To live fast or not: growth, vigor and longevity of old-growth ponderosa pine and lodgepole pine trees

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Summary Old trees of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) were studied to determine volume growth patterns in relation to leaf area. Ponderosa pine trees varied in age from 166 to 432 years and were about 77 cm in diameter; lodgepole pine trees varied in age from 250 to 296 years and were about 31 cm in diameter. With the exception of several ponderosa pine trees less than 200 years old, trees of both species had flattened tops, heavy branches, and foliage distribution characteristically found only in the oldest trees. After trees were felled, annual volume increments were determined from crossdated radial increments measured on discs at 4-m height intervals, and leaf areas were determined based on leaf area/branch sapwood area ratios for 1/5 sections of the crown for each tree.

In ponderosa pine, three distinct volume growth patterns occurred: (1) a gradual increase in annual volume growth until felling; (2) a more rapid increase in growth to a plateau that persisted for a century or more; and (3) a rapid increase in growth followed by a generally sudden decrease in growth to less than half the earlier rates, and persisting at these lower rates for as long as seven decades. In lodgepole pine, fewer trees exhibited the sudden growth decline observed in ponderosa pine. Most short-term growth variations in ponderosa pine were synchronized among all trees, suggesting a common climatic signal. In lodgepole pine, annual variations in volume growth were slight.

Volume growth in the most recent years before felling was weakly correlated with leaf area at the time of felling ($r^2 = 0.45$ for both species). However, in both species, trees having a high volume growth rate and leaf area at the time of felling had grown slowly when young, whereas trees having low volume growth rate and leaf area at felling grew rapidly when young. Thus a wide range of early and late growth patterns can lead to old-growth conditions in these species. Growth efficiencies (grams of dry matter per m² total leaf area) were generally higher for trees having the lowest leaf areas, and in almost all cases were below 100 g m^{-2}.

Keywords: annual volume growth increment, dendrochronology, growth efficiency, Pinus contorta, Pinus ponderosa, stem analysis, tree-ring measurement, tree vigor.

Introduction

Old-growth forests provide unique features involving stand and tree structure and function in the forested landscape. Typically, old-growth stands have patterns of tree growth and internal distribution of fixed carbon, accumulation of detritus, and perhaps resistance to insects and disease that are quite different from those of younger stands (Spies and Franklin 1991, Kaufmann et al. 1992, Moir 1992, Ryan and Waring 1992). Through timber harvest and other land use impacts, the amount of old-growth forest has been reduced in the western United States and many other areas of the world. To maintain or restore the old-growth condition, information is needed about the growth and development of trees that eventually achieve old age. Conducting experiments on forest community dynamics that compare possible stand treatments leading to old-growth conditions could take hundreds of years.

It is possible, however, to study the growth history of existing trees to learn retrospectively how old trees developed. One goal of such studies is to determine how early stand conditions allow certain trees to reach old age. Another goal is to understand better the variation in growth patterns of individual trees, and to identify patterns of growth that lead to achievement of large size and persistence. This information would be helpful in determining how mature stands might be managed to create the old-growth condition as early as possible and to allow the condition to persist. Such information would also be useful in determining how biotic and abiotic stresses contribute to the loss of vigor and eventually lead to mortality in old trees (Waring 1987).

Study of the development of old-growth features in forest stands requires a better understanding of the distinguishing characteristics of old trees. It is easier to see differences between mature and old-growth trees in certain pine species than in spruce, fir and other conifers. In ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), for example, old trees typically have very little terminal leader growth, and the top of the crown becomes flattened as lateral branches reach nearly the same height as the terminus. In addition, branches throughout the bole become larger in diameter, and lower branches often droop as they become older. A fairly prominent feature of old ponderosa pine

and lodgepole pine trees is that the lateral branches near the top of the crown become thicker and nearly free of foliage near the bole. Changes in both branch characteristics and foliage distribution along shoots are much less useful in distinguishing old trees from mature trees in other conifer species in the central and southern Rocky Mountains.

