Biomass accumulation over the first 150 years in coastal Oregon *Picea-Tsuga* forest

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Abstract. Production and mortality are the component processes that together determine the biomass dynamics of forests. Due to the significant role of forests in the global carbon cycle, it is important to assess how these two processes affect the maximum biomass attained by forests, as well as the dynamics leading up to and following peak biomass. We address these questions for two sets of plots in *Picea sitchensis-Tsuga heterophylla* forest on the northern Oregon coast that originated from a catastrophic wildfire in the 1840s, using new data on dynamics of live trees and stocks of coarse woody debris (CWD). The set of plots closest to the ocean and occupying steeper, more dissected terrain with areas of thin soils has lower biomass, lower net primary production (NPP) of bole wood and higher tree mortality as a fraction of standing biomass. The two sets of plots have similar CWD levels, most of which has accumulated in the last 25 yr. The present disparity in biomass between the two sets of plots appears to be the result of lower NPP on the low-biomass plots for the entire 140+ yr history of the forest. Over the 58 yr that the high-biomass plots have been measured (from stand age 85 to 143 yr), NPP of bole wood has declined by 41%. Only ca. 6% of this decline can be accounted for by an increase in maintenance respiration of woody tissues. For both sets of plots relative constancy of biomass in the long term appears likely, due to a short time lag in tree regeneration, asynchronous tree mortality and little overall decline in NPP of bole wood in recent decades. However, since tree mortality as a fraction of standing biomass is higher on the low-biomass plots, and NPP of bole wood is slightly lower, the difference in biomass between the two sets of plots should increase if current rates of production and mortality persist.

Keywords: Coarse woody debris; Long-term biomass dynamics; Net primary production; *Picea sitchensis*; Tree mortality; Tree recruitment; *Tsuga heterophylla*.

Abbreviations: CHEF = Cascade Head Experimental Forest; CWD = Coarse woody debris; DBH = Diameter at breast height; NCRNA = Neskowin Crest Research Natural Area; NPPB = Net primary production of boles.

Introduction

Forests play an important role in the global carbon cycle, with natural dynamics and human management of forests largely determining whether the terrestrial biosphere is a net source or sink for carbon (Dixon et al. 1994). Hence, to understand the role of forests in the global carbon cycle, it is necessary to explain the dynamics of biomass accumulation and the patterns of change after maximum accumulation (Cooper 1983).

Temporal patterns of biomass change in forests and their causes are also long-standing, fundamental issues for basic and applied ecology at regional and local scales, both for the aggrading phase leading to maximum biomass and for the following period (Peet 1981, 1992; Cooper 1983; Pare & Bergeron 1995; Cohen et al. 1996). In this paper we investigate the interaction between production and mortality in determining differences in maximum biomass attained on two sets of plots in mature forest of *Picea sitchensis* and *Tsuga heterophylla* on the Oregon coast. We also reconstruct temporal patterns in the aggrading phase, and use observations of live tree dynamics and coarse woody debris stores to explore potential trends in the period following maximum biomass. Long-term observations of tree growth and mortality, in association with inventories of coarse woody debris, make it possible to assess the relative importance of production and mortality in controlling biomass of forests during and after the aggrading phase.

The amount of standing biomass of tree boles at any given time represents the integration of net primary production of boles (NPPB) and tree mortality from the initiation of the stand until the time in question. Thus, tree mortality could limit maximum standing biomass. In a previous paper (Greene et al. 1992) we reported high local variation in biomass in 140 yr-old plots in forest dominated by *Picea sitchensis* and *Tsuga heterophylla* on the Oregon coast. One set of plots (CHEF); (Harcombe 1986; Harcombe et al. 1990) had relatively high biomass (750Mg/ha in 1988), whereas another nearby set of plots (NCRNA); (Greene et al. 1992) had

considerably lower biomass (462 Mg/ha in 1989). Based on long-term observations of live trees on the two sets of plots, a number of alternative scenarios could be developed to explain the current difference in standing biomass. A key, but missing, piece of evidence for discriminating among alternative explanations was measurements of CWD (Greene et al. 1992). If the two sets of plots had had similar levels of production, and therefore had similar biomass at some time in the past, the difference in current biomass would be a result of higher loss to mortality in the low-biomass plots, and those plots would have substantially higher CWD (Greene et al. 1992). An alternative hypothesis is that if the difference in standing biomass was caused by long-term differences in production, then CWD would not differ substantially between the plots. Thus, the alternative to higher CWD on the low-biomass plots would be higher NPPB on the high-biomass plots during the aggrading phase. During the period that both sets of plots were measured NPPB has declined (Harcombe et al. 1990; Greene et al. 1992). The alternatives are not mutually exclusive, in that the low-biomass plots may have had both higher mortality and lower NPPB in the past. Implicit in both scenarios is the assumption that the rate of CWD decomposition has been the same on the two sets of plots. This is reasonable, given the similarities in climate and biota (Harmon et al. 1986).

Recently, the issue of decline in NPPB after a peak relatively early in forest development (i.e. well before the biomass peak) has come under scrutiny (Gower et al. 1996; Ryan et al. 1997). Until the renewed interest, the most widely accepted explanation for the decline in NPPB during stand maturation has been increasing respiration due to increasing amounts of non-photosynthetic tissue (Kira & Shidei 1967; Sprugel 1985). Recent work, however, suggests that respiration of non-photosynthetic tissue may account for only a small portion of the decline in NPPB during stand development and that a variety of other causes are more important including reduced leaf area, reduced assimilation efficiency of canopies or changes in allocation from above-ground wood production to below-ground production (Gower et al. 1996; Ryan & Waring 1992; Ryan et al. 1997).

With respect to long-term trends after the peak in biomass accumulation, there are several possibilities. Peet (1981, 1992) summarized empirical patterns and created a theoretical framework that could account for many different patterns of biomass variation over time. The basic patterns include sigmoidal increase of biomass to an asymptote, or sigmoidal increase to a peak, followed by a decline with or without oscillations. According to Peet (1981), the different temporal patterns are caused by different degrees of synchrony of tree mortal-

ity and whether or not there are time lags in tree regeneration. Where tree mortality is asynchronous and tree regeneration continuous, there is likely to be no decline from peak biomass. Time lags in tree regeneration lead to oscillations in biomass, which are accentuated where tree mortality occurs in pulses.

In this paper, we present new measurement data for live trees and data on CWD stocks and inputs over time. These data allow us to assess the relative importance of production and mortality in causing the current difference in standing biomass between stands. We also reconstruct NPPB, mortality, accumulation of biomass and CWD accumulation over the life of these stands to gain further information about the degree and timing of differences between them. Finally, we use the data to distinguish among alternative patterns of biomass dynamics proposed by Peet (1981) during the period following peak biomass.

