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ECOSYSTEMS

Succession May Maintain High Leaf Area: Sapwood Ratios and Productivity in Old Subalpine Forests

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ABSTRACT

Old forests are generally believed to exhibit low net primary productivity (NPP) and therefore to be insignificant carbon sinks. This relationship between age and NPP is based, in part, on the hypothesis that the biomass of respiratory tissues such as sapwood increases with age to a point where all photosynthate is required just to maintain existing tissue. However, this theoretical connection between respiration:assimilation ratios and forest productivity is based on age-dependent trends in the sapwood:leaf ratios of individual trees and even-aged stands; it does not take into account such processes in natural forests as disproportional increases in shade-tolerant species over time and multiple-age cohorts. Ignoring succession and structural complexity may lead to large underestimates of the productivity of old forests and inaccurate estimates of the ages at which forest productivity declines. To address this problem, we compared biomass allocation and productivity between whitebark pine, a shade-intolerant, early-successional tree species, and subalpine fir, a shade-tolerant, late-successional species, by harvesting 14 whitebark pines and nine subalpine firs that varied widely in dbh and calculating regression models for dbh vs annual productivity and biomass allocation to leaves, sapwood, and heartwood. Late-successional subalpine fir allocated almost twice as much biomass to leaves as early-successional whitebark pine. Subalpine firs also had a much lower allocation to sapwood and higher growth rates across all tree sizes. We then modeled biomass allocation and productivity for 12 natural stands in western Montana that were dominated by subalpine fir and whitebark pine varying in age from 67 to 458 years by applying the regressions to all trees in each stand. Whole-stand sapwood:leaf ratios and stand productivity increased asymptotically with age. Sapwood:leaf ratios and productivity of whitebark pine in these stands increased for approximately 200–300 years and then decreased slowly over the next 200 years. In contrast, sapwood:leaf ratios of all sizes of subalpine fir were lower than those of pine and productivity was higher. As stands shifted in dominance from pine to fir with age, subalpine fir appeared to maintain gradually increasing rates of whole-forest productivity until stands were approximately 400 years old. These results suggest that forests such as these may continue to sequester carbon for centuries. If shade-tolerant species that predominate late in succession maintain high assimilation-to-respiration ratios in other forests, we may be underestimating production in old forests, and current models may underestimate the importance of mature forests as carbon sinks for atmospheric CO_2 in the global carbon cycle.

Key words: allometry; biomass allocation; carbon cycle; climate change; forest productivity; growth efficiency; leaf area; productivity; sapwood; succession.

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INTRODUCTION

As conifer forests age, net primary productivity (NPP) increases rapidly during early succession, but it is believed to decrease to very low or even negative rates in older forests (Bazzaz 1979; O'Neill and DeAngelis 1981; Pearson and others 1984; Ryan 1991; Ryan and Waring 1992; Gower and others 1994; Murty and others 1996; Ryan and others 1997). A widely cited hypothesis for this decline in productivity is that allocation to leaves decreases or reaches a steady state, while allocation to sapwood increases, creating conditions where total respiration costs equal or even exceed gross photosynthetic assimilation (Yoda and others 1965; Odum 1969; Kira and Shidei 1967; Whittaker 1975; Waring and Schlesinger 1985; Kimmins 1997). The relationship between biomass allocation and NPP has not been rigorously tested (see Gower and others 1995), and there are several alternative hypotheses (Vitousek and Reiners 1975; Van Cleve and others 1981; Gholz and others 1985; Ryan and Waring 1992; Yoder and others 1994; Gower and others 1996; Murty and others 1996; Ryan and Yoder 1997; Ryan and others 1997). Furthermore, evidence from stand analyses in some natural forests indicates that biomass can continue to accumulate for hundreds of years (MacMahon 1980; Franklin and others 1981; Kimmins 1997; Tappeiner and others 1997). However, the biomass allocation–productivity paradigm is still central to forest ecology, and it affects the estimation of global carbon budgets. For example, increasing respiration:assimilation ratios are implicit as the mechanistic background for the management practice of replacing old "overmature" or "decadent" forests with younger even-aged stands to increase forest productivity (Smith and others 1997). The respiration: assimilation hypothesis is also the theoretical basis for the assumption that old forests play a minor role as an active carbon sink in global models (Detwiler and Hall 1989; Jarvis 1989; Dixon and others 1994; Mellilo and others 1995).

A weakness in the current conceptual relationship between forest age, sapwood:leaf allocation, and productivity, however, is that models for sapwood:leaf ratios in whole forests, as they age, have been extrapolated from age-dependent allocational patterns of single species (Turner and Long 1977; Attiwill 1979), even-aged stands (Braastad 1975; Long and Smith 1992; Ryan and Waring 1992; Ryan and others 1997), the combination of many species into a single ratio (Kira and Shidei 1967), or, as in Odum's (1969) influential treatise, on generalized theoretical connections between algal microcosms and Kira and Shidei's results. Although increasing sapwood:leaf mass ratios with age are the rule for individual trees and must eventually occur in undisturbed forests, successional shifts in the community species composition and multi-age cohorts (see Haight and Monserud 1990; O'Hara 1996) that typify many natural forests may maintain low sapwood:leaf ratios and high forest productivity for much longer than predicted by allocational changes in single species or even-aged stands.

Interspecific comparisons of leaf:sapwood (defined as the cross-sectional area at the base of the live crown) ratios for conifer species in the literature show a correlation between leaf:sapwood proportions and site aridity (Waring and Schlesinger 1985; Margolis and others 1995; Kimmins 1997). This correlation suggests that the xeric conditions that occur in some early-successional sequences (Geiger and others 1995) may favor species that have relatively low leaf-to-sapwood ratios (that is, low transpiration area and high water storage volume). As forests age, low-light conditions may favor species with high leaf-to-sapwood ratios, an assumption that is generally supported by pairwise comparisons of species that are believed to form general successional sequences in western coniferous forests (Table 1). The observation that leaf areas and leaf:sapwood ratios of late seral species are typically higher than those of early-successional species supports the hypothesis that successional processes maintain a favorable balance of assimilation and respiration and productivity in older forests. Long-term recruitment after stand initiation may amplify the species-specific effects of late seral species on respiration:assimilation ratios. However, little information is available on the biomass allocation of early and late seral species growing under the same climatic conditions at the same site. Most of the ratios presented in Table 1 were collected at different study areas, or over a wide range of biophysical conditions within study areas; thus, they only provide an inference of trends that might occur during succession in conifer forests. Compounding our lack of knowledge of the effects of succession on biomass allocation and productivity is the scarcity of field studies comparing productivity among forests of different ages but in similar habitats.