In an earlier study of lodgepole pine, Kaufmann and Watkins (1990) reported that trees differed widely in their leaf area even though they had nearly the same bole size and tree age. Trees with higher leaf areas had deeper crowns and the needles occurred along a greater twig length than in low-vigor trees. Furthermore, trees with high leaf area had a larger sapwood volume and lower heartwood volume than trees with low leaf area. In this paper, we focus on the pattern of growth over the life of old ponderosa pine and lodgepole pine trees and its relationship to leaf area.

Methods and materials

Initial studies were done on lodgepole pine growing in an old-growth stand in the Fraser Experimental Forest near Fraser, Colorado. The stand occurs at an elevation of 3100 m and is on a 15--20° south-facing slope. Twenty trees were sampled in a 1-ha area. The trees had crowns characterized by flattened tops, large diameter branches, and foliage distribution suggesting slow shoot growth compared with younger trees in other stands. The trees were selected to be similar in bole size (mean diameter at breast height (dbh) of 31.4 cm, range 28.0--34.1 cm), and height varied from 19.8 to 24.1 m (mean 22.0 m). The trees were 250--296 years old at breast height (mean 273 years), and they were selected to have a wide range of total leaf area (9.7--224 m^2). Applying the ponderosa pine growth rate classification system (Thomson 1940) to the sampled lodgepole pine trees, the classifications would fall between 4B and 4D, based on advanced age and medium to weak vigor classes.

Trees were felled, and measurements were made of total height, depth of crown, and diameters at various heights along the bole. The live crown length was divided into five sections, and within each section, a representative large branch was selected for leaf area calculations. On this branch, the total leaf area of the foliage was determined based on a leaf area/dry weight conversion factor developed on a subsample of foliage. The ratio of total branch leaf area to branch sapwood area was estimated from a branch cross section taken 15 cm from the bole. This ratio was used to estimate leaf area for each crown fifth, using the sapwood area of cross sections from all other branches in that fifth.

Thin cross sections were taken from the bole near the base (0.2 m above the ground), at 1.37 m, at each 4-m interval above the ground to the top of the bole, and at the base of the crown. On each section, sapwood and heartwood cross-sectional areas were determined, as well as radial growth increments at 10-year intervals on two radii. Volume growth increments were determined for each bole section using the 10-year radial growth increment data. The radial increment data were not crossdated using dendrochronology techniques, and although

the magnitude of errors associated with the 10-year increment data is probably not large, there may be some inaccuracy resulting from not detecting missing rings.

Recognition of the difficulties associated with ring detection in lodgepole pine led to development of a video-based tree-ring measuring system for use on ponderosa pine (Kaufmann, unpublished data). The ponderosa pine portion of the study was conducted on a site having older trees and a greater potential for complications arising from missing rings. This site was in the Long Valley Experimental Forest about 90 km south of Flagstaff, Arizona, on the Coconino Plateau. The site was relatively flat, having local relief of no more than about 30 m over a study area of about 25 ha. The forest stand was characterized by an overstory of old trees in several age groups, and most of the area had one or several age classes of younger trees creating additional canopy layers, stemming from lack of fire during this century. Most of the sampled trees had crown structures that typically appear in trees over 200 years old, although several trees in the sample of 24 were younger than this. The sample trees had a mean dbh of 76.6 cm (range 65.4--85.3 cm) and a mean height of 33.9 m (range 29.5--37.4 m). Age ranged from 166 to 432 years at breast height, and total leaf areas ranged from 162.3 to 1202.3 m^2. Applying Thomson's (1940) growth rate classification, the sampled ponderosa pine trees were primarily in the range of 4A to 4C, representing advanced age and vigor classes from full to light. The ponderosa pine trees appeared to be in slightly higher vigor classes than the lodgepole pine trees.

With the exception of the radial increment data and the fact that the lowest bole disc was sampled at 0.4 m rather than 0.2 m, measurements on individual ponderosa pine trees were similar to those on lodgepole pine. Radial increments were measured with a video system that included a computer and monitor for program control using a menu system; a separate terminal, monitor and software library for gantry control and image capture; and an x, y, z gantry system with a digital monochrome camera for tree-ring observation. Data were collected on four radii for each bole cross section, with the total number of radial increment measurements in the study exceeding 150,000. Surface preparation with fine sandpaper was a critical step for minimizing errors. Resolution for each measurement was 0.026 mm. To resolve potential inaccuracies caused by missing or false rings, measurements on all radii were crossdated using known marker years (low radial increments in drought years) identified in chronologies developed for this and other sites in the region (Stokes and Smiley 1968, Swetnam et al. 1985), with crossdating confirmed using COFECHA (Holmes 1983 and unpublished improvements). Analyses were more intensive for the ponderosa pine data because the crossdating is believed to have reduced ambiguity to a minimum compared to the lodgepole pine data set.

