Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age

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Summary   Although it is generally accepted that the rate of accumulation of biomass declines as forests age, little is known about the relative contributions to this decline of changes in net primary production (NPP) and tree mortality. We used 10–15 years of observations of permanent plots in three small watersheds in and near the H.J. Andrews Experimental Forest, Oregon, to examine these issues. The three watersheds are of similar elevation and potential productivity and support young (29 years at last measurement), mature (~100 years) and old (~400 years) forest dominated by *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg. Accumulation of tree bole biomass was greatest in the young stand, reaching ~7 Mg ha^{-1} year^{-1} in the last measurement interval. Bole biomass accumulation was relatively constant (~4–5 Mg ha^{-1} year^{-1}) in the mature stand, and there was no net accumulation of bole biomass in the old-forest stand. The NPP of boles increased with time in the young stand, from ~3 to ~7 Mg ha^{-1} year^{-1}, but was nearly constant in the mature and old-forest stands, at ~6 and 3–4 Mg ha^{-1} year^{-1}, respectively. Mortality increased slowly in the young stand (from < 0.1 to 0.3 Mg ha^{-1} year^{-1}), but fluctuated between 1–2 and 2–6 Mg ha^{-1} year^{-1} in the mature and old-forest stands, respectively. Thus, declining biomass accumulation with stand age reflects, in approximately equal amounts, both decreasing NPP and increasing mortality.

Keywords: old-growth forest, permanent plots, tree growth, Tsuga heterophylla, western Cascade Range.

Introduction

Forests play an important role in the global carbon cycle, largely determining whether the terrestrial biosphere is a source or sink of CO_2 to the atmosphere (Dixon et al. 1994). Thus, it is important to understand the dynamics of biomass accumulation of forests (Cooper 1983). It is generally accepted that the rate of accumulation of biomass peaks relatively early in the life of a stand (at the time of canopy closure or peak stand leaf area), and declines thereafter (Turner and Long 1975, Grier et al. 1989, Ryan et al. 1997). For example, Grier et al. (1989) reported that the rate of biomass accumulation for *Pseudotsuga menziesii* (Mirb.) Franco forests in the Pacific Northwest peaks at about 20 years of age, although this species often dominates stands for 500 years in the absence of disturbance (Franklin and Halpern 2000). Most of the data in support of the decline in biomass accumulation derive from chronosequence-based studies (e.g., Ryan et al. 1997). Direct observations of changes in forest production and biomass over time are few, but represent the most unambiguous means of documenting the phenomenon (Peet 1981).

Biomass accumulation is the net result of production and mortality. Although production has been the subject of many short-term studies, there are few long-term studies that compare the relative contributions of changing production and mortality rates to long-term trends of biomass accumulation (Ryan et al. 1997). Based on the few relevant studies, Ryan et al. (1997) suggested that declining growth of surviving trees is more important than increased tree mortality in explaining decreased production as stands age. However, this does not rule out the possibility that increased mortality contributes to a decline in biomass accumulation as stands age. In very old stands, biomass accumulation is often assumed to decline to zero (Peet 1981, Grier et al. 1989). Although there may be no net change in live biomass, old forests may maintain relatively high rates of production (Grier et al. 1989); however, this cannot be assessed without knowledge of biomass loss through mortality. Ultimately, understanding the role of old forests in carbon cycling and storage requires accurate measurements of both production and mortality (Grier et al. 1989).

This study concerns biomass of tree boles. Data on other components of biomass (e.g., tree foliage and branches, understory plants and roots) were not available. Previous work has shown that tree boles account for about 40 to 70% of aboveground plant production in young *Pseudotsuga* forests (Turner and Long 1975, Keyes and Grier 1981), and about 30% of production in an old forest (M.E. Harmon et al., unpublished data). With respect to total production (i.e., including roots), tree boles account for 30 to 60% in young *Pseudotsuga* forests

(Keyes and Grier 1981), and about 20% in an old forest (M.E. Harmon et al., unpublished data).

Our objective was to document temporal trends in biomass accumulation in young, mature and old-growth forests of *Pseudotsuga menziesii*, and to assess how production and mortality change with stand age. Specifically, we attempted to answer the following questions. (1) Does the rate of biomass accumulation in tree boles at the stand level decline with stand age and, if so, does increased tree mortality contribute to the decline? (2) Do old-growth forests continue to accumulate bole biomass?