Study area

The two sets of plots are located in close proximity on the north Oregon coast (45° 4' N, 123° 56' W; Fig. 1) in the *Picea sitchensis-Tsuga heterophylla* (Sitka spruce-western hemlock) zone of Franklin & Dyrness (1988). The existing forest cover developed after the Nestucca
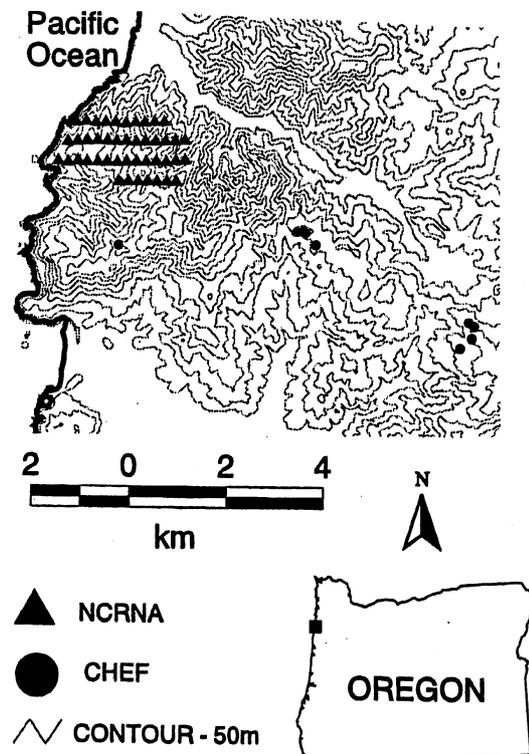

Fig. 1. Location of *Picea-Tsuga* permanent plots in Cascade Head Experimental Forest (CHEF) and Neskowin Crest Research Natural Area (NCRNA) on the northern Oregon coast.

Burn, a huge, catastrophic crown fire that occurred in the late 1840s (Morris 1934; Munger 1944; Harcombe 1986). The Nestucca Burn is likely to have killed most trees within the fire area (Munger 1944). All of 157 trees cored on the CHEF plots established after the fire (Harcombe 1986). Tree core data are not available for the NCRNA plots but, based on age-DBH relationships for the cored trees from the CHEF plots, it appears that in 1979 as many as 5 trees/ha may have been survivors of the Nestucca Burn.

While tree densities and basal area differed between the two sets of plots at the most recent measurement (1993 for CHEF, 1994 for NCRNA), other aspects of forest structure and composition were similar (Table 1). Trees per ha and basal area were ca. 50% greater on the CHEF plots. On both sets of plots, *Tsuga heterophylla* accounted for ca. 90% of stems and 50% of basal area. Mean tree sizes were similar on the two sets of plots, with *P. sitchensis* about twice as large as *T. heterophylla.*

The prevailing climate for both sets of plots is cool and wet with annual precipitation of 2496 mm, falling mostly between late fall and spring. Fog drip can add as much as 800 mm precipitation during the summer months (Ruth 1954). Mean annual temperature is 10.3°C for nearby Otis, Oregon (Franklin & Dyrness 1988). The CHEF plots are mostly situated several km inland from the Pacific Ocean on gentle, generally south or west-facing slopes. The NCRNA plots are directly adjacent to the Pacific Ocean and occur on highly dissected, moderate to steep slopes at all aspects (Fig. 1). The soil parent material in both sets of plots is primarily tuffaceous siltstones (Greene 1982; Harcombe et al. 1990), though basalt bedrock can cause significant local modifications of the soil profile, especially in the NCRNA plots. The texture of the soil in the CHEF plots is silt loam to silty clay loam throughout all soil horizons (J. Norgren & C.T. Dyrness unpubl.). Few rocks are found in any soil layer (< 5%). The soil is generally friable through the B2 horizon, becoming much firmer in lower horizons. Structure of the soil is fine granular through the A horizons, becoming a mix of weaker subangular particles in the B horizons, with more massive structure in the lowest horizons. Fine, medium and coarse roots are found throughout the A horizon, fine and medium roots in the B horizon, with virtually no roots in the C horizon. Soil depths exceed 1.5 m in all the CHEF plots. Soils at the NCRNA plots are not as well characterized (Greene 1982). Because these plots are on steeper, more dissected slopes where bedrock is often seen close to the surface we infer that the soils are not as deep and probably contain more gravel and rocks.

Table 1. Summary of forest structure for CHEF and NCRNA plot sets. $n = 9$ for CHEF (measured in 1993) and $n = 44$ for NCRNA (1994). All trees ≥ 5 cm DBH were included. Values are means with standard errors in parentheses.

| | Trees per ha | | | |
	CHEF		NCRNA	
Total	734	(102)	499	(95)
Picea sitchensis	94	(24)	47	(5)
Tsuga heterophylla	638	(114)	446	(95)
	Basal area (m²/ha)			
Total	104	(6)	65	(5)
P. sitchensis	52	(13)	28	(3)
T. heterophylla	51	(10)	37	(8)
	Quadratic mean diameter (cm)			
P. sitchensis	83	(2)	85	(8)
T. heterophylla	35	(4)	40	(2)

Methods

The two sets of plots were established at different times, employing different designs. The nine CHEF plots, each 0.4 ha in size, were established in 1935 on various sites throughout the Experimental Forest. Plot locations were selected to be representative of the post-Nestucca Burn age-class of *Picea sitchensis-Tsuga heterophylla* forest in the vicinity of Cascade Head Experimental Forest (Brieglieb 1940; Munger 1946), although there is apparently no detailed record of the process of site selection. The 44 NCRNA plots were established in 1978 and 1979, each nominally 0.1 ha in size; area of the NCRNA plots varies due to differences in slope. The NCRNA plots were systematically located 200 m apart on parallel transects 400 m apart. Although the two sets of plots differ with respect to number and size of plots, measurements on individual trees are identical (see below), the total area sampled is similar and the frequency of measurement has been the same since the NCRNA plots were established. Inclusion of data for the CHEF plots for the period before establishment of the NCRNA plots makes direct examination of a much longer interval of stand development possible. All values are reported on a slope-corrected, horizontal area basis.

Coarse woody debris stores

The mass of CWD was estimated using the fixed area plot method (Harmon et al. 1987; Harmon & Sexton 1996). Measurements were made in 1993 for the CHEF plots and in 1994 for the NCRNA plots. The dimensions of all CWD > 10 cm diameter and > 1 m long were measured in both sets of plots. In addition, the species, decay class and tag number (if found) of each piece were recorded. For each tagged piece, the number

of years since death was defined as the measurement year (i.e. 1993 or 1994) minus the middle year of the measurement interval in which the tree was recorded as dead. Five decay classes were distinguished using a modified version of the system of Sollins et al. (1987) and Graham & Cromack (1982). Class 1 was the least decayed (i.e. bark and wood sound, fine twigs present), class 3, intermediate in decay (i.e. some bark present, heartwood decaying but still capable of supporting weight) and class 5 was the most decayed (i.e. bark entirely absent, wood decayed into a structureless mass). We modified this classification system to account for the fact that moss growth was considerably faster in these coastal forests than in the inland forests of the Cascade Range where the classification was originally developed.