Results

Annual volume growth for ponderosa pine, summed for all sections of the bole by year, varied greatly among trees. The pattern of volume growth generally fell into three categories

(Figure 1). For some trees (6 of 24), the annual volume growth increment increased linearly with only modest variations for 200–350 years, and with no clear tendency to level off or decline (Figure 1, top panel). For another group of trees (9 of 24), the annual volume growth increment increased more rapidly and fairly linearly for no more than 100 years, then varied around a relatively stable value for 100–250 years (Figure 1, middle panel). For a third group (9 of 24), the annual volume growth increment increased rapidly and often leveled off, but then decreased (Figure 1, bottom panel). The decrease in volume growth was gradual in only several trees. Generally the decrease was sudden, dropping in seven of the nine trees in this category to less than half the previous rate in less than 10 years. The decrease was not synchronized among trees, however, and occurred between just a few years and as much as 70 years before sampling. Following the rapid growth decline, some ponderosa pine trees exhibited a gradual increase in annual volume growth but never approached the earlier growth rates. Generally, similar growth patterns were observed in lodgepole pine, except that fewer trees experienced a rapid decline in growth to a lower rate.
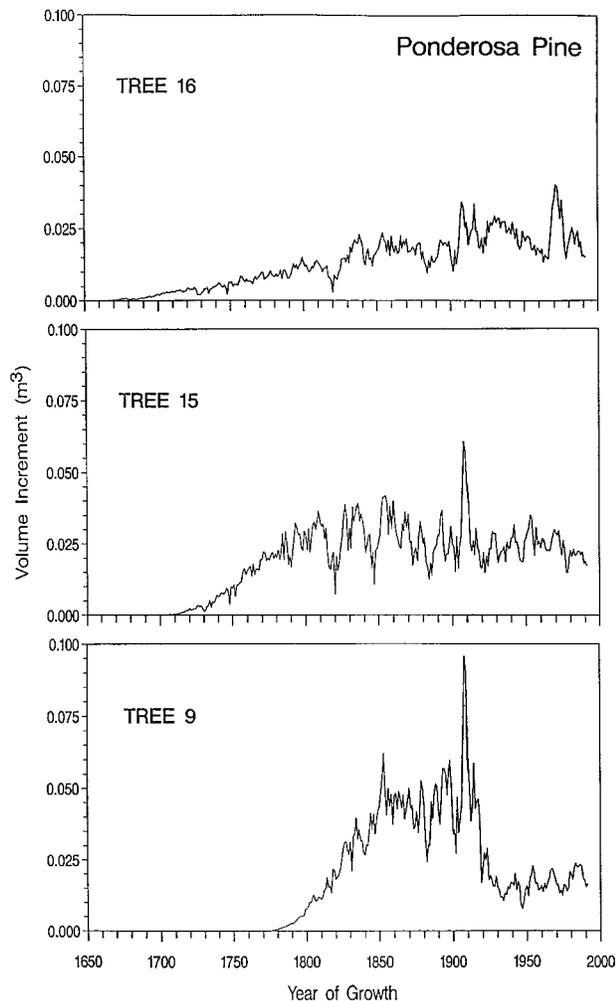
The annual growth rates for ponderosa pine were examined for synchrony among trees to determine if climatic variation contributed to the within-tree variations in growth shown in Figure 1 (Figure 2). High-frequency growth variations attributable to year-to-year variations in climate were detected using a 30-year cubic smoothing spline (Cook et al. 1990). This process allows the separation of short-term variations in growth from long-term trends caused by other factors such as competition or infrequent disturbance effects. Results indicated a high degree of synchrony among trees, suggesting that climate had a significant influence on growth of the ponderosa pine trees at this site. Although yearly data were not available for lodgepole pine, other studies indicate that growth of lodgepole pine and other conifers in subalpine forests in the central Rocky Mountains are not particularly responsive to climatic signals (W. Shepperd, personal communication).