Study area

We used long-term records of forest dynamics from three small watersheds included in the H.J. Andrews Experimental Forest Long-Term Ecological Research site (Van Cleve and Martin 1991, Acker et al. 1998). The three watersheds were in or near the Andrews Forest, Oregon, and occupy a similar range of elevations (Table 1). The climate is characterized by mild, wet winters and warm, dry summers (Bierlmaier and McKee 1989). In watersheds of the Andrews Forest, mean monthly temperatures are 0.6 °C in January and 17.8 °C in July. Mean annual precipitation is 2302 mm, but only 6% falls between June and August (Bierlmaier and McKee 1989). Compared with the Andrews Forest, Hagan Block (location of the mature watershed) is slightly warmer in winter and cooler in summer, and may receive slightly more precipitation (Klopsch 1985). All three watersheds are within the western Cascades geologic province, characterized by volcanic bedrock and steep, dissected topography (Franklin and Dyrness 1988). On watersheds at Andrews Forest, soil parent materials are mostly colluvium derived from andesite and greenish tuffs and breccias; soils are relatively deep and well drained (Rothacher et al. 1967, Dyrness 1969). Detailed, published soil descriptions are not available for the Hagan watershed. Potential productivity of the watersheds appears to be similar, based on classification of vegetation (using reproducing tree species and understory composition) and mean site index values for these vegetation types (32–34 m, Table 1; see Hemstrom et al. 1987).

Differences in stand history among the three watersheds contrast with their proximity to each other and similarity in environment. The watershed supporting the young trees was clear-cut between 1962 and 1966, and logging debris was burned in 1966 (Halpern 1988). *Pseudotsuga menziesii* was aerially seeded and planted by hand over a 5-year period (repeatedly in locations where regeneration failed), although relative contributions of artificial and natural regeneration are unknown (Halpern 1988). The mature stand originated after wildfires in the 1850s and 1890s (Klopsch 1985). The old-growth forest originated after catastrophic wildfire in the late 1500s (based on ages of the oldest *P. menziesii*), although portions of the watershed burned again during the 1800s (Teensma 1987).

At the most recent sampling, tree basal area of the young stand was about one-third that of the mature and old-growth stands (Table 2). Among the three study stands, dominance of *P. menziesii* was greatest in the mature stand and tree species richness was lowest in the mature stand (Table 2). Hardwood species (*Acer macrophyllum* Pursh, *Castanopsis chrysophylla* (Dougl.) DC and *Prunus emarginata* (Dougl.) Walp.) and *Tsuga heterophylla* (Raf.) Sarg. accounted for most of the remaining tree basal area in the young stand; *T. heterophylla* alone accounted for nearly all of the remaining tree basal area in the old-growth stand.

Because each tree age class is represented by a single stand, direct inferences to a larger population of forest stands is precluded. However, given the close proximity of the three study stands and their similarity in elevation and potential productivity, it is likely that differences between them are primarily a result of differences in stand history, especially age.

Methods

Between 1980 and 1982, a series of circular, fixed-area plots were established along transects placed perpendicular to the major stream channel of each watershed. Plots were evenly spaced along each transect at intervals of 30.5 m (young stand) or 100 m (mature and old-growth stands). The first plot on each transect was located a random distance from the ridgeline defining the boundary of the watershed. There were 132, 96 and 67 plots in the young, mature and old-growth stands, respectively. Because of differences in density of tree stems, smaller plots were used in the young stand. The nominal plot sizes were 250 m^2 in the young stand and 1000 m^2 in the mature and old-growth stands. However, horizontally projected areas of the plots vary because of differences in slope. All values are reported on a slope-corrected, horizontal area basis.

Table 1. Location, size, elevational range and site index of the study areas.

