	0.4	0.8	0.4

decline to 4–7 Mg·ha^{-1}·year^{-1} over the last 20 years in the older growth and yield plots (Fig. 2; Table 3). Adding 4–7 Mg·ha^{-1}·year^{-1} in fine litter and branch input (Grier 1976; Sollins 1982) gives a total current aboveground net primary productivity of 10–14 Mg·ha^{-1}·year^{-1} at age 138. The maximum value of 15–20 Mg·ha^{-1}·year^{-1} NPPB is in the range observed for temperate mixed forests (Lieth 1975), but is somewhat lower than that estimated for a single 26-year-old *Tsuga* stand nearby (25 Mg·ha^{-1}·year^{-1}; Fujimori 1971; Grier 1976).

The early peak in NPPB in the densest young plots is not consistent with an expected smooth decline in NPPB between ages 37 and 90. To reach 570 Mg·ha^{-1} at 85 years from a starting biomass of 360 Mg·ha^{-1} at 37 years (high-density spacing trials), average biomass increment must be only 5.1 Mg·ha^{-1}·year^{-1} for the unmeasured interval. Thus, an early peak in NPPB would have to be accompanied with either a peak in mortality loss or a depression in NPPB between 37 and 85 years, or both, rather than a continuous increase in biomass and gradual decline in NPPB. Heavy thinning mortality does occur in dense young stands, so a mortality peak is conceivable; a period of depressed productivity could also occur if trees surviving intense thinning are slow to recover because of small crowns and low root

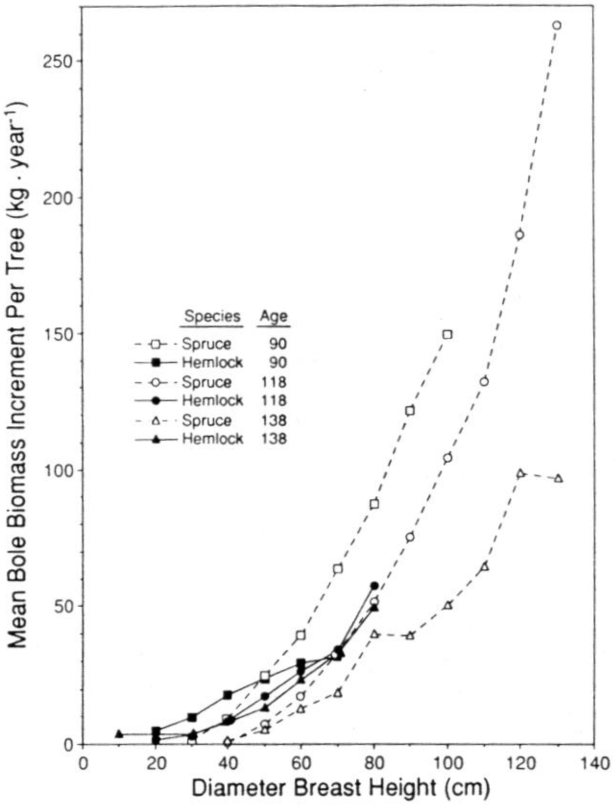

FIG. 3. Mean biomass increment per tree vs. dbh class for *Tsuga heterophylla* and *Picea sitchensis* at three different stand ages (90, 118, and 138 years).

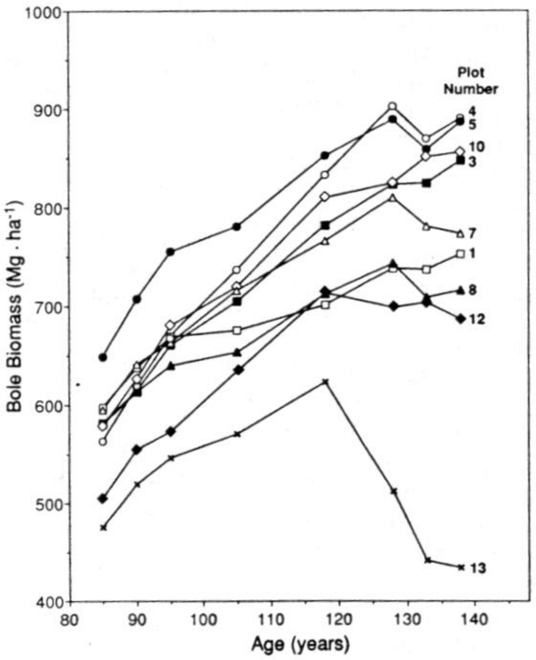

FIG. 4. Total biomass of boles in each of nine 0.4-ha sample plots.