Fire exclusion policies have led to large-scale successional changes in conifer forests throughout North America (Arno 1980), where early seral, single-stratum forests have been replaced by late-successional species (Covington and Moore 1992; Quigley and Arbelbide 1997). Over the last 60–80 years, western forests have seen an expansion of

Table 1. Ratios of Projected Leaf Area to Sapwood Cross-sectional Area for Early- and Late-successional Conifer Species Pairs in the Northern Rocky Mountains

Early Succession (m^2/cm^2)	→	Late Succession (m^2/cm^2)
Pinus ponderosa (.17–.25)	→	*Pseudotsuga menziesii* (.25–.70)
Pinus ponderosa (.17–.25)	→	*Abies grandis* (.51)
Pinus contorta (.11–.30)	→	*Pseudotsuga menziesii* (.25–.38[a])
Pinus contorta (.11–.30)	→	*Abies lasiocarpa* (.75)
Pinus contorta (.11–.30)	→	*Tsuga heterophylla* (.46)
Pseudotsuga menziesii (.25–.38[a])	→	*Abies lasiocarpa* (.75)
Pseudotsuga menziesii (.25–.38[a])	→	*Abies grandis* (.51)

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[a] *Pseudotsuga menzeisii* is highly variable in sapwood:leaf ratios. Here we report ratios for the interior variety (*P. menzeisii, glauca*); the interior, coastal varieties (var. *Douglasii*) have much higher ratios.

Biomass ratios are taken from Waring and Schlesinger (1985), Kimmins (1987), Callaway and others (1994), Margolis and others (1995). Successional trends are taken from Pfister and others (1997, Appendix B).

shade-tolerant firs (*Abies*) and interior Douglas-firs (*Pseudotsuga menzeisii* var. *glauca*) (Monnig and Byler 1992; O'Laughlin and others 1993). In subalpine forests of the interior northwest, fire suppression, beetle epidemics, and introduced pathogens have contributed to dramatic shifts from shade-intolerant, early-successional whitebark pine (*Pinus albicaulis* Engelm.) to shade-tolerant, late-successional subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Arno and Pederson 1983; Keane and others 1990; Keane and Arno 1993). Because this subalpine ecosystem is simple in composition and is currently undergoing large-scale successional changes, it provides a good opportunity to investigate successional effects on sapwood:leaf allocation and growth, as well as changes in forest productivity with age. We compared biomass allocation, growth rate, and growth efficiency between whitebark pines and subalpine firs of different sizes in western Montana and extrapolated these measured relationships to whole forests by applying the regression models for individual trees to known size classes of trees in forests ranging in age from 67 to 458 years.

SPECIES

Whitebark pine is a slow-growing, long-lived species common in the subalpine zones and timberline of southwestern Canada and the western United States (Arno and Hoff 1989). It is more abundant on the dry inland slopes of mountains and absent from most of the wettest areas. On very dry sites, whitebark pine may form climax stands (Weaver and Dale 1974), but in most forests in which it occurs it is a long-lived seral component of forests that are codominated by subalpine fir (Pfister and others 1977). Subalpine fir is widely distributed in the United States and Canada. In the subalpine forests of the northern Rockies, it is common in the coolest and wettest habitats (Alexander and others 1990), and in sites too moist for whitebark pine it forms the timberline. The shift from whitebark pine to fir over time is often altered by wildfire, with intervals ranging from 50 to 300 years (Arno 1980). Whitebark pine seeds are dispersed and carried large distances by Clark's nutcracker (Tomback 1982), and it is usually the earliest colonist on these burned sites (Arno 1986; Keane and others 1994). Whitebark pine seeds are a crucial component of the diet of black and grizzly bears, red squirrels, and Clark's nutcrackers (Ferner 1974; Tomback 1982; Mattson and others 1991). Whitebark pine–dominated forests also protect snowpack in high-elevation watersheds and delay snowmelt (Arno and Hoff 1989). Whitebark pine is decreasing rapidly in many parts of its range as a result of mountain pine beetle outbreaks, successional replacement by shade-tolerant subalpine firs, and the introduced white pine blister rust, *Cronartium ribicola* (Keane and Arno 1993; Keane and others 1994).

SITE

To build regression models for biomass allocation and growth, we harvested 14 whitebark pines and nine subalpine firs from an approximately 5 ha area, at 2300 m elevation, in the Sapphire Mountains of the northern Rockies (46°05′N, 114°50′W) approximately 90 km south of Missoula, Montana. We worked with a smaller sample size for firs because the crown structure of these trees appeared to be highly consistent with dbh and because sapwood:leaf ratios for subalpine fir have been documented elsewhere in the Rockies (Kaufman and Troendle 1981; Margolis and others 1995). To lessen our impact on beleaguered pristine whitebark communities, we chose a site that had already been disturbed in the early 1960s by partial cutting of the overstory trees. For consistency and to maintain conditions as similar as possible to that found in undisturbed forests, within this area we sampled trees in closed stands that had canopies that were not in contact with the canopies of neighbors. As a result of working on a disturbed site and selecting trees that were not densely packed, however, our results probably show higher growth rates and lower sapwood:leaf ratios than those of trees in dense stands (Dean and Long 1986; Keane and Weetman 1987). The site is on a northwest-facing 10%–15% slope; the substrate is granitic; and mean temperatures for July and January for this habitat type are 14°C and –10°C, respectively (Pfister and others 1977). None of our sample trees were infected with blister rust.

METHODS

Allometry and Biomass Allocation

Trees of each species were selected to represent their typical ranges of diameters at 140 cm above ground (dbh). Measurements and calculations of allometry and biomass allocation follow Callaway and others (1994). Total tree height and the basal diameter of all live branches on each bole were measured on trees cut at the base. We cut 3–5-cm-thick transverse disks at 2-m intervals from each bole; an additional section was cut at the base of the live crown. Disks were stained when necessary with bromecresol green (Kutscha and Sachs 1962) to distinguish sapwood from heartwood, and the cross-sectional areas of sapwood, heartwood, and bark on each disk were traced on clear acetate. The area of each component on the acetate was cut out and weighed. The mass of the acetate was converted to area by multiplying by the specific area (in square centimeters per gram) of the acetate. The volume (in cubic meters) of each component in each 2-m bole section was calculated using the areas of the disks at each end of the sections in the following equation:

$$\text{Volume} = ((A_1 + A_2)/2) \times 2\text{ m}$$

where A_1 = initial area in square meters and A_2 = terminal area in square meters. Bole volume was calculated by summing all sections for each tree. Volume of each component was converted to mass using the specific gravity (in kilograms per cubic meter) of the heartwood, sapwood, and bark. Specific gravity for each species was determined using known dimensions and dry mass of wood cores and bark cores collected from randomly chosen sections.

Four to five branches were selected randomly and removed from each subalpine fir tree, and three to four branches were removed from each whitebark pine. For subalpine firs, each branch was separated into a primary branch (the main axis attached directly to the bole), secondary branches, and leaves. The branches of whitebark pine were often larger and more complex, so each branch was separated into terminal branches (those bearing leaves), all other branches, and leaves. The primary branches of firs and all nonterminal branches of pines were cut into 0.5-m-long sections, and the diameters of heartwood, sapwood, and the total branch were measured at the end of each cross section. Cross-sectional areas were calculated from these measurements, and volumes were calculated using the previous equation modified for 0.5-m sections. All nonprimary branches of firs and terminal branches from pines were collected with the leaves and sorted, dried at 60°C, and weighed. Cross-sectional areas of heartwood, sapwood, and bark were measured on random subsamples and used to estimate volumes of the smaller branches. Specific weights of the wood and bark of the boles were used to convert secondary branch volumes to the mass allocated to heartwood, sapwood, and bark (see Callaway and others 1994).