Dimensional measurements for logs included the end and middle diameters and the total length inside the plots. DBH, top diameter and length of snags were recorded. In the case of broken snags, the top diameter was obtained by measuring the large end of the resulting log (if it could be located), or by making a visual estimate. Diameters to the nearest 1 cm were measured using 100 cm calipers or diameter tapes. Log length to the nearest 0.1 m was estimated using ultrasonic distance measuring devices (Sonin Combo Pro; Sonin Inc., Scarsdale, New York, USA) or tape measures. Snag height was estimated to the nearest 0.1 m using meter sticks for heights less than 3 m, site-specific diameter-height regressions for snags with intact tops and a clinometer and an ultrasonic distance measuring device for snags > 3 m tall with broken tops. The volume of each piece was calculated using Newton's formula for logs and a cone frustum for snags (Harmon & Sexton 1996). CWD mass was calculated by multiplying the volume of each piece by the species and decay class-specific density (Harmon & Sexton 1996). Mass and volume were summed for each plot by species, decay class and position (snag versus log).

Three of the 44 NCRNA plots (9, 13, 32) were unsafe to inventory because of the quantity of large, jumbled coarse wood and intermingled growth of shrubs. The volume of CWD in these plots was estimated from the live volume killed by windstorms since establishment of the plots. This is probably an underestimate of total CWD volume on these plots. Nevertheless, the amount added by windstorms was approximately twice that of the other plots. Comparison with other plots with heavy wind damage indicated the underestimation on these plots to be < 30% at maximum and < 15% if the major fraction of mortality was recent. Based on visual inspection of the pieces in these plots we assumed that the bulk of these logs were in decay class 2.

Measurements of live trees

On both sets of plots, all trees > 5 cm DBH (1.37 m) were tagged. The CHEF plots were measured in 1935, 1940, 1945, 1955, 1968, 1978, 1983, 1988 and 1993 and the NCRNA plots in 1978/79, 1984, 1989 and 1994. At each measurement, trees that had grown to > 5 cm DBH since the previous measurement (ingrowth) were tagged. Dead trees were recorded at each measurement. Mortality checks were also made during some of the years between measurements (CHEF 1950, 1961, 1979-1986; NCRNA 1980-1990).

To estimate volume and biomass of bole wood and bark from DBH, we used separate sets of allometric equations developed from optical dendrometer measurements for the two sets of plots. The form of the equations was:

$$V = C * B_0 * D^{B_1} \qquad (1)$$

where V = volume, B_0 and B_1 are regression coefficients, C is a factor to correct for bias introduced by back-transformation from logarithmic to arithmetic units (Sprugel 1983) and D = DBH. Separate equations were developed for each species (*Picea sitchensis, Tsuga heterophylla, Pseudotsuga menziesii* at CHEF; *P. sitchensis* and *T. heterophylla* at NCRNA). For the CHEF plots, equations were developed for five different measurement years and the set of equations closest in time to each measurement was used. A single set of equations was developed for the NCRNA plots and was used for all four measurements. Separate equations were necessary for the two sets of plots because of differences in allometry: for a given DBH, trees at NCRNA are shorter and have less biomass than trees on the CHEF plots (Greene et al. 1992). To convert volume to biomass, we used published wood density values for the three species. Details of development of the equations and parameter values are given in Harcombe et al. 1990 (CHEF plots) and Greene et al. 1992 (NCRNA plots). 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:

$$NPPB = dB + M \qquad (2)$$

where dB is the difference in standing live bole biomass between one measurement period and the next (including ingrowth) 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 measurement interval (Harcombe et al. 1990).

Reconstruction of stand dynamics

Biomass accumulation at any point in time equals the difference between production and mortality integrated over time. This simple, mass-balance constraint allowed us to explore the logical implications of our records of biomass, NPPB, M and CWD for temporal patterns of production, mortality and biomass during the aggrading phase of stand dynamics. The investigation involved fitting curves of NPPB and M to the observed data based on the following assumptions:

1. There is a lag of some years after the stand-initiating disturbance before appreciable bole production;

2. Bole production rises steeply, following a parabolic curve (Peet 1981; Binkley & Greene 1983; Harcombe et al. 1990; Ryan et al. 1997) then declines linearly to the first observed value of NPPB;

3. There is a lag of some years before appreciable bole mortality;

4. Bole mortality rises linearly to match the general trend of observed values (i.e. extreme mortality events in the observed record are recognized as deviations from the general trend); and

5. The rate of CWD decay has been constant over time and space.

The first assumption requires that all trees died in the stand-initiating disturbance. As mentioned previously, a small number of trees are likely to have survived the Nestucca Burn, especially on the NCRNA plots. However, given the severity of the fire (Munger 1944) and the sensitivity of both *Picea sitchensis* and *Tsuga heterophylla* to fire (Agee 1993), it is clear that biomass and productive capacity were almost completely removed by the fire. The post-disturbance lag in production is also a consequence of only including trees >5 cm DBH in biomass calculations. *Tsuga heterophylla*, for example, typically takes 4 years to reach breast height on productive sites (Wiley 1978) and then would require additional growing seasons to reach 5 cm DBH.

The time lag before appreciable bole mortality represents a period early in stand development when trees that have survived the seedling stage experience little competition (Oliver & Larson 1990; Kenkel et al. 1997). In addition, once started self-thinning mortality typically affects the smallest trees in a population (Peet & Christensen 1987; Kenkel et al. 1997), further delaying a noticeable effect in terms of biomass.

The final two assumptions represent parsimonious use of our data or published information for the region, respectively. We consider it unlikely that there is a systematic difference between the plot sets in the rate of decay of CWD, since the controlling factors of temperature, moisture, oxygen, substrate quality and decomposer

organisms (Harmon et al. 1986) are likely to be quite similar in both locations.

We set the lag before appreciable bole production to 10 yr (cf. Binkley & Greene 1983) and the CWD decay rate to 3% per year (Sollins 1982; Spies et al. 1988). We then applied the set of assumptions separately to the CHEF and NCRNA data and fitted NPPB and M curves to the observed data. First we varied the length of the time lag before appreciable bole mortality in order to match the measured CWD. Then we varied the magnitude and timing of the peak of NPPB to match the first observed biomass values. We tested whether NPPB could have peaked at the first observed value. If this was not the case, the peak in NPPB was incrementally increased and shifted back in time until the first value of biomass was matched.

We tested the sensitivity of the reconstruction approach to variability in the two quantitative parameters to which we assigned assumed values: the lag before bole production and the CWD decay rate. Using the data from the CHEF plots, we increased or decreased each parameter by 10%, and compared the resulting time and magnitude of peak NPPB to values from the standard reconstruction (Swartzman & Kaluzny 1987).