	Young stand	Mature stand	Old-growth stand
Location	Andrews Experimental Forest (Watershed 1)	Hagan Block Research Natural Area	Andrews Experimental Forest (Watershed 2)
Size (ha)	100	470	230
Elevational range (m)	440–1080	460–1000	450–1040
Site index (m) (SE)[1]	32.3 (0.2)	33.0 (0.2)	33.5 (0.4)

[1] Mean 50-year site index for *P. menziesii* (King 1966), derived from vegetation classification of Hemstrom et al. (1987).

Table 2. Forest composition and structure for the study areas.

	Young	Mature	Old-growth
Tree basal area ($m^2 ha^{-1}$)[1]	22.4	66.7	71.6
% of basal area of *P. menziesii*	80	98	68
No. of other tree species[2]	11	9	11

[1] At most recent measurement.
[2] Species with trees ≥ 5 cm DBH.

On all three watersheds, trees were tagged and periodically measured and checked for mortality. In the mature and old-growth stands, all trees ≥ 5 cm DBH (diameter at breast height, 1.37 m) were sampled. In the young stand, all trees ≥ 1.37 m tall were sampled. Those large enough to hold a nail (typically ≥ 2 cm DBH) were tagged and measured at breast height; for smaller stems, a tag was affixed to a main branch with wire, and stem diameter measured at ground level (basal diameter, DBA). Several of the hardwood species in the young stand (principally *A. macrophyllum*, *C. chrysophylla*, *Cornus nuttallii* Aud. and *P. emarginata*) tended to grow in clusters as stump sprouts rather than as individual stems. For these clusters, stems < 5 cm DBH were tallied in one of two size classes, 0 to 3 cm and 3 to 5 cm DBH, and larger stems were tagged and measured at breast height. Measurements were made in the young stand in 1980, 1984, 1988, 1991 and 1995, and in the mature and old-growth stands in 1981–1982, 1988 and 1994.

The method of computing bole biomass for individual stems varied with type of measurement (DBH, DBA, cluster tallies) and tree species. For coniferous species with DBH measurements, we developed local models of inside-bark volume as a function of DBH. These models were based on regional models of inside-bark volume as a function of DBH and tree height (Browne 1962). In developing the models, we exploited data sets with simultaneous DBH and height measurements of trees on the three watersheds and other study sites in and near the Andrews Forest. Because *P. menziesii* was abundant in all three watersheds, and because the relationships between DBH and height, and hence DBH and volume, are likely to change with stand age, we developed separate models for *P. menziesii* for each watershed. We used nonlinear regression to generate the volume–DBH models; sample sizes ranged from 64 to 611; R^2 values were between 0.89 and 0.97. To compute bark volume, species-specific mean ratios of bark volume to wood volume were calculated from an optical dendrometer data set from western Oregon and Washington (data set AND001 in Michener et al. 1990). Published values of wood and bark density were used to convert volume to mass. For hardwoods with DBH measurements (and clusters tallied in DBH classes), allometric equations from Means et al. (1994) were used to compute mass.

For coniferous trees with DBA measurements, species-specific models were developed to convert DBA to DBH so that the local volume–DBH models could be used. The DBA to DBH models were developed by linear regression from simul-

taneous measurements of DBA and DBH on trees in the young stand. Sample sizes ranged from 113 to 1916; r^2 values were between 0.68 and 0.72. For hardwood species, allometric equations described by Means et al. (1994) were used to compute mass, with one exception. The maximum diameter used in developing the equation for *C. chrysophylla* by Means et al. (1994) was 5.5 cm DBA. Thus, for trees > 6 cm DBA, a model for conversion of DBA to DBH was developed, similar to the models for coniferous species ($n = 47$, $r^2 = 0.57$), and the appropriate allometric equation on DBH was used.

At each measurement interval, we computed both live and dead bole biomass for each plot. Mass of dead trees was based on the last live measurement of a stem. Net primary production of boles (NPPB) was calculated as:

$$NPPB = \Delta B + M, \qquad (1)$$

where ΔB is the difference in live bole biomass between one measurement and the next and M is bole biomass of trees that died since the last measurement (see Acker et al. 2000 for details). This is equivalent to calculating the sum of biomass increments for all stems that survived from the previous measurement to the current measurement (Harcombe et al. 1990). Both NPPB and M are reported on a per-year basis.