Leaves were removed from each branch, dried at 60°C, and weighed to the nearest gram. Fresh subsamples were chosen from one randomly chosen branch from each tree and measured for one-sided leaf area with MOCHA (Jandel Inc., San Rafael, CA, USA) image analysis software. Specific leaf areas (SLA, $\text{m}^2 \cdot \text{kg}^{-1}$) of the subsamples were used to convert leaf mass to projected leaf area.

Growth Analyses

We measured the width of the five most recent annual rings (1991–95) for all 23 trees at three different places on each disk section. This width was subtracted from all disk sections, and bole biomass was recalculated using the 5-year preharvest estimates of tree size. The 5-year preharvest mass was subtracted from current bole mass for each tree and divided by five to estimate current annual aboveground bole productivity. The annual productivity of the bole, as a percentage of current bole mass, was used to estimate branch productivity. Because whitebark pine allocates proportionally more biomass to branches than subalpine fir with age (see Results), our calculations may yield slightly disproportional underestimates of pine productivity. Leaves from 10 randomly chosen branches from different trees (in the case of subalpine fir there were only nine sample trees, so one other branch was chosen at random from the entire branch pool) for each species were separated into the sample year's current growth, and that of all previous years, prior to drying and weighing. From these samples we developed estimates of the proportion of total leaf mass that was a single year's production. This ratio was applied to the canopies of all trees to estimate an annual rate of leaf productivity for each species. Bole, branch, and leaf productivity were summed as an estimate of total aboveground net primary productivity (ANPP) for each species by dbh. We then calculated growth efficiency as grams of wood produced per square meter of projected leaf surface area (Waring 1983).

Projections of Allocation and Productivity to Whole Forests

We constructed biomass allocation and ANPP estimates for forests using empirical data from 12 natural stands in the Bob Marshall Wilderness in Montana, 300–400 km north of the harvest site. These stands varied in age from 67 to 458 years old, appeared to have regenerated after stand-replacing fires, and were sampled using standardized ECODATA methodology (Keane and others 1994). One 400-m^2 circular plot was located in each stand, and all tree stems were classified into 5-cm size classes. In each plot 10–20 trees of various sizes, but including the largest trees, were cored as close to the ground as possible and aged by adding the age at the height of the core to regression estimates for the number of years the tree took to reach core height. To control for variation in microclimate among stands and to calibrate microclimate between these stands and the harvested stand, we chose only stands that were the same habitat type (*Abies lasiocarpa–Luzula hitchcockii*) (Pfister and others 1977) as the stand used for harvests. Over 95% of the basal area in these stands consisted of whitebark pine and subalpine fir. We entered the median dbh for each dbh class (for example, 7.5 in the 5–10-cm class) into the regression models that were developed using the harvested whitebark pine and subalpine fir to calculate sapwood mass, leaf mass, and ANPP. Sapwood mass, leaf mass, and ANPP of all dbh classes were summed for each plot and scaled to tM/ha.

Time-based models were built using the age of the oldest cored tree in each stand for stand age, which assumed that no trees existed in the stand prior to that time. On average, the oldest subalpine firs sampled in these stands were 45 years younger than the oldest whitebark pines. Therefore, whitebark pine and whole-stand allocation and ANPP were extrapolated to time zero and subalpine fir biomass and ANPP to 45 years after time zero. To provide a simple null model for stands without subalpine fir and without recruitment over time, we used the biomass allocation and productivity regressions from harvested whitebark pines to model biomass allocation and productivity of a theoretical, even-aged, whitebark pine stand. This stand began with 400 3.8-cm dbh stems/ha at 50 years (a rounded figure from the two youngest natural stands), underwent 30% mortality every 50 years, and had all surviving trees grow into the next largest age class every 50 years. These inputs were designed so that modeled stands at 450 years in age would have tree densities in the greater-than-50-cm dbh classes that were similar to our natural stands, which exceeded 400 years in age. This kind of consistent mortality may be unrealistic for many natural stands, but it is representative of a much larger data set on stand dynamics in the Bob Marshall Wilderness (Keane and Arno 1993).

Statistical Analyses

Whole-tree leaf mass, bole component masses, and branch component masses were regressed on dbh using logarithmic regressions for each species (compare Whittaker and Woodwell 1968; Chapman and Gower 1991; Callaway and others 1994). Leaf area was regressed against cross-sectional sapwood area at dbh, and sapwood mass:leaf mass ratios and sapwood volume:leaf area ratios were regressed against dbh using simple regression models ($Y = a + bX$) for each species. For small trees that had branches near or to the ground, we substituted the diameter at the base for dbh.

For each species, different logarithmic least squares regressions ($\log Y = a + b \log X$) were calculated using branch basal area as the independent variable and total sapwood, total bark, total heartwood, and leaf mass as dependent variables. These regression equations were then applied to all branch bases measured on each tree to estimate total biomass of branch components on whole trees.

To compare biomass allocation at the branch level, leaf area for individual branches was regressed against branch diameter using logarithmic regression models and against cross-sectional sapwood area at the base using simple regressions. Regression models for whitebark pines and subalpine firs were compared statistically for species effects and slope differences using general linear models (GLM) procedures (Statistical Analysis Software 1996). Significant species by dbh (or cross-sectional sapwood area at the base of live crown)

Table 2. Regression Models for Biomass Allocation among Sapwood, Bark, Heartwood, Leaves, and Height for Subalpine Fir and Whitebark Pine in Western Montana

		Regression Model	r^2
Leaf mass (LM)[a]	Subalpine fir	logLM = –1.170 + 1.949(logdbh)	0.98
	Whitebark pine	logLM = –1.409 + 1.925(logdbh)	0.98
Bole sapwood (BSW)[a]	Subalpine fir	logBSW = –1.634 + 2.349(logdbh)	0.99
	Whitebark pine	logBSW = –1.599 + 2.412(logdbh)	0.99
Bole heartwood (BHW)[a,b]	Subalpine fir	logBHW = –2.351 + 2.902(logdbh)	0.99
	Whitebark pine	logBHW = –3.525 + 3.570(logdbh)	0.94
Bole bark (BB)[a]	Subalpine fir	logBB = –2.036 + 2.328(logdbh)	0.98
	Whitebark pine	logBB = –1.754 + 1.951(logdbh)	0.94
Total branch sapwood (BrS)[a,b]	Subalpine fir	logBrS = −2.195 + 2.163(logdbh)	0.96
	Whitebark pine	logBrs = –3.161 + 2.994(logdbh)	0.94
Total branch heartwood (BrHW)[a,b]	Subalpine fir	logBrHW = –2.778 + 2.266(logdbh)	0.95
	Whitebark pine	logBrHW = –4.498 + 3.384(logdbh)	0.95
Total branch bark (BrB)[a,b]	Subalpine fir	logBrB = –1.779 + 1.836(logdbh)	0.98
	Whitebark pine	logBrB = –1.754 + 1.951(logdbh)	0.94

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[a] *Equations with significant species effects in GLM.*

[b] *Equations with significantly different slopes (significant species by dbh interactions in GLM).*