The assumptions used to reconstruct the time trends of NPPB and M have been assembled into a computer program in the QuickBASIC language (Anon. 1985-1988). The program, a more fully developed explanation of the underlying ideas and test data sets are accessible via the worldwide web at http://www.fsl.orst.edu/lter/pubs/res_rpts/curv_fit.htm

Sapwood respiration

Over the course of observations there has been a decrease in the rate of the bole biomass accumulation in both sets of plots (Harcombe et al. 1990; Greene et al. 1992). Because we wished to investigate whether changes in sapwood biomass and its maintenance respiration would account for the observed changes in the rate of accumulation of bole biomass, we estimated the mass of sapwood of each species using the equations in Harcombe et al. (1990). These equations predict the proportion of sapwood volume for individual trees from DBH. This proportion was multiplied by the bole biomass of each tree to calculate sapwood mass.

Maintenance respiration of boles is highly correlated with sapwood volume in many species of conifers (Ryan 1990; Ryan et al. 1995). To calculate the maintenance respiration of boles at each measurement period we multiplied the mass of sapwood by 0.01 /yr, the proportion Ryan et al. (1995) estimated for a stand of *Tsuga heterophylla* at low elevation on the western slope of the Oregon Cascade Range (Runyon et al.

1994). The *T. heterophylla* stand in Ryan's study had an annual maintenance respiration of 3.24 Mg ha^{-1} yr^{-1} (assuming a 0.5 ratio of carbon to biomass; Edwards et al. 1981) and a sapwood biomass of 323 Mg/ha (assuming a sapwood density of 0.42 Mg/m^3; Ryan et al. 1995). The estimate of maintenance respiration by Ryan et al. (1995) was based on an annual temperature of 9.2 °C; this value is quite close to the temperature experienced at both CHEF and NCRNA plots, which are higher in elevation and thus cooler than the Otis meteorological station (Greene 1982). As there are no published estimates of the ratio of maintenance respiration to sapwood mass for *Picea sitchensis* or *Pseudotsuga menziesii*, we assumed that these species would have similar values to those of *T. heterophylla*.

Dating mortality events

We took two approaches to assessing whether CWD of different decay classes represents mortality in different periods in the past. First, we compared the decay class and the time since death for tagged pieces of CWD. Second, we regressed the mass of trees observed dying in various intervals in the past on CWD in different decay classes.

We selected regression models to investigate based on the distribution of time since death of tagged pieces by decay class. Decay classes 1 and 2 were examined both separately and together due to the substantial overlap in ages. Due to the relatively short duration of measurement of the NCRNA plots, only regressions of mortality mass on CWD in decay classes 1 and 2 were investigated. For each decay class or combination of decay classes considered, regressions with mortality from alternative time periods were examined. For significant regressions, transformations of the dependent variables were employed where necessary to satisfy assumptions of linear regression. The three NCRNA plots on which CWD was not measured due to unsafe conditions were excluded from regressions.

Results and Discussion

Coarse woody debris

Mean total CWD mass was slightly higher on the CHEF plots than the NCRNA plots (155 vs 144 Mg/ha), not lower as predicted under the hypothesis of higher mortality on the NCRNA plots ($p = 0.80$ in a one-tailed Wilcoxon rank-sum test; Anon. 1989b). For both sets of plots, most CWD was in decay classes 2 and 3 (Fig. 2). The two sets of plots differed with respect to the distribution of CWD ($p < 0.001$ in a likelihood-ratio χ^2 test

(Anon. 1989a)). Class 3 was the most common on the CHEF plots (50% of total CWD), whereas class 2 was the most common on the NCRNA plots (46% of total CWD) (Fig. 2). Low CWD in classes 4 and 5 suggests that residual CWD from the stands that burned in 1850 has essentially disappeared; this disappearance seems likely, considering that, at a 3 %/yr decay rate (Sollins 1982; Spies et al. 1988), only ca. 1% of the residual mass would remain after 140 yr.

For the CHEF plots, we compared the time since death for tagged pieces in decay classes 1, 2, 3 and 4 (there were only two tagged pieces in decay class 5). The percentage of tagged pieces decreased with decay class:

62% for decay class 1;
57% for decay class 2;
31% for decay class 3;
9% for decay class 4.

Though the range of time since death within each decay class was broad, the bulk of observations of decay classes 1 and 2 were distinct from those of decay classes 3 and 4 (Fig. 3). Median ages for the decay classes were:

1.5 yr for decay class 1;
6 yr for decay class 2;
18.5 yr for decay class 3;
27 yr for decay class 4.

For the NCRNA plots, all tagged pieces were in decay classes 1, 2 and 3, with considerable overlap of classes 2
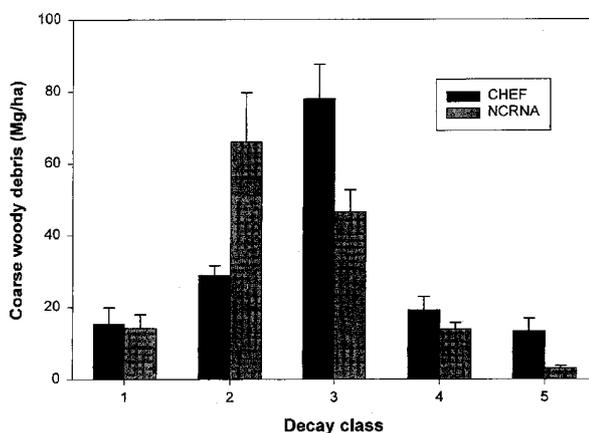
Fig. 2. Mass of coarse woody debris by decay class for CHEF and NCRNA plots. Inventories were conducted at stand ages 143 yr for CHEF plots and 144 yr for NCRNA plots. Values are means ($n = 9$ for CHEF and $n = 44$ for NCRNA); bars represent standard errors.
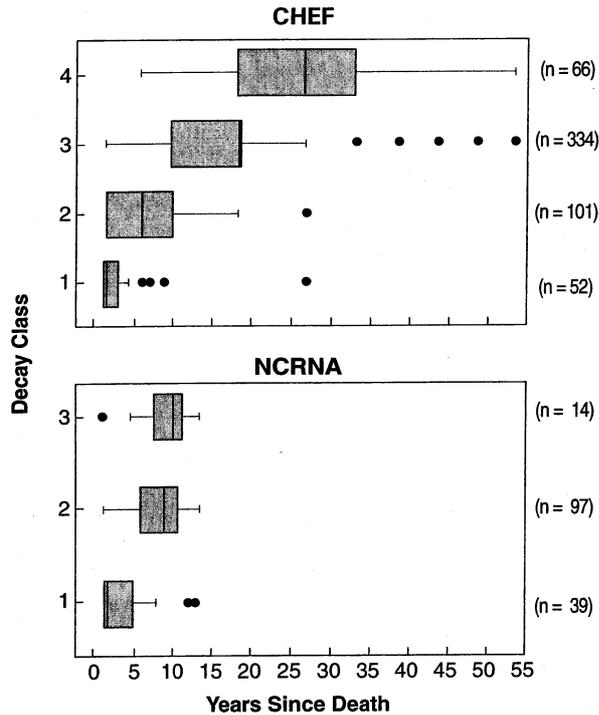
Fig. 3. Time since death by decay class for tagged pieces of coarse woody debris on CHEF and NCRNA plots. Boxes represent the middle 50% of observations (i.e., between 25th and 75th percentiles, or lower and upper quartiles). Vertical lines correspond to the median value. Horizontal lines extending from boxes include values up to the upper quartile plus 1.5 times the interquartile range (difference between upper and lower quartile) or the lower quartile minus 1.5 times the interquartile range. Circles represent more extreme values.

and 3 (Fig. 3). Again, the percentage of tagged pieces decreased with decay class:

37% for decay class 1;
21% for decay class 2;
2% for decay class 3.