Results

Trends in the rate of accumulation of tree bole biomass varied considerably among the three watersheds (Figure 1). In the young stand, bole biomass accumulated at a rate that increased over time (Figure 1a), from 2.8 Mg ha^{-1} year^{-1} in the first interval to 6.8 Mg ha^{-1} year^{-1} in the most recent interval. In the mature stand, bole biomass accumulated at a relatively constant rate (Figure 1b): 4.0 Mg ha^{-1} year^{-1} in the first interval and 4.8 Mg ha^{-1} year^{-1} in the second interval. In the old-growth stand, the direction of change of biomass was not consistent over time. Bole biomass accumulated at a rate of 2.3 Mg ha^{-1} year^{-1} in the first interval, whereas it decreased at a rate of 2.2 Mg ha^{-1} year^{-1} in the second interval.

Net primary production of boles (NPPB) increased with time in the young stand, but was relatively constant in the mature and old-growth stands (Figure 2a). In the young stand, NPPB was 2.8 Mg ha^{-1} year^{-1} in the interval that ended at Age 18 years (1984), and 7.2 Mg ha^{-1} year^{-1} in the interval that ended at Age 29 years (1995); although NPPB increased with time, the rate of increase declined in the last measurement interval. In the mature stand, NPPB was about 6 Mg ha^{-1} year^{-1} in both intervals. In the old-growth stand, NPPB was between 3 and 4 Mg ha^{-1} year^{-1} in both intervals.

Both the mean and variability in tree mortality differed among watersheds (Figure 2b). In the young stand, tree mortality was low and varied little among plots; rates increased from < 0.1 Mg ha^{-1} year^{-1} in the first measurement interval to 0.3 Mg ha^{-1} year^{-1} in the last interval. In the mature stand, mortality was 2.3 Mg ha^{-1} year^{-1} in the first interval and 1.3 Mg ha^{-1} year^{-1} in the second interval. Among the three watersheds, mortality was most variable in both time and

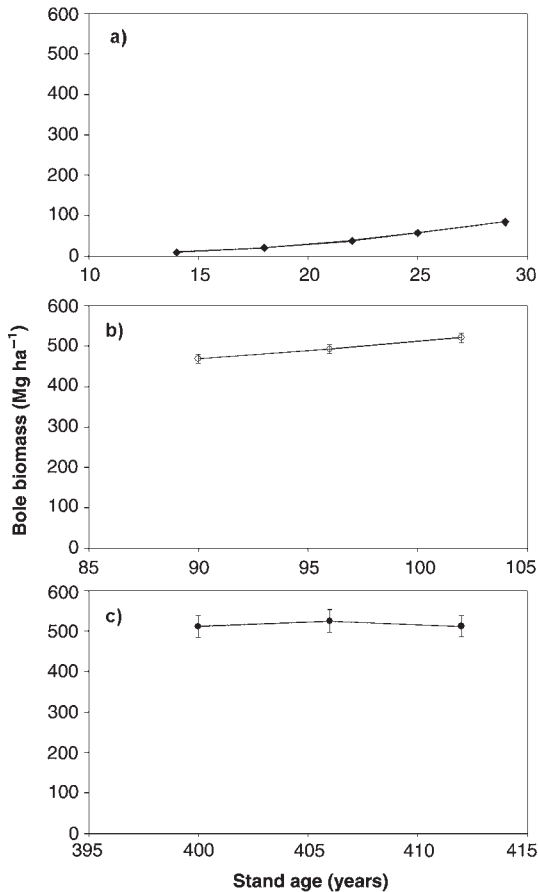Figure 1. Changes in bole biomass with time for the young (a), mature (b) and old-growth (c) watersheds. Error bars are ± 1 SE.
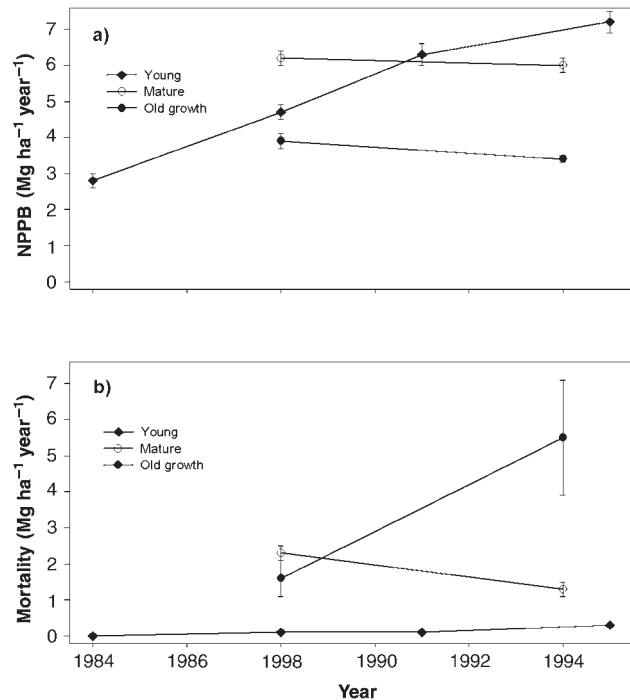