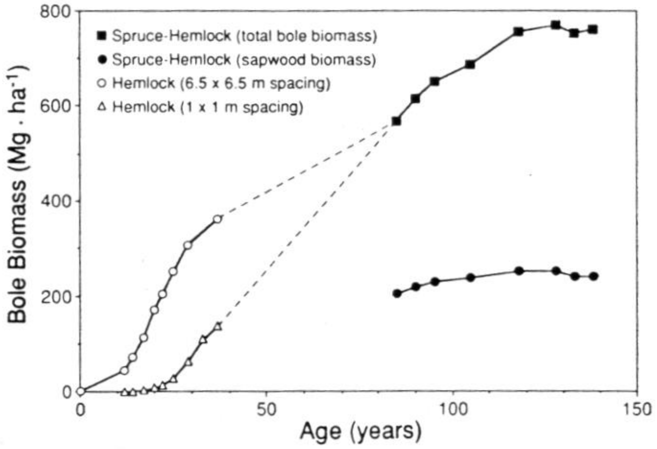

FIG. 5. Mean biomass of boles over nine 0.4-ha sample plots.

assume that NPPB in the older plots began to increase later and peaked at a lower value than in the densest young plots. Such a delay might be the result of low initial stocking density (cf. low-density young plots) or shrub competition.

The NPPB minimum in the penultimate measurement period (age 128–133) may have been due to the 1981 storm that reduced the number of living trees and the amount of foliage on the remaining trees. The overall decline from age 85 to 138 involves both fewer stems and slower growth per tree: both species declined about equally in NPPB (47% for *Picea* and 42% for *Tsuga*) and in number of stems (29 and 31%, respectively). However, *Picea* declined more in average NPPB per tree (26%) than did *Tsuga* (15%), in part because of a strong decline in diameter-specific growth with age (Fig. 3). In spite of the decline in *Picea*, that species still contributed more NPPB per tree than *Tsuga* (24% of all stems at age 138, but 48% of the NPPB).

In the last two measurements (ages 133 and 138), mass of new stems (ingrowth) of *Tsuga* was 3.3 and 6.0 $\mathrm{Mg \cdot ha^{-1}}$, respectively. Bolewood production by the stems first recorded in 1983 averaged 0.2 $\mathrm{Mg \cdot ha^{-1} \cdot year^{-1}}$ during the 1983–1988 period. Our observations and some measurements show that considerable advance regeneration is present. Therefore, ingrowth may continue to be an important component of productivity in these plots.

The ratio of mortality loss to NPPB was less than 0.01 in the young plots and was 0.20 at 90 years. The average over the last 20 years was slightly greater than 1.0. This convergence in trends in NPPB and mortality suggests that steady-state bole biomass may have been reached.

Bole biomass

Bole biomass curves for the nine plots show maxima at 600–900 $\mathrm{Mg \cdot ha^{-1}}$ (Fig. 4, Table 4), near the high end of the range reported for this forest type (e.g., McKee et al. 1982) or calculated from volume tables for *Tsuga* (Barnes 1962). Variation in bole biomass among plots was strongly related to abundance of *Picea* (Kendall's $\tau = 0.67$; $p < 0.05$). Of the nine plots, three are still increasing in bole biomass, four have declined slightly in the last 10–20 years, and one, which experienced major blowdown at age 122, has declined substantially over the last 20 years. The average bole biomass over all plots peaked at age 128 (Fig. 5), with a subsequent decline of less than 2%. This peak is later than that for *Pinus taeda* L. (50–80 years; Peet 1981) or *Alnus rubra* Bong. (45 years; Zavitkovski and Stevens 1972), but earlier than that for *Pseudotsuga menziesii* (>500 years; T. Spies and J.F. Franklin, personal communication). The overall temporal pattern in biomass accumulation is roughy sigmoid, with maximum accumulation occurring between 25 and 60 years, depending on initial density (Fig. 5). Sap-

TABLE 4. Total bolewood biomass (Mg·ha^{-1}) by plot and measurement interval (stand age in years)

	Stand age							
Plot	85	90	95	105	118	128	133	138
1	598.7	638.6	670.1	676.1	701.1	739.0	738.0	753.3
3	582.1	615.4	661.3	705.3	782.8	823.6	825.2	847.9
4	564.4	620.2	672.0	737.9	833.4	902.6	869.2	890.4
5	649.1	707.5	755.2	780.0	852.5	889.3	858.5	888.0
7	595.6	642.7	664.4	716.3	766.3	810.8	780.4	773.6
8	580.5	613.4	640.2	654.3	712.2	743.4	708.2	716.9
10	578.3	627.1	682.0	720.0	810.0	824.9	851.9	856.4
12	505.3	555.9	573.9	635.0	713.6	699.6	704.8	687.5
13	475.8	519.2	546.1	571.1	623.8	513.0	441.1	434.0
Mean	570.0	615.6	651.7	688.5	755.1	771.8	753.0	760.9
SE	17.1	17.8	20.4	20.7	24.5	39.4	49.4	47.7

wood biomass increased between ages 85 and 138 from 205 to 241 Mg·ha^{-1} (Fig. 5). As a fraction of total bole biomass, it declined from 36 to 32%.