Median ages were

1.5 yr for decay class 1;
 9 yr for decay class 2;
10.5 yr for decay class 3.

Ages of CWD in decay classes 1, 2 and 3 were compared between the two sets of plots with two-tailed Wilcoxon rank-sum tests (Snedecor & Cochran 1980; Anon. 1989b). For decay class 1, there was no significant difference in the distribution of ages ($p = 0.16$). For decay classes 2 and 3, differences were significant ($p = 0.015$ and $p = 0.002$, respectively). However, the direction of the difference was not consistent, as CWD in decay class 2 tended to be older on NCRNA plots while the opposite was true for decay class 3 (Fig. 3).

There is a significant correspondence between inventoried CWD of different decay classes and mortality observed over various intervals in the past (Table 2) for some, but not all, combinations of decay class and plot set. For the CHEF plots, the regressions of mortality mass 15 - 24 yr and 10 - 24 yr ago on CWD in decay class 3 were both highly significant. For the NCRNA plots, the regressions of mortality mass at various intervals between 0 and 14 yr ago on CWD in decay classes 1 and 2, separately and combined, were all highly significant. The analysis of decay class of pieces with known time of death confirms that most of the CWD present on both sets of plots corresponds to tree mortality in the last 20 years (Fig. 3).

If the biomass difference between the two sets of plots in 1994 had been caused by higher recent mortality in the NCRNA plots, then CWD would be greater at NCRNA than at CHEF (Greene et al. 1992). That CWD was not greater at NCRNA indicates that the large difference in biomass between the NCRNA and the CHEF plots is not a consequence of higher recent mortality at NCRNA. This leaves a long-term difference in NPPB as the most reasonable explanation for the difference in accumulation of above-ground live biomass over 150 yr of stand development.

Net primary production, mortality and live biomass of bole wood

Net primary production of bole wood was not significantly different between the two sets of plots for two of the three measurement intervals. Values were most similar for the first interval, ending at age 133/134 yr:

CHEF, 6.2 Mg ha^{-1} yr^{-1}, s.e. 0.3;
NCRNA, 5.8 Mg ha^{-1} yr^{-1}, s.e. 0.6; $p = 0.54$; two-tailed *t*-test, df = 50.9 by Satterthwaite correction due to unequal variance (Anon. 1989b).

For the second interval, ending at age 138/139 yr, production of bole wood was significantly greater for the CHEF plots:

CHEF, 6.8 Mg ha^{-1} yr^{-1}, s.e. 0.3;
NCRNA, 4.5 Mg ha^{-1} yr^{-1}, s.e. 0.4; $p = 0.0001$; two-tailed *t*-test, df =36.6

In the most recent interval (up to age 143/144 yr), production was greater on the CHEF plots, but the difference was not significant:

CHEF, 6.7 Mg ha^{-1} yr^{-1}, s.e. 0.6;
NCRNA, 5.0 Mg ha^{-1} yr^{-1}, s.e. 0.4; $p = 0.10$
in two-tailed *t*-test with df = 51 (assumption of equal variance not violated).

Over the more than 60 years of observation, net production of bole wood has declined on the CHEF plots (Fig. 4). Although variation from one interval to the next has increased over time, the decrease in NPPB

Table 2. Regressions of mass lost to mortality on CWD mass. $n = 9$ for CHEF and 41 for NCRNA (see text for details).

Plot set	Tree mortality during interval (years ago)	CWD decay class	P-value	Regression model	R^2
CHEF	0-4	1	0.06	n/a	n/a
CHEF	0-9	1	0.24	n/a	n/a
CHEF	5-9	2	0.07	n/a	n/a
CHEF	0-9	2	0.5	n/a	n/a
CHEF	0-14	2	0.06	n/a	n/a
CHEF	0-9	1 and 2	0.16	n/a	n/a
CHEF	0-14	1 and 2	0.08	n/a	n/a
CHEF	15-24	3	0.002	$\log(M) = 2.58 + 0.0118*CWD$	0.73
CHEF	10-24	3	0.0004	$\log(M) = Ð0.329 + 1.07*\log(CWD)$	0.83
CHEF	25-37	4	0.11	n/a	n/a
CHEF	15-37	4	0.86	n/a	n/a
NCRNA	0-4	1	0.0001	$\sqrt{M} = 1.69 + 0.102*CWD$	0.46
NCRNA	0-9	1	0.0003	$\sqrt{M} = 4.09 + 0.093*CWD$	0.27
NCRNA	5-9	2	0.003	$\sqrt{M} = 1.84 + 0.026*CWD$	0.18
NCRNA	0-9	2	0.01	$M = 25.3 + 0.441*CWD$	0.14
NCRNA	0-14	2	0.0001	$\sqrt{M} = 4.92 + 0.052*CWD$	0.37
NCRNA	0-9	1 and 2	0.0001	$\sqrt{M} = 2.41 + 0.042*CWD$	0.4
NCRNA	0-14	1 and 2	0.0001	$\sqrt{M} = 3.74 + 0.057*CWD$	0.51

from the first interval to the last interval is highly significant (mean change – 4.7 Mg ha^{-1} yr^{-1}, s.e. 0.8; p = 0.0003 in two-tailed t-test, df = 9).

Biomass lost to mortality was not significantly different between the plot sets for any of the three intervals of measurement. Mortality was high in the first interval:

CHEF, 10.0 Mg ha^{-1} yr^{-1}, s.e. 1.9;
NCRNA, 11.0 Mg ha^{-1} yr^{-1}, s.e. 2.4; p = 0.73, 37.5 d.f.

but mortality was lower in the second interval
CHEF, 4.9 Mg ha^{-1} yr^{-1}, s.e. 1.0;

NCRNA, 6.4 Mg ha^{-1} yr^{-1}, s.e. 1.6; p = 0.42, df = 45.3
and in the third interval:

CHEF, 6.1 Mg ha^{-1} yr^{-1}, s.e. 1.3;
NCRNA, 5.5 Mg ha^{-1} yr^{-1}, s.e. 1.6; p = 0.75, df = 34.7.