Examination of the relationship of growth to leaf area was necessarily limited because the only data available for leaf area for the sample trees were at the time of sampling; however, these data do provide some basis for interpreting how trees behave at old ages. The relationships between annual volume growth and leaf area for lodgepole and ponderosa pine are

Figure 1. Annual volume growth in ponderosa pine showing three distinct growth patterns over the life of the tree.
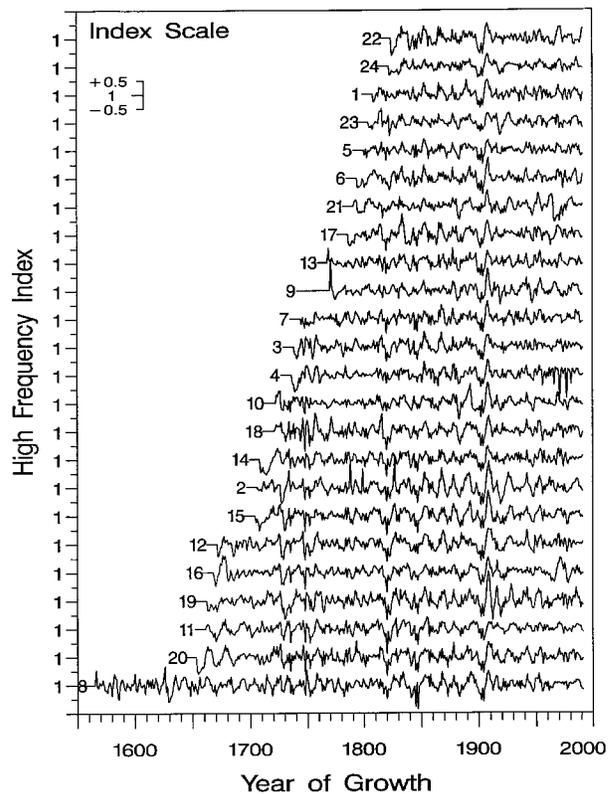

Figure 2. High-frequency index of variability in annual volume growth for ponderosa pine after data were detrended using a 30-year cubic smoothing spline. Numbers to the left of each curve indicate tree numbers. Simultaneous peaks or troughs occurring for all trees indicate an impact of some variable affecting volume growth of the entire stand. For example, low index values in 1902 and 1904 followed by high index values several years later corresponded to a severe drought followed by a wet period.

shown in Figures 3 and 4, respectively. The mean annual volume growth was determined for the last 10 years for lodgepole pine and 5 years for ponderosa pine, roughly corresponding to the needle retention time for each species. Trees with higher leaf areas at the time of sampling generally had higher mean annual growth rates during their final years compared with trees having lower leaf areas at sampling.

Data in Figures 3 and 4 are useful for stratifying the sample trees into groups. For both species, trees having highest or lowest leaf areas and mean annual volume growth rates during their most recent years were placed into groups for analysis of their earlier growth patterns. Strong differences were observed in the growth histories of these extreme groupings (Figures 5 and 6). In both species, trees having low leaf areas and volume growth rates at the time of sampling had high growth rates when young, whereas trees having high leaf areas and volume growth rates at sampling had much lower growth rates when young. Thus trees that appeared most vigorous at sampling grew slowly when young, whereas trees that appeared to be in poor vigor and, in some cases, near death at sampling had been much more vigorous when young. The remainder of the sampled trees had varying growth patterns generally intermediate between the extreme groupings.

Growth efficiencies were calculated for the last 10 years of growth for lodgepole pine and the last 5 years for ponderosa pine. Mean annual volume growths shown in Figures 3 and 4 were converted to mass using a specific gravity of 0.4 g cm^{-3}, and mass was divided by leaf area. In both species, growth efficiency appeared to decline with increasing leaf area, and in almost all cases, it was below 100 g m^{-2} leaf area (Figures 7 and 8).