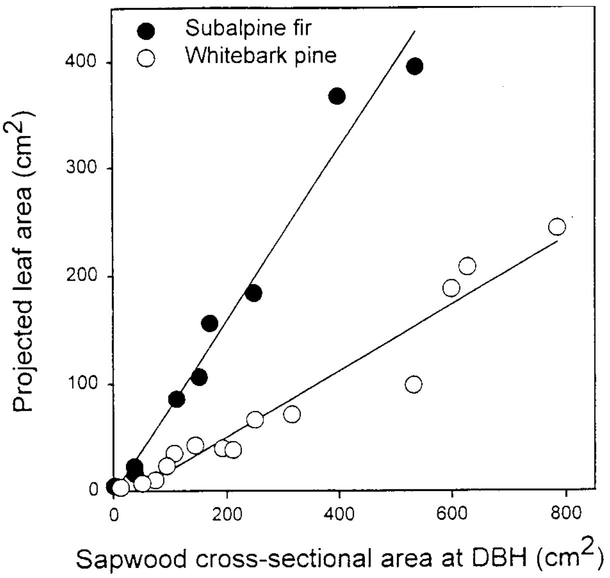

Figure 1. Whole-tree projected leaf area (LA) versus cross-sectional sapwood area (SA) at dbh for subalpine fir and whitebark pine in subalpine forests of western Montana. For subalpine fir, LA = –1.42 + 0.80(SA), r^2 = 0.97. For whitebark pine, LA = –10.86 + 0.31(SA), r^2 = 0.94. Slopes differed significantly, GLM, $F_{SA \times species} = 56.56$, $P < 0.0001$.

interactions identified significantly different slopes. To compare patterns of aboveground biomass allocation for whitebark pines and subalpine firs of the same diameters, we used the regressions to develop models for hypothetical trees of 15- and 50-cm dbh.

We used ANCOVA to test for differences between whitebark pine and subalpine fir over time on stand allocation ratio, ANPP, and biomass. Significant stand age by species interactions were considered to indicate that species effects over time were different.

RESULTS

Biomass Allocation and Growth at the Tree Scale

Subalpine fir trees of all diameters allocated significantly more biomass to leaves and less to sapwood than similar-sized whitebark pines (Table 2, Figures 1, 2), but the difference between species was greater for larger trees. Leaf area to cross-sectional sapwood area ratios, measured as the slopes of the regression lines, were 0.80 for subalpine fir and 0.31 for whitebark pine, respectively (Figure 1), and larger individuals of the late-successional species were able to support over twice as much foliage per unit of conducting tissue. For entire trees, sapwood:leaf mass ratios were two to three times higher for whitebark pine than for subalpine fir, depending on the dbh of the trees (Table 2 and Figure 2). This difference was due to much larger volumes of sapwood and low leaf proportions in pine, and differences in pine wood density (0.46 ± 0.01, 1 S.E., g/cm^3 compared to 0.40 ± 0.01 g/cm^3 for fir). For leaf cohorts at least 1 year old, specific leaf area was 3.3 ± 0.3 m^2/kg (1 S.E.) for fir and 3.0 ± 0.2 m^2/kg for pine. We evaluated mass ratios to em-

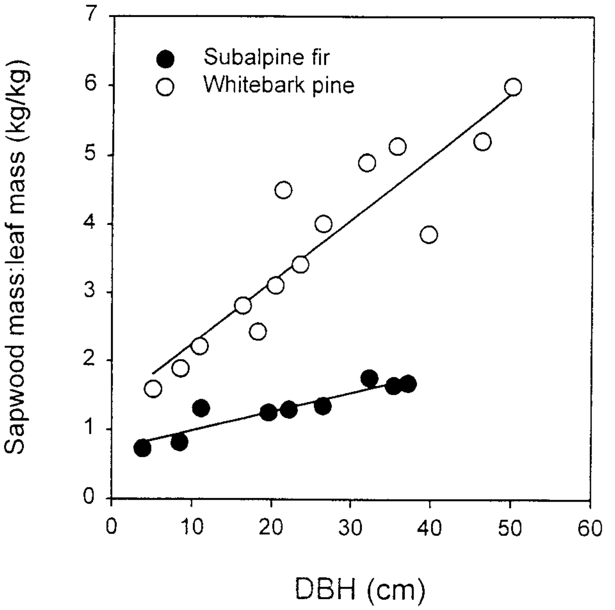

Figure 2. Whole-tree sapwood mass:leaf mass (SLM) versus dbh for subalpine firs and whitebark pines. For subalpine fir, SLM = 1.271–0.020(dbh), r^2 = 0.77. For whitebark pine, SLM = 0.541–0.009(dbh), r^2 = 074. Slopes differed significantly, GLM, $F_{\text{dbh} \times \text{species}}$ = 14.48, P = 0.0012.

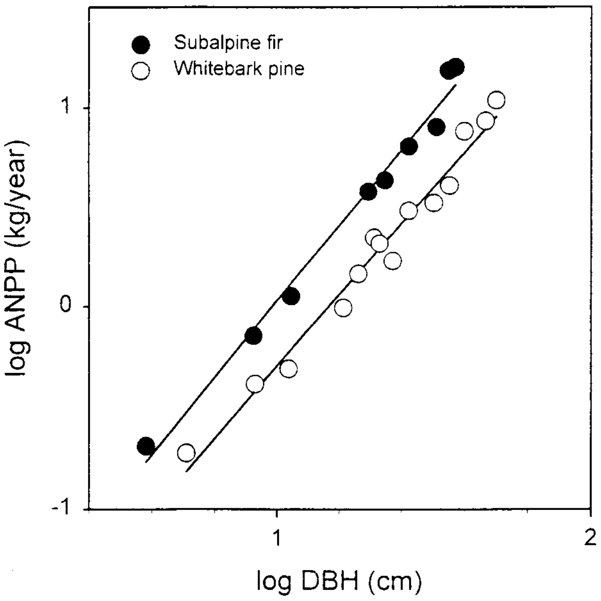

Figure 3. Whole-tree annual net primary productivity (ANPP) versus dbh of subalpine fir and whitebark pine in western Montana. For subalpine fir, log(ANPP) = –1.870 + 0.1.903(logdbh), r^2 = 0.99. For whitebark pine, log(ANPP) = –2.080 + 1.788(logdbh), r^2 = 0.98. Slopes did not differ significantly, but the effect of species did, GLM, F_{species} = 100.47, $P < 0.0001$.

phasize the effects of carbon allocation on photosynthetic gain and respiration losses.

Whitebark pines developed larger branches, with models of 50-cm dbh trees allocating over 15% of their total aboveground biomass to branches. In contrast, 50-cm dbh firs allocated only 8% of their aboveground biomass to branches. Allocation patterns within the branches also varied between the species. Of the 138 kg of branches on a modeled 50-cm dbh whitebark pine, 61% of the total mass was sapwood, as compared to 45% in subalpine fir branches. This difference appeared to be due, in part, to more extensive development of heartwood in firs.