Over the period that both sets of plots have been observed, CHEF and NCRNA have had similar percentages of standing trees among those dying (49% and 47%, respectively). This suggests that mortality due to competition and other biotic factors is of similar impor-
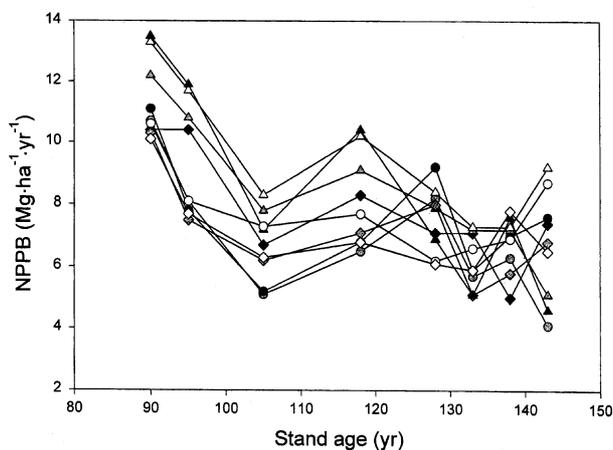
Fig. 4. Annual net primary production of bole wood plus bark versus stand age for CHEF plots. Each of the nine plots is represented by a unique symbol to facilitate recognition of trends.
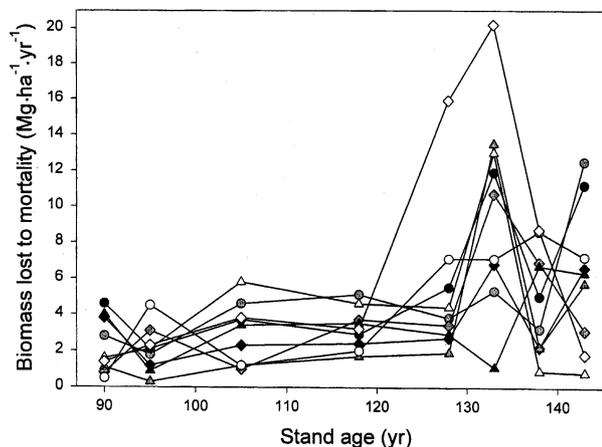
Fig. 5. Annual loss of biomass due to tree mortality versus stand age for CHEF plots. Each of the nine plots is represented by a unique symbol to facilitate recognition of trends.
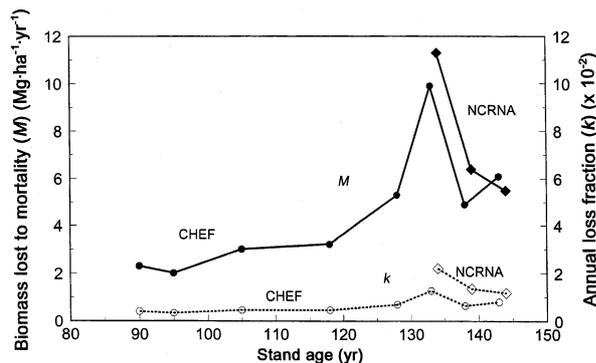
tance on both sets of plots.

Over the 60 years of observations annual mortality has increased on the CHEF plots (Fig. 5). The increase in mortality from the first interval to the last interval is significant (mean change 3.8 Mg ha^{-1} yr^{-1}, s.e. 1.1; p = 0.009; two-tailed t-test, df = 9). Variability between plots and from one interval to the next has increased over time.

The greatest observed loss of biomass to mortality occurred at about the same age, 133/134 yr, for both sets of plots (Fig. 6). This peak is related to two major wind events that occurred in 1981 and 1983. A relatively recent peak in biomass lost to mortality is consistent with the distribution of CWD by decay class. This is further evidence that early differences in NPPB is a more probable explanation than early differences in mortality for the current difference in above-ground biomass between the two plots sets.

Over the period of observation, the fraction of live biomass lost to mortality has consistently been higher on the NCRNA plots than on the CHEF plots (Fig. 6). For the first three decades, annual loss rate was between 0.003 and 0.005 for the CHEF plots. The peak in annual loss rate was at the same age for both sets of plots, 133/134 yr. Annual loss rate peaked at 0.013 on the CHEF plots and dropped to 0.008 in the most recent interval. The highest annual loss rate on the NCRNA plots (0.022) was observed in the first measurement interval. Annual loss rate on the NCRNA plots dropped to 0.012 in the most recent interval.

The maximum observed biomass values for both the CHEF and the NCRNA plots (774.6 Mg/ha, s.e. 39.1, and 499.0 Mg/ha, s.e. 38.4, respectively) occurred at age 128 and 129 yr (Harcombe et al. 1990; Greene et al. 1992). Biomass changed little for both sets of plots over the most recent measurement interval (0.3% increase for CHEF; 0.4% decrease for NCRNA).

Thus, over the period of observation of both sets of plots, live biomass has consistently been higher on the CHEF plots while differences in NPPB and mortality have been minimal. Since the analysis of CWD suggested that production, rather than mortality, explains the differences in biomass between the two sets of plots, it appears that production on the two sets of plots must have been markedly different at some time prior to the establishment of the NCRNA plots in 1979. The plausibility of this speculation can be addressed by reconstructing dynamics of biomass and CWD.

Reconstruction of stand dynamics

The reconstruction of stand dynamics supports the conclusion that NPPB has been higher on the CHEF

Fig. 7. Reconstruction of biomass dynamics for the aggrading phase for CHEF and NCRNA plots, constrained by initial biomass of zero and measured biomass, mortality, NPPB and CWD. **a**. Annual NPPB; **b**. Annual loss of biomass to tree mortality; **c**. Live biomass of tree bole wood plus bark (B) and CWD. Observed and reconstructed trends for NCRNA plots are marked with open circles.
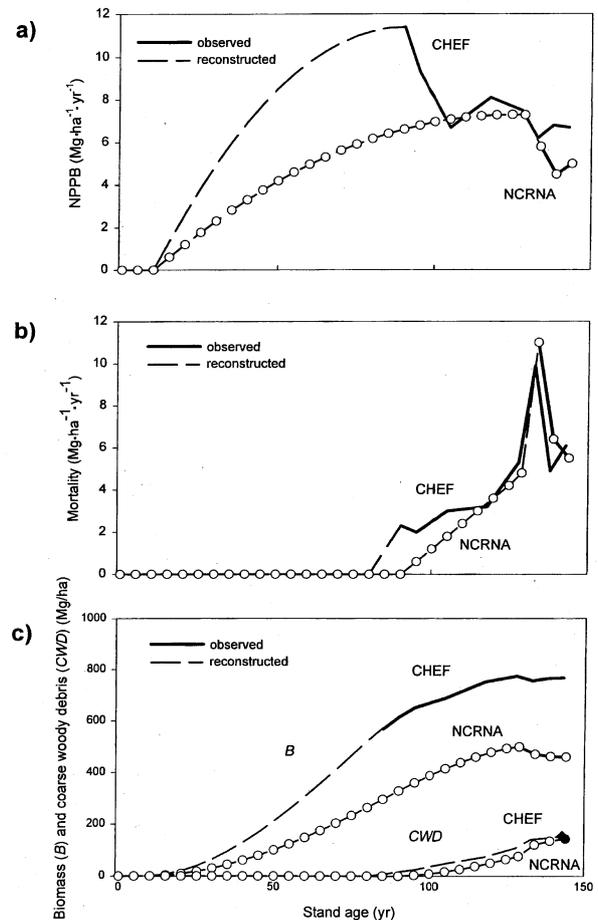