Discussion

Bole biomass in these *Tsuga–Picea* plots levelled off at about 120 years as NPPB declined and mortality increased. The convergence of mortality and NPPB in the range of 5–7 Mg·ha^{-1}·year^{-1} suggests that bole biomass may remain roughly constant. In contrast, yield tables for *Tsuga* (Barnes 1962) show increasing volume through 300 years to a value about 20% higher than volume at age 120.

Declining NPPB over time could be cause by reduced photosynthetic fixation of carbon, reduced allocation to boles, or increasing bole respiration. In this system, there is some evidence for reduced leaf area, in that trees in these plots had very shallow crowns (crown ratios of <15%) compared with trees in older plots on the Olympic Peninsula of Washington (M.E. Harmon, personal observation). On the other hand, there is no published evidence for declining leaf litter fall with stand age in conifers (Vogt et al. 1986). Reduced photosynthesis might be the result of unfavorable weather conditions, but the smooth decline over 80 years is not what one would expect if weather were responsible. Increased bole respiration could account for the reduction in NPPB. Even though inner bark and sapwood reach a constant thickness at a relatively small diameter (Lassen and Okkonen 1969; Smith and Kozak 1971), we found that *Picea* and *Tsuga* sapwood mass increased about 20% over the period of observation. Therefore, increased bole respiration might account for some of the decline in NPPB. This is consistent with measured increases in stem respiration with tree size in *Pinus contorta* Dougl., which could account for about 13% of the decline in NPPB with tree size (Ryan 1988).

Increased allocation of photosynthate to roots could also reduce NPPB. Fine-root production in a 180-year-old *Abies amabilis* (Dougl.) Forbes stand was 70% greater than that in a 23-year-old stand (Grier et al. 1981). In contrast, fine- and mycorrhizal-root biomass in the forest floors of *Pseudotsuga* plots increased only until canopy closure, remaining constant in older plots (Vogt et al. 1983). We know of no data on changes in fine-root biomass with age for *Picea–Tsuga* forests. Increased allocation to roots is expected if soil fertility declines because of nutrient immobilization in forest floor material (Keyes and Grier 1981). However, the soils in this region are highly productive. In all likelihood, reduced photosynthesis, increased bolewood respiration, and decreased allocation of photosynthate to boles all contribute to the decline in NPPB with time.

It is too early to tell whether bole biomass will continue to increase, as suggested by *Tsuga* yield tables (Barnes 1962), remain constant, as suggested by the convergence of production (NPPB) and loss (mortality), or decline. Increases in the range suggested by the yield tables (ca. 1 Mg·ha^{-1}·year^{-1}) are undetectable over the short time period of the present study. However, the increase shown in the yield tables may not apply to the plots we studied, as individual plots with substantial blowdown were likely excluded in the yield study, thus raising the average biomass for older plots. For individual plots, bole biomass may continue to increase in the absence of mortality or it may decline if blowdown is substantial. Averaging over several plots in the case reported here suggests that on a slightly broader scale, bole biomass may reach an asymptote relatively early in succession if plots experiencing mortality are not excluded.

With respect to a decline in bole biomass, our results suggest that the transition to steady state need not involve a decline in areas as small as 4 ha (the total plot area sampled was 3.6 ha). The major factors contributing to the apparent absence of a decline in bole biomass with age seem to be asynchrony in the onset of mortality and the small size of disturbance patches relative to the area sampled. Though mortality loss may fluctuate by 30–50% from one measurement period to the next, in absolute terms it remains a small fraction of the steady-state biomass.

The empirical value for the minimum area within which average bole biomass approaches a steady state is consistent with the predictions of Shugart and West (1981) for forests characterized by small disturbances such as single-tree gaps. They suggest that "quasi-equilibrium" biomass is reached in areas approximately 50 times average disturbance size. In other words, having 50 or more disturbance patches assures that eventually patches in all stages of recovery will be present, and so average biomass becomes roughly constant over time. In this *Picea–Tsuga* system, modal gap size is 700–800 m^2 (Taylor 1990), and so the estimated equilibrium landscape unit for bole biomass is 3–4 ha.