Figure 2. Changes in net primary production of boles (NPPB) (a) and mortality of boles (b) with time for the three watersheds. Each value represents a mean for the measurement interval preceding the point; error bars are ± 1 SE.

space in the old-growth stand, averaging 1.6 Mg ha^{-1} year^{-1} in the first interval and 5.5 Mg ha^{-1} year^{-1} in the second interval (Figure 2b).

Discussion

The three stands illustrate three distinct trends in the rate of accumulation of bole biomass: positive and increasing in the young stand; positive and constant in the mature stand; and fluctuating between positive and negative in the old-growth stand. Thus, our observations support the generally accepted notion that biomass accumulation declines with stand age. Although the lack of replication limits the generality of our results, previous investigations have reached similar conclusions. Rate of biomass accumulation in the young stand peaked at about the same stage of stand development (Age 30 years) as reported by Turner and Long (1975). The observed maximum rate of accumulation (6.8 Mg ha^{-1} year^{-1}) was slightly greater than that reported by Turner and Long (1975) (~6 Mg ha^{-1} year^{-1}), and within the range reported by Keyes and Grier (1981) for 40-year-old *P. menziesii* stands on low and high productivity sites (5.1 and 9.9 Mg ha^{-1} year^{-1}, respectively). It is unclear at present whether leaf area, production and biomass accumulation have peaked in the young

stand. In their chronosequence study, Turner and Long (1975) reported increasing foliar biomass up to Age 73 years (although tree production peaked at Age 42 years). Both continued measurement and retrospective analysis of leaf area trends are warranted for our young stand. The most variable aspect of biomass changes among the three watersheds was tree mortality in the old-growth stand. Only continued observation can reveal whether live bole biomass will remain relatively constant in the old-growth stand over the long run (although see results of DeBell and Franklin 1987).

A decrease in net primary production and an increase in tree mortality both contributed to the observed decrease in biomass accumulation with stand age. The difference in NPPB between the highest observed value for the young stand and the mean value for the old-growth stand was ~4 Mg ha^{-1} year^{-1}. Biomass loss through mortality was minimal for the young stand, and averaged ~4 Mg ha^{-1} year^{-1} for the old-growth stand. Thus, the apparent decrease in biomass accumulation with stand age appears to be the result, in roughly equal parts, of a decrease in production and an increase in mortality. This conclusion does not conflict with the findings of Ryan et al. (1997) who concluded that tree mortality is probably not the cause of the decline in NPP with stand age. However, Ryan et al. (1997) did not directly address the causes of the change in biomass accumulation with stand age.

Over 12 years of observation, live bole biomass was essentially constant in the old-growth stand. Nevertheless, net primary production of boles was still considerable, averaging

about half the largest value observed in the young stand. DeBell and Franklin (1987) observed similar trends in a 36-year study of an old-growth *P. menziesii*–*T. heterophylla* forest in Washington state: production and mortality essentially balanced, resulting in no net change in live volume; and production was roughly half the maximum for young stands on similar sites. Thus, old-growth forests in the Pacific Northwest can maintain relatively high rates of production, with the carbon captured most likely accumulating as dead wood. As Grier et al. (1989) have cautioned, to ignore tree mortality can result in a serious underestimate of the productivity of old-growth forests.

Acknowledgments

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