Fig. 6. Annual loss of biomass due to tree mortality (solid line) and annual fractional biomass loss (dashed line) versus stand age for CHEF and NCRNA plots.

plots for most of the life of the current stands (Fig. 7a). NPPB on both sets of plots appears to have diverged in the first decades of growth, reaching a maximum discrepancy at age 75 yr, shortly before NPPB peaked on the CHEF plots. Since then, NPPB of the plots has apparently been converging to a lower value. For most of the life of the current stands, gross mortality on the two sets of plots has been similar (Fig. 7b).

As a consequence of production and mortality trends, the reconstruction also demonstrates that over the life of the current stands, biomass has always been higher on the CHEF plots (Fig. 7c). Moreover, it appears that at no time since establishment of the current stand has CWD been higher on the NCRNA plots than on the CHEF plots. Biomass on the CHEF plots approached and fluctuated around a plateau, whereas biomass on the NCRNA plots apparently peaked later and then declined slightly to a plateau. Since biomass has consistently been lower on the NCRNA plots while gross mortality has been similar, the fraction of biomass lost to mortality has consistently been higher on the NCRNA plots. Further investigation of this apparent difference in disturbance regime between the two sets of plots would be worthwhile.

Although the reconstruction depends, in part, on assumptions concerning the shape of the time trend of NPPB prior to establishment of the plots, it is severely constrained by the biomass value of zero at stand initiation and observed biomass, mortality, NPPB and CWD values. The sensitivity analysis demonstrates both the degree of this constraint, and that the reconstruction method is robust to small changes in parameter values that decrease net accumulation of living and dead mass (Table 3). Small increases (10%) in either the lag before appreciable NPPB or the decay rate of CWD, do not alter substantially the estimates of the magnitude or timing of peak NPPB. Small decreases in these parameters result in an inability to reconcile estimated trends with observations. That is, there is no set of values of the lag before appreciable

mortality, maximum NPPB and the year of maximum NPPB that will simultaneously match the observed values of CWD and initial measured biomass, NPPB and mortality. The long duration of records of tree mortality and growth, in conjunction with the CWD inventory, imposes severe limits on plausible dynamics prior to plot establishment. In particular, observed tree mortality is closely enough matched to inventoried CWD that there is very little room for CWD generated prior to plot establishment.

The reconstruction should be viewed as a parsimonious extrapolation of the available data. A radically different reconstruction would require a larger number of more complex assumptions. For example, an earlier peak in NPPB would require a corresponding early increase in rates of both mortality and decomposition to make the increase in wood produced early in the life of the stands disappear. However, we cannot rule out the possibility that tree species composition was markedly different early in the history of these stands, or that decomposition rates have fluctuated due to climatic variability. Either of these factors could make the history of these stands more complicated than our simple scenario.

A difference between the two sets of plots in NPPB is the logical explanation for differences in standing biomass. However, the difference in NPPB for the period when both were measured (1978-1994) is too small to account for this difference. Therefore, NPPB differences must have been greater at some time in the past; the reconstruction indicates that at its peak, NPPB was ca. 60% higher at CHEF than at NCRNA (Fig. 7a). This difference may be related to better site quality at CHEF due to gentler slopes and deeper soils. Recent mapping shows considerable heterogeneity of bedrock geology in the study area (Snavely et al. 1996), which could contribute to differences in potential productivity between the plots.

In addition to indicating the magnitude of difference between the plots in maximum NPPB, recon-

Table 3. Sensitivity analysis of reconstruction of biomass dynamics.

| Reconstruction scenario | Parameters (inputs) | | Estimates (outputs) | | |
	Lag before appreciable NPPB (yr)	Annual rate of CWD decay	Lag before tree mortality (yr)	Maximum NPPB (Mg ha^{-1} yr^{-1})	Time of maximum NPPB (yr)
Standard	10	0.03	80	11.4	90
Test 1	11	0.03	85	11.4	90
Test 2	9	0.03	No solution possible[1]		
Test 3	10	0.033	40	11.9	86
Test 4	10	0.027	No solution possible[1]		

[1]See text for explanation.

struction of the time trend of NPPB for the CHEF plots is consistent with the observation that NPPB peaks relatively early in development of spruce-hemlock stands (Fujimori 1971; Grier 1976). However, our reconstruction suggests that the peak in NPPB occurs at 90 yr for the CHEF plots rather than the 25 - 40 yr predicted by Harcombe et al. (1990). The NPPB peak at 90 yr is two decades later than the oldest ages for peak forest growth in chronosequence studies reviewed by Ryan et al. (1997), which were reported for other species of spruce. The reconstruction also illustrates the decline in NPPB associated with even-aged stands (Ryan & Waring 1992; Gower et al. 1996; Ryan et al. 1997).

Sapwood respiration

In the CHEF plots, sapwood biomass increased from 216 Mg/ha at age 85 yr to a high of 262 Mg/ha at age 128 yr. This was followed by a decline to 253 Mg/ha at age 133 yr. Since then, sapwood biomass in these plots has remained relatively constant at 252 Mg/ha. In the NCRNA plots there was a similar decline in sapwood biomass from 154 Mg/ha at 129 yr and declining to 142 Mg/ha at 134 yr. From 134 to 144 yr sapwood biomass in the NCRNA plots was ca. 139 Mg/ha. This was 55% of that estimated for the CHEF plots over a similar time period, a reflection of the lesser amount of bole biomass on the NCRNA plots. The decrease in sapwood biomass between 128/129 yr and 133/134 yr was probably caused by wind-related mortality, which removed large trees with high sapwood biomass.