Canopy architecture differed substantially between firs and pines. A 50-cm dbh subalpine fir was projected by regression models to be 23.6 m tall and on average supported 32.4 ± 4.5 (1 S.E.) branches per meter of bole. A 50-cm dbh whitebark pine was projected to be 18.2 m tall and only had 15.6 ± 1.2 branches per meter (t_{species} = 4.34, df = 21, $P <$ 0.001). Low branch density and long branches in this early seral, shade-intolerant species seems to maintain an open crown architecture in which light can penetrate throughout the canopy.

ANPP of subalpine firs was higher than that of whitebark pines of all ages (Figure 3), with firs of all sizes producing significantly more mass per year than pines.

Biomass Allocation and Productivity at the Whole-Stand Level

Our reconstruction of stand biomass allocation from the field data suggested that subalpine fir maintained a substantially lower whole-forest sapwood: leaf ratio than would be predicted from the biomass allocation of either even-aged stands or naturally developing stands of whitebark pine (Figures 4, 5). Unlike whitebark pine, for which sapwood:leaf ratio was high and continued to increase throughout our range of forest stand ages, subalpine fir populations maintained very low and stable sapwood: leaf ratios throughout the 450-year seral sequence. Individual subalpine firs increased sapwood:leaf ratios slowly with dbh (Figure 2), and many young firs became established late in stand development, even in the oldest stands (Figure 6). For example, in the two oldest stands (406 and 458 years), there were 1013 and 1160, respectively, individual subalpine firs in the 1–5-cm size class per hectare and 445 and 395 individuals/ha in the 5–10-cm size class. Based on the growth rates from our harvested trees, these firs were estimated to contribute an average of 20% of the ANPP of these two stands.

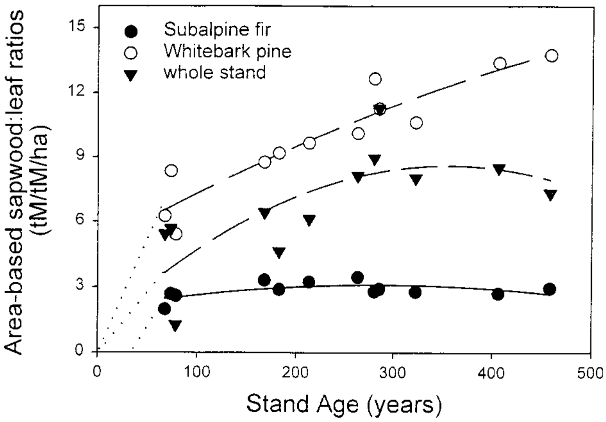

Figure 4. Whole-stand sapwood:leaf mass ratios for 12 subalpine forest stands of different ages in the Bob Marshall Wilderness. Curves were fit as second-order regressions. ANCOVA for whitebark pine and subalpine fir, $F_{age} = 64.82$, df = 1,23, $P < 0.001$; $F_{species} = 19.11$, df = 1,23, $P < 0.001$; $F_{age \times species} = 52.33$ df = 1,23, $P < 0.001$.

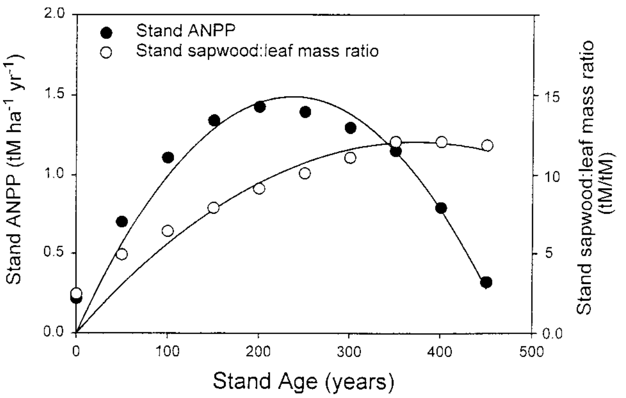

Figure 5. Simulated whitebark pine stand productivity and biomass allocation without subalpine fir and without recruitment over time. This model used regressions from harvested whitebark pines to model biomass allocation and productivity of a theoretical whitebark pine stand over 450 years. This stand began with 400, 3.8 cm dbh stems/ha at 50 years (derived from the two youngest natural stands), underwent 30% mortality every 50 years, and had all surviving trees grow into the next largest age class every 50 years. These inputs were designed so that modeled stands at 450 years in age had similar tree densities in the greater-than-50-cm dbh classes to our natural stands that exceeded 400 years in age. Curves were fit as second-order regressions.

Our empirical models suggest that the maintenance of low stand sapwood:leaf area ratios by subalpine fir has the potential to maintain high rates of stand productivity even in forests more than 400 years old (Figure 7). The contrast is illustrated by comparing whole-stand ANPP in the natural forests to the general pattern of productivity over time in our null model ANPP (Figure 5). The latter shows the classic pattern of rapid increases in ANPP and then decreasing ANPP as sapwood:leaf ratios continue to rise. In the natural forests, ANPP of whitebark pine declined in the oldest stands, but high growth rates and recruitment rates of late-successional subalpine fir sustained gradually increasing rates of whole-stand ANPP for this species during the 450-year span of our sample stands. The role of subalpine fir in maintaining stand ANPP is evident in comparisons of the proportional contribution of each species to stand productivity at different stand ages. In the three youngest stands, whitebark pine contributed 67% of the stand productivity, but in

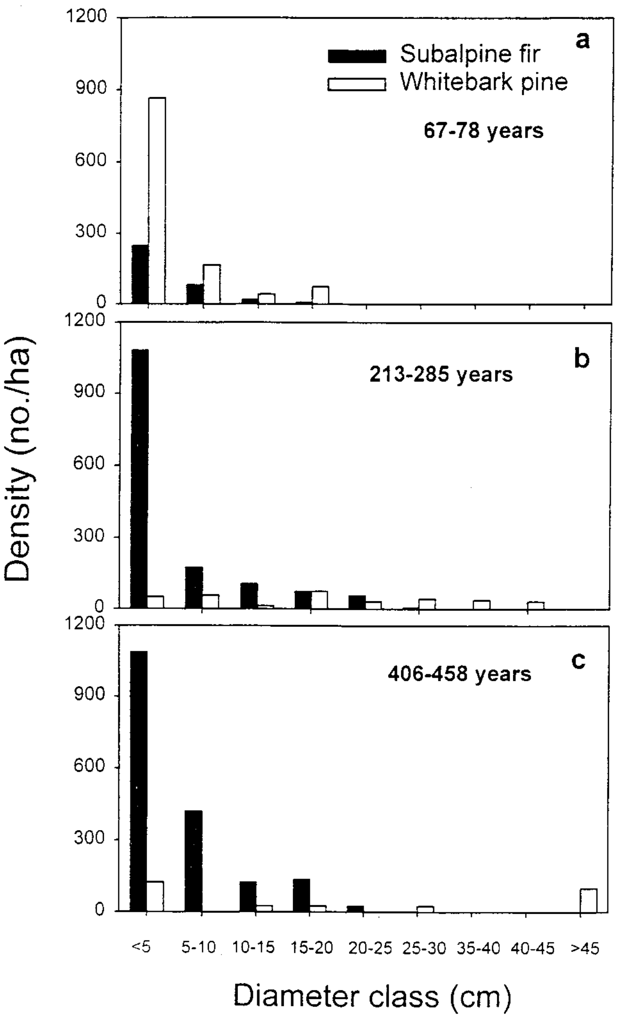

Figure 6. Size class distributions for whitebark pine and subalpine fir in (a) the three youngest, (b) four stands of intermediate age, and (c) the two oldest stands sampled in the Bob Marshall Wilderness.