Large-scale blowdown or synchronous mortality of canopy trees could alter the scenario of asymptotic approach to a steady-state biomass at 120 years. The former certainly can occur, though rough estimates suggest that blowdown of even one whole plot occurs on the order of once in 450 years (Harcombe 1986); the probability that several of the nine plots, which are scattered over 3000 ha, would blow down in one storm is very small. Some have argued that synchronous senescence or death is common in even-aged stands (e.g., Mueller-Dombois 1987 and references therein), but such a phenomenon has not been described for *Tsuga–Picea* stands, and life-spans for both species are in the 400+ year range (Franklin and Waring 1979). Another factor that could contribute to long-term biomass fluctuations is slow recovery due either to recruitment inhibition by canopy dominants, or to nutrient immobilization in coarse woody debris (Peet 1981; Sprugel 1985). While there was a long period of recruitment inhibition early in the developmental history of this forest (Harcombe 1986), substantial advance regeneration now exists in these plots, and recruitment into the tree size classes following blowdown in plot 13 began within 20 years of the disturbance. In any case, the asynchrony among plots in the onset of mortality reduces the poential importance of regeneration lags, as they would be masked by the asynchrony of tree death.

In addition to synchrony of mortality and lags in regeneration, one other population-level process, species replacement, can affect the pattern of long-term biomass change during forest development following fire (Shugart and West 1981; Shugart and Noble 1981). In the plots described in this study, the possibility exists for a modest decline in biomass due to replacement of *Picea* by *Tsuga*. Such a possibility seems more likely in other systems where the differences in maximum size between a seral species and its successor are greater. One such example is replacement of a massive, long-lived seral dominant (*Pseudotsuga menziesii*) by a smaller, shorter lived climax dominant (*Tsuga heterophylla*) in old-growth forests in the mountains and interior valleys of western Oregon and Washington (T. Spies, personal communication). Models of these forests suggest long-term declines on the order of 25% from a maximum of about 800 $\mathrm{Mg \cdot ha^{-1}}$ (Dale et al. 1986).

The above discussion highlights mortality as a key process influencing the pattern of bole biomass accumulation and the steady-state bole biomass attained by a system. Declining NPPB due to increasing maintenance cost (including respiratory load plus any increased allocation to fine-root production) is the other important pattern influencing bole biomass accumulation. The relative importance of maintenance cost and bolewood mortality in limiting bole biomass increase might be assessed as follows: Assume that the maximum measured NPPB (which occurs during early forest development when wood respiration and fine-root turnover are low) is the amount of photosynthate available to meet any increase in maintenance costs and to replace mortality loss, if crown photosynthesis, and respiratory efficiency do not decline. This photosynthate is first drawn upon to meet maintenance costs, and any remaining is available for bolewood production. Then at steady state, when NPPB = mortality loss, NPPB/NPPB(max.) is the fraction of available photosynthate going to replace mortality loss, and 1 – (NPPB/NPPB(max.)) is the fraction going to meet maintenance costs of above- and below-ground woody tissue (including fine-root replacement). In this system, if we assume that NPPB = 5 $\mathrm{Mg \cdot ha^{-1}}$ and NPPB(max.) is 10–20 $\mathrm{Mg \cdot ha^{-1}}$, replacement of mortality loss accounts for 25–50% of the available photosynthate and maintenance cost accounts for 50–75%. If a lower, more conservative value is taken for NPPB(max.), the proportion of carbon allocated to maintenance would be lower. Thus we conclude that while increasing maintenance cost is important in limiting biomass increase, mortality loss is also important. Furthermore, mortality may be more important from the standpoint of control: if mortality loss rate is low, then biomass will be higher, and more of the available photosynthate will be lost via respiration; if mortality loss rate is high, then biomass will be lower, and more of the photosynthate will be available for wood production. In a more immediate sense, mortality loss is much more variable in time and space than NPPB and maintenance cost and so contributes more strongly to temporal and spatial variation inbole biomass.

Conclusion

While theory and some models have predicted an intrinsic response during succession involving a peak in biomass followed by a decline to steady state, it was not observed in this and other empirical studies, in spite of conditions that might promote it (e.g., few species, blowdown, and a seral dominant individually more massive than its successor). Our study suggests that one important reason for the lack of the biomass peak is asynchrony in the onset of mortality. Here, disturbance begins in some plots well before maximum biomass is reached in others, so there is little or no decline to the steady state. It may be that in other systems the lag in the onset of mortality is longer and the increase once it begins is steeper than in this system, where high winds are frequent. Where the causes of individual tree falls may be less assuredly storm related, senescence or synchronous mortality may play a larger role. A consequence of this difference is that in forests like this *Tsuga–Picea* forest, mortality is important relative to maintenance cost in controlling steady-state biomass.

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