Changes in maintenance respiration for sapwood paralleled those of sapwood mass for both sets of plots (Fig. 8) using our method of estimating sapwood respiration. These changes demonstrate that the decline in NPPB is not a consequence of increasing respiratory load. Over the period of observation, NPPB on
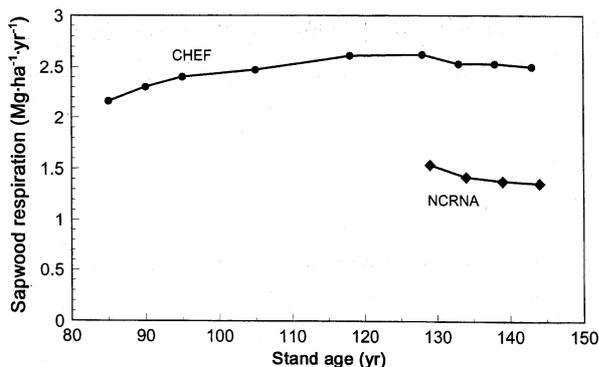
the CHEF plots declined from 11.4 to 6.7 Mg ha^{-1} yr^{-1}, while estimated sapwood respiration rose from 2.2 Mg ha^{-1} yr^{-1} to 2.5 Mg ha^{-1} yr^{-1}, accounting for only ca. 6% of the decline in NPPB. Declining NPPB with forest age is more likely due to a combination of declining leaf area, reduced photosynthesis per unit leaf area and increased below-ground allocation (Gower et al. 1996; Ryan et al. 1997). Assessing the relative magnitudes of these and other changes contributing to declining NPPB is an important area for future research.

Biomass dynamics after the peak

Our observations of mortality, recruitment and NPPB allow us to evaluate which of Peet's (1981, 1992) scenarios for biomass dynamics after the peak are most applicable: declining biomass, periodic oscillations or relative constancy with random fluctuations. Although long-term decline in biomass cannot be ruled out based on existing data, several observations suggest that it is unlikely. First, NPPB seems to be levelling off in the range of 5 to 7 Mg ha^{-1} yr^{-1} in both sets of plots; sequestration of resources would result in a continuing long-term decline in NPPB. Second, inspection of NPPB values for plots regenerating after blowdown indicates that NPPB in post-disturbance plots can be high. This suggests that as the forest ages and the plots come to have a more even distribution among various biomass and disturbance classes and stages of recovery, mean NPPB over all plots will not fall substantially and mean biomass will not decline. In addition, the large accumulation of CWD, which could lead to a decline in nutrient availability (Gower et al. 1996), does not appear to be inhibiting production. Finally, there are documented examples of high-biomass, old-growth hemlock-spruce stands in Washington (483-830 Mg/ha at 205 to 266 yr; McKee et al. 1982) and Alaska (ca. 450 to 750 Mg/ha for ages ca. 200 to 390 yr; Alaback 1982), suggesting that live biomass may be relatively stable for intervals longer than the current age of our stands.

Biomass oscillation in the period after the peak could be caused by a long interval between the opening of stands due to tree mortality and the onset of tree regeneration (Peet 1981). This seems unlikely in the present instance, since tree regeneration can commence prior to opening of the canopy, and regeneration lags that do occur are short. For example, relatively large ingrowth numbers were recorded on several NCRNA plots that had high initial biomass and experienced no mortality during the first measurement interval. Substantial ingrowth (40 stems ha^{-1} yr^{-1}) was observed on NCRNA plots with biomass values as high as 744 Mg/ha; only six of the 44 NCRNA plots had higher biomass

Fig. 8. Mean annual sapwood maintenance respiration versus stand age for CHEF and NCRNA plots.

values at the beginning of the interval. Thus mortality within a plot is not required to trigger recruitment. Concerning regeneration lags, six of the 10 NCRNA plots that lost at least 50% of their biomass over the course of the study did not show a lag: recruitment occurred in all three measurement intervals. The other four plots experienced most mortality in the first interval (1979-1984) and had no ingrowth until the last interval (1989-1994), indicating a maximum recruitment lag of ca. 10 yr. For CHEF plot 13, significant tree mortality due to wind-throw commenced at 122 yr (Harcombe et al. 1990). Ingrowth on this plot was first recorded at 133 yr (492 stems/ha), indicating a recruitment lag of between 6 and 11 yr. Thus, in the absence of advanced regeneration or chronic recruitment due to low stocking, there appears to be a recruitment lag of ca. 10 yr.

Another reason that biomass oscillation is unlikely is that the large temporal variability in windstorm damage would seem to reduce the likelihood of synchronous onset of mortality (cf. Peet 1981,1992). Because plots do not necessarily break up in a single wind-throw event (Harcombe et al. 1990), recruitment can commence while there is sufficient canopy remaining to maintain relatively high levels of NPPB. By the time the original canopy is gone, the newly recruited cohort will have attained high NPPB. The net result is that overall NPPB does not decline due to a recruitment time lag.

Thus, according to the theory of long-term biomass dynamics (Peet 1981, 1992), this system appears to lack the conditions for peak/decline (synchronous mortality of a dominant age class, replacement of species with large maximum tree size by species with smaller maximum tree size, long-term declines in resource availability) or periodic oscillation (synchronous mortality and/or recruitment time lags). Thus, relative constancy of biomass appears more likely than the alternatives.

Constant biomass over time implies a balance between NPPB and mortality. This condition can be formulated as equality between NPPB and the product of biomass and annual loss fraction (Reiners 1983; Harcombe et al. 1998). We used this formulation to assess the hypothetical constant biomass implied by current NPPB and annual loss fraction. This hypothetically stable state is best viewed as a long-term value, about which biomass will fluctuate.

To estimate current NPPB and mortality we used the mean of the last three intervals. For the CHEF plots, with current NPPB of 6.6 $Mg\,ha^{-1}\,yr^{-1}$ and annual loss fraction of 0.0091, the hypothetical constant biomass is 725 Mg/ha. For NCRNA, with current NPPB of 5.1 $Mg\,ha^{-1}\,yr^{-1}$ and annual loss fraction of 0.0158, the hypothetical constant biomass is 323 Mg/ha. Thus, for the CHEF plots, based on current production and mor-

tality rates, constant biomass would be ca. 6% lower than the present value. For the NCRNA plots, constant biomass would be ca. 30% lower than at present.

Hypothetical constant values of CWD can be calculated similarly. Since mortality equals production when biomass is constant, the input rate would equal the NPPB values stated above. Assuming a 3%/yr decay rate, stable CWD values would be 220 Mg/ha for CHEF and 170 Mg/ha for NCRNA. Thus under hypothetical stable conditions based on current production and mortality rates, the sum of live bole biomass and CWD would be ca. 20 Mg/ha (2%) greater than at present for CHEF. For the NCRNA plots, the sum of live bole biomass and CWD under hypothetical stable conditions would be ca. 110 Mg/ha (20%) lower than at present.

Long-term biomass dynamics in the post-peak phase is most likely to be characterized by relative stability with random fluctuations. If current production and mortality rates prevail, the long-term mean of live, above-ground biomass will be somewhat lower than at present for both CHEF and NCRNA. While differences in production appear to explain current differences in live bole biomass between the plot sets, future trends in mortality may be more important for long-term biomass dynamics, as mortality has fluctuated much more than production in recent decades.

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