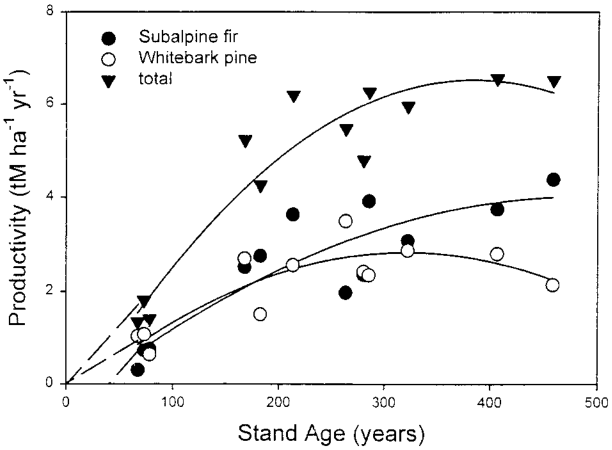

Figure 7. Whole-stand annual productivity rates for 12 forest stands of different ages in the Bob Marshall Wilderness. Curves were fit as second order regressions. ANCOVA for whitebark pine and subalpine fir, $F_{age} = 33.22$, df = 1,23, $P < 0.001$; $F_{species} = 1.14$, df = 1,23, $P = 0.298$; $F_{age \times species} = 3.59$, df = 1,23, $P = 0.073$.

the three oldest stands the trend was reversed, with subalpine fir contributing 62% of the whole-stand productivity.

DISCUSSION

Subalpine forests in our study appear to sustain continued, gradual increases in ANPP over 3 to 4 centuries. Even at 400–450 years, we found no evidence for a decline in productivity. As stands aged, late-successional subalpine fir appeared to play a major role in maintaining low sapwood:leaf ratios and productivity. These findings support others that indicate that evergreen conifer forests may remain highly productive for centuries.

Weaver and Dale (1974) estimated that stands dominated by whitebark pine in environments drier than that studied here gradually increased in productivity over several hundred years. Grier and Logan (1977) estimated ANPP of 450-year-old Douglas fir–western hemlock forests in the northwest United States at 10.8 $tM \cdot ha^{-1}y^{-1}$, whereas ANPP in 100-year-old and 150-year-old stands was estimated at 12.7 and 9.5–10.5 $tM \cdot ha^{-1}y^{-1}$, respectively (Fujimori and others 1976; Gholz 1982). Stands of Pacific silver fir (*Abies amabilis*) measured by Grier and others (1981) only decreased from 6.4 to 4.6 $tM \cdot ha^{-1}y^{-1}$ over 157 years. However, these productivity rates do not integrate the effects of tree mortality over time (as do ours). DeBell and Franklin (1987) argued that biomass loss to mortality may roughly equal that gained by net productivity in old Douglas fir–western hemlock forests, but estimates of annual biomass lost as "coarse woody debris" in mature to old northwestern forests are extremely variable, ranging from 0.5 to 30.0 $tM \cdot ha^{-1}y^{-1}$ (Harmon and others 1986). We applied the mortality coefficient estimated by Turner and others (1995) for Douglas fir and spruce fir forests in the Rocky Mountains (0.50% of standing biomass) to the total biomass of forests in the studies cited above and calculated that 3.6–4.4 $tM \cdot ha^{-1}y^{-1}$ of biomass should be lost to mortality. The differences between ANPP and mortality suggest that even old stands of a number of different forest types may maintain substantial positive rates of productivity.

In our study, productivity may have been sustained because late-successional, shade-tolerant subalpine fir had much lower apparent respiration: assimilation ratios, higher growth rates, and higher growth efficiencies than early-successional whitebark pines. Our calculations of the projected leaf area to sapwood cross-sectional area ratio for subalpine firs (0.80) was similar to that determined in other forests (0.75) (Kaufman and Troendle 1981; Margolis and others 1995). However, the causal relationship between sapwood:leaf ratios and forest productivity has been challenged in a number of studies showing that respiration rates per sapwood volume decrease with tree age and size.

Ryan (1991) found that the total respiration rates of Englemann spruce (*Picea englemanii*), also a common subalpine species in the northern Rockies, decreased with tree diameter. Maintenance respiration of ponderosa pine also decreases with tree size in mesic and xeric environments (Carey and others 1997). In boreal forests, old stands of jack pine (*Pinus banksiana*) had lower maintenance respiration rates per unit of sapwood than young stands (Lavigne and Ryan 1997). Ryan and Waring (1992) found that the maintenance respiration rates (per unit ground area) of a 40-year-old stand of subalpine *Pinus contorta* (61 $g \cdot m^{-2} \cdot y^{-1}$) did not differ from that of a 245-year-old-stand (79 $g \cdot m^{-2} \cdot y^{-1}$); they could not explain the dramatic decline they observed in wood production. In general, maintenance respiration appears to account for only 5%–12% of carbon fixation for most forests (Ryan and others 1995). These data and the alternative hypotheses for age-related declines in forest productivity explored by Murty and others (1996), Ryan and others (1997), and Ryan and Yoder (1997) demonstrate a need to reevaluate the mechanisms that determine forest productivity over time and the models that are currently used to estimate forest productivity at regional and global scales.

Subalpine fire contributes disproportionally to high-stand leaf area, and high leaf area shows a strong correlation with stand productivity in many other forest types (Fassnacht and Gower 1997). Our projections of size-based regression models to whole stands supports the hypothesis that successional species replacement in these forests maintains favorable assimilation to respiration ratios and high ANPP for much longer than would be predicted by simple trajectories of sapwood:leaf ratios of single species or even-aged stands. As environmental conditions change over time such that subalpine fir is favored, both fir recruitment over long time periods and low rates of sapwood accumulation for individual fir trees contribute high proportions of assimilatory tissue and low proportions of heterotrophic tissue at the stand level.

We caution that our calculations of growth rates and growth efficiencies may be higher than for other, similar stands, for two reasons. First, we harvested trees from stands that had been thinned 30 years before our study, and increases in the widths of the annual rings of some of the harvested trees indicated that they may have been released from competitive inhibition. Other investigators have shown that canopy position or stand density can affect sapwood:leaf ratios (Pearson and others 1984; Keane and Weetman 1987; Dean and Long 1986; Hungerford 1986; Naidu and others, forthcoming). The annual growth increment at dbh of subalpine fir and whitebark pine harvested for this study averaged 2.20 ± 0.50 mm (1 S.E.) and 1.20 ± .40 mm, respectively. These figures are substantially higher than those we have collected for other old subalpine forests in the region. Annual increments at dbh from whitebark pines and subalpine firs from three other stands between 2,200 and 2,400 m elevation ranged from 0.44 ± 0.05 to 0.61 ± 0.11 for firs and 0.18 ± 0.11 to 0.22 ± 0.06 for pines (Callaway 1998). These differences suggest that our estimates of whole-stand productivity may be several times higher than that in many other subalpine forests dominated by these species. However, the greater differences between the growth rates for whitebark pine and subalpine fir in these other forests (Callaway 1998) suggest that whitebark pine in other forests may show an even more rapid proportional drop in growth relative to fir than predicted by our models, and there may be a greater relative effect of subalpine firs on the maintenance of productivity over time.