Discussion

These results suggest that, for the two species of pine investigated, trees having visible old-growth characteristics of crown shape, branching and foliage distribution can achieve these characteristics through a wide range of early growth patterns. Both trees growing very rapidly during their first century and their counterparts in the same stand that had grown very slowly could reach old-growth status. Data for the ponderosa pine trees in this study and from other observations not reported here suggest that old-growth features become prominent in this species by about 200 years. All trees in the lodgepole pine study were well over 200 years old, and it is not possible with this data set to estimate the age at which lodgepole old-growth features are acquired. It is also not possible to determine unequivocally whether rapid early growth leads to early development of old-growth crown characteristics. If some of the
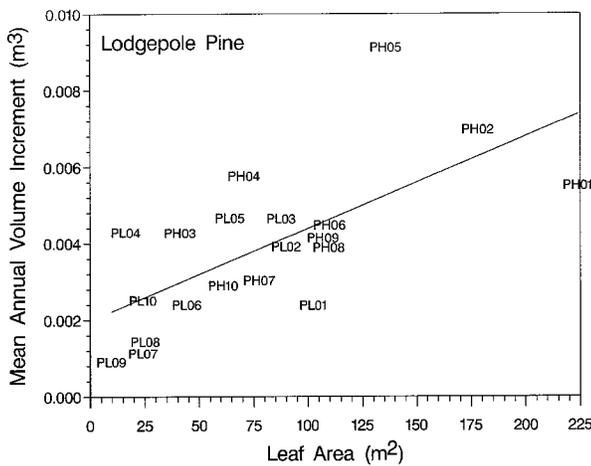

Figure 3. Mean annual volume growth of lodgepole pine trees for the last 10 years before sampling in relation to total leaf area at the time of sampling ($r^2 = 0.45$). Numbers indicate sample tree number.
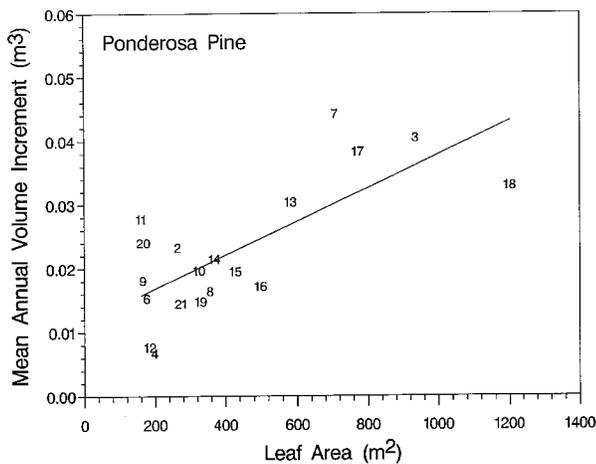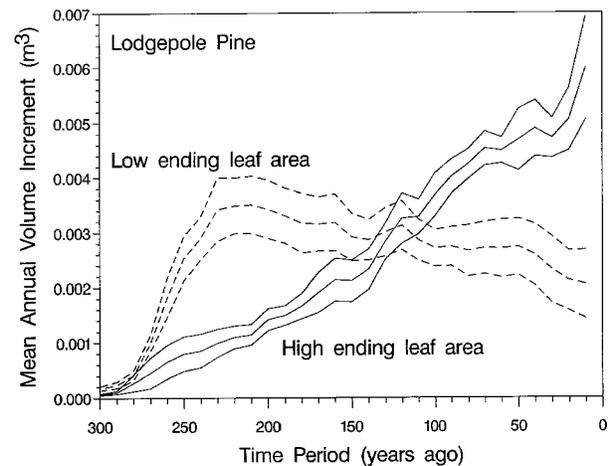

Figure 4. Mean annual volume growth of ponderosa pine trees over 200 years old for the last 5 years before sampling in relation to total leaf area at the time of sampling ($r^2 = 0.45$). Numbers indicate sample tree number. Five trees were eliminated because they were too young, but they would not have changed the relationship shown.

Figure 5. Mean annual volume increment over the life of lodgepole pine trees having the five highest (> 107 m^2) or five lowest (< 30 m^2) ending leaf areas. Measurements were made for 10-year intervals counting back from the year of sampling. The middle line is the mean of five trees in each group, and the upper and lower lines represent ± 1 standard error.