A second caveat is that our regression models are built from pines no older than 228 years and firs no older than 140 years. These regressions were used to predict stand allocation and growth for pines up to 458 years old and firs up to 263 years old. These discrepancies in age probably do not have large effects on our estimates of forest biomass allocation because allocation is strongly related to tree size, rather than age, and is reasonable for relative comparisons of species-specific effects on forest productivity. In our two oldest stands, 28% of the productivity of whitebark pine and none of the productivity of subalpine fir (the oldest fir was in a middle-aged stand) could be attributed to trees outside the age limits of our regressions. Thus, even conservative estimates of forest productivity would still show substantial biomass accumulation in the oldest forests.

Our estimates of stand productivity overlap with the figures shown in tables of yield capability as determined by Pfister and others (1977). Their estimates of stand (bole) ANPP for this forest type ranged from 0.1 to 0.7 $\mathrm{tM \cdot ha^{-1}y^{-1}}$. Our estimates ranged from approximately 0.5 to 2.5 $\mathrm{tM \cdot ha^{-1}y^{-1}}$, which is low compared to other types of forests (Waring and Schlesinger 1985; Franklin 1988; Peet 1988). However, we included leaf and branch ANPP, which roughly doubled estimates for boles. Furthermore, our calculations explicitly included measurements of growth in the upper bole, which was greater than growth at dbh, the height at which conventional bole growth rates are determined.

Our data may also overestimate the contribution of new recruits to whole-stand ANPP. The smallest subalpine firs and whitebark pine in our harvest did not appear to be as suppressed as those in stands sampled for whole-stand allocation. In the 12 stands sampled in the Bob Marshall Wilderness, the average ages of firs and pine 2.5–5-cm dbh were 65.4 ± 7.1 (1 S.E.) and 75.5 ± 10.0, respectively. The 4–10-cm dbh trees in our harvest were 20–70 years old. Our predictions of the contribution of young firs to whole-stand ANPP would be too high when small individuals are more suppressed than those used in our harvest-based models.

Due to harsh physical conditions, canopy closure may be more gradual in subalpine forests than in lower elevation forests, and gradual canopy closure may create opportunities for continuous recruitment that may not occur in other forests (Peet 1980). If other types of forests show substantially less recruitment after initial stand establishment than we and others (Tomback and others 1993; Callaway 1998) have observed for subalpine forests, the effects of succession on whole-stand biomass allocation will be less. Recruitment over time is highly variable among forest types and varies even among similar subalpine forests of the Rockies (Peet 1988). However, there is extensive evidence for recruitment of trees long after stand initiation in many coniferous forests, including those dominated by *Pseudotsuga menzeisii* and *Tsuga heterophylla* (Franklin and Hemstrom 1980; Huff 1995), *Pinus strobus* and *Tsuga canadensis* (Abrams and Orwig 1996), and mixed species in the northern Rocky Mountains (Arno and others 1997). Even though these forests, and ours, show distinct differences in proportional abundance, either early or late after stand initiation, it should be noted that none of these forests follow a strict pattern of relay floristics, and "early" and "late" successional species may be found in forests of different ages.

Our models of stand allocation and growth were also affected by recent whitebark pine mortality due to the nonnative whitebark pine blister rust. The basal area of dead whitebark pines averaged 13% of the total basal area over all stands (R. E. Keane unpublished), but some mortality was natural and not due to blister rust. Mortality due to blister rust is much more common for larger pines, and because larger trees always have higher sapwood:leaf ratios, our estimates of sapwood:leaf ratios in old stands of whitebark pine may have been low in comparison to stands without blister rust. Therefore, our calculations of the proportional contribution of firs to sapwood:leaf ratios in old stands may be high. High mortality rates of large pines due to nonnative factors certainly introduce underestimates of stand ANPP and the contribution of pine to ANPP. However, we could not detect any systematic relationship between whitebark pine mortality and stand productivity as the percent basal area of dead whitebark pine in stands was not correlated with either total stand ANPP ($r = 0.37$, $P = 0.24$) or the proportion of ANPP attributed to firs ($r = 0.01$, $P = 0.97$). However, virtually all whitebark stands in northern Montana, Idaho, and Washington are experiencing mortality due to blister rust that appears to be accelerating the conversion of these forests to subalpine fir.

Correlations between sapwood:leaf ratios and the successional status of conifers has not been considered explicitly in the literature, which is not surprising. Large-scale and gap-scale disturbances may create hotter and perhaps drier conditions (Geiger and others 1995) that can favor species with the ability to store large amounts of water in their tissues. Conversely, once early-successional trees have become established, the forest floor often becomes more mesic and light levels decrease. These conditions favor species that allocate proportionally more biomass to leaves (Waring and Schlesinger 1985; but see Naidu and others forthcoming), and long-term water storage capacity may not be as essential. We correlated sapwood:leaf ratios reported for a number of species in the literature with their reported light compensation points and shade tolerance rankings (after Wenger 1984) (Figure 8). We found that sapwood:leaf ratios showed a high negative correlation with shade tolerance, indicating that the general allocational differences reported here for whitebark pine and subalpine fir may occur in other forests.

We have emphasized the potential for long-term productivity in these subalpine forests; however, fire is an integral part of this ecosystem and occurs at 50- to 300-year intervals (Arno 1980). These fires are often stand-replacing (Losensky 1990). Whitebark pines have a dispersal advantage after large fires because Clark's nutcrackers (*Nucifraga columbiana*) cache whitebark pine seeds into burns from great distances (Tomback and others 1990). Subalpine fir suffers much higher mortality in light ground fires than whitebark pine, and natural fire regimes are presumed to maintain forests dominated by whitebark pine (Arno 1986; Arno and Hoff 1989).

Aboveground carbon sequestering in forests is the difference between carbon gained as ANPP and carbon lost due to mortality and decomposition (net ecosystem productivity, Turner and others 1995). Although our time sequence of stands incorporates mortality, we applied the mortality coefficient of Turner and others (1995) for spruce fir forests in the Rocky Mountains (0.50%) to the total biomass of the oldest forest that we studied to estimate the potential for mortality to cause underestimates in carbon sequestering. We calculated that roughly 0.5 $\text{tM} \cdot \text{ha}^{-1}\text{y}^{-1}$ of biomass should be lost to mortality. This is a relatively small proportion of the approximately 1.5–2.5 $\text{tM} \cdot \text{ha}^{-1}\text{y}^{-1}$ that old stands produced; it suggests that even the oldest stands may be carbon sinks. As a further precaution against misinterpreting the effects of ANNP on carbon acquisition in these stands, we used dbh–total tree biomass regressions to estimate changes in biomass of living trees in stands over time and found that biomass accumulation also continued to increase until approximately 400 years (Figure 9).

Direct comparisons of the productivity of forests of different specific ages are rare in the literature (see Ryan and others 1997), and the theoretical connections between specific forest ages, biomass allocation, net ecosystem productivity (see Turner and others 1995), and net annual productivity in forests is vague. Yet there appear to be strong regional differences (Turner and others 1995). How-

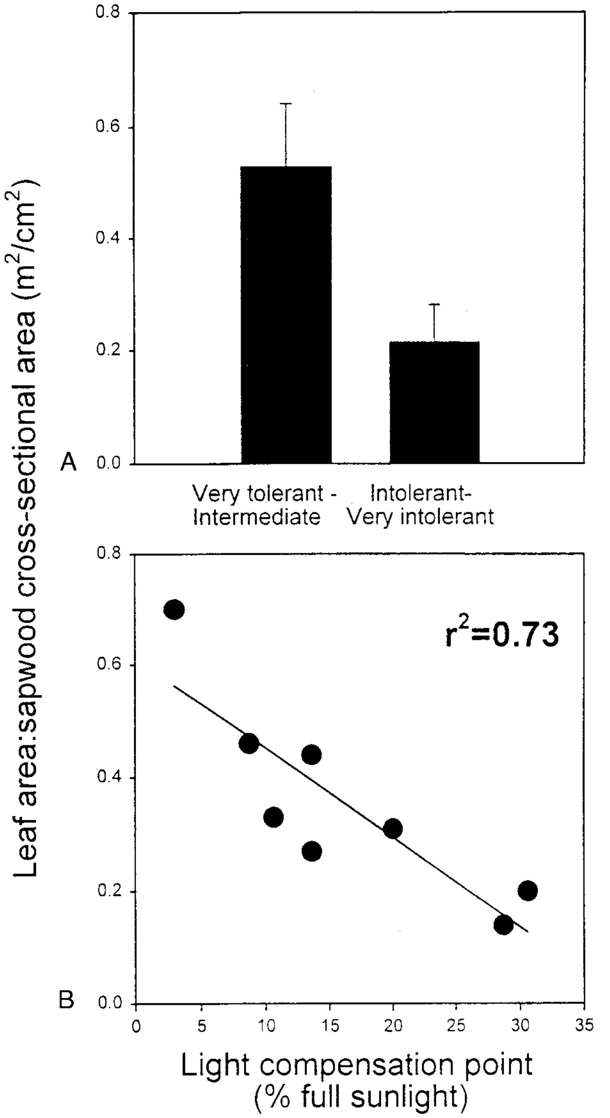

Figure 8. (**A**) Means and 95% confidence limits for leaf:sapwood ratios for shade-tolerant and shade-intolerant evergreen conifer species. Shade-tolerant bar includes species from the "very tolerant," "tolerant," and "intermediate" classes of Wenger (1984); the shade-intolerant bar includes species from the "intolerant" and "very intolerant" classes. (**B**) Regression relationship between light compensation point (percentage of full sunlight) and leaf area:sapwood cross-sectional area ratios for evergreen conifer species. Species used were *Abies grandis,*[1,2] *Abies lasiocarpa,*[1,3,4] *Picea abies,*[1,2] *Picea englemanii,*[1,2] *Pinus albicaulis,*[3,4] *Pinus contorta,*[1,2] *Pinus ponderosa,*[1,2] *Pinus sylvestris,*[1,2] *Pseudotsuga menziesii.*[1,2] [1]Leaf:sapwood ratio from Margolis et al. (1995). [2]Compensation point from Kimmins (1997). [3]Leaf:sapwood ratio from this study, or data from this study average with others. [4]Compensation point from R. M. Callaway, unpublished data.

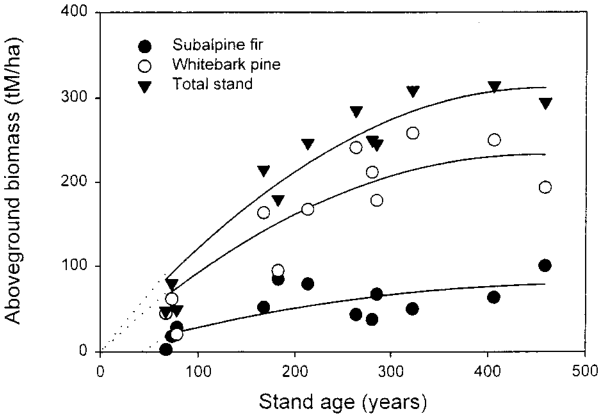

Figure 9. Whole-stand biomass for 12 forest stands dominated by whitebark pine and subalpine fir of different ages in the Bob Marshall Wilderness. Curves were fit as second order regressions. ANCOVA for whitebark pine and subalpine fir, $F_{age} = 33.21$, df = 1,23, $P < 0.001$; $F_{species} = 0.20$, df = 1,23, $P = 0.663$; $F_{age \times species} = 10.02$ df = 1,23, $P = 0.005$.

ever, this theoretical connection plays an important role in the harvesting of public and private forests (Smith and others 1997) and estimates of global carbon budgets (Melillo and others 1995). For example, Melillo and others (1995) state that "old-growth forests accumulate little if any carbon" and that only forests that are regrowing from cutting in the early to mid-1900s are accumulating significant amounts of carbon. Clearly, overestimating the rate at which the productivity of old forests declines will underestimate the potential of old forests to sequester atmospheric carbon. The perception that mature forests are not productive, and thus do not do their part in the global carbon crisis, has even led to congressional proposals to harvest and replace them with young forests (see Harmon and others 1990).

Coniferous forests cover 24% of the terrestrial surface of the globe and are especially important because they store large amounts of carbon at mid- to high- latitudes, where the consequences of climate change are likely to be the greatest (Houghton and others 1991; Gucinski and others 1995). Conifer biomes have the potential to affect feedback among biosphere carbon fluxes and storage (Neilson and King 1992), but many models of carbon storage and flux for conifer forests do not account for succession as described here (see Dixon and others 1994). Sedjo (1992) argued that temperate forests are an important global carbon sink, basing his argument primarily on recent forest expansion and regrowth. If successional shifts maintain low sapwood:leaf ratios and productivity in coniferous forests, as described here for subalpine forests, old forests may contribute to the role of temperate forests or "northern land biota" as a "missing sink" (Kauppi and others 1992; Sedjo 1992; Ciais and others 1995; Keeling and others 1996). Our results indicate that successional effects on long-term productivity of forests should be considered in global climate models. However, before we can conclude that succession maintains higher rates of productivity and carbon storage in forests in general, much more evidence from other forest types is necessary.

In summary, shade-tolerant, late-successional subalpine fir appears to maintain low sapwood:leaf ratios in subalpine forests via inherently low sapwood:leaf area of individual trees, low rates of increase in sapwood:leaf ratios (lower regression slopes) with size, and high recruitment rates over hundreds of years of stand development. In general, late-successional and shade-tolerant species have relatively low sapwood:leaf ratios, suggesting that the temporal patterns reported here for subalpine forests may occur in other forests. The effects of succession on the maintenance of productivity should be measured in other forests; if late-successional species are found to maintain favorable sapwood:leaf ratios in other ecosystems, we may be greatly underestimating the productivity and carbon storage potential of old forests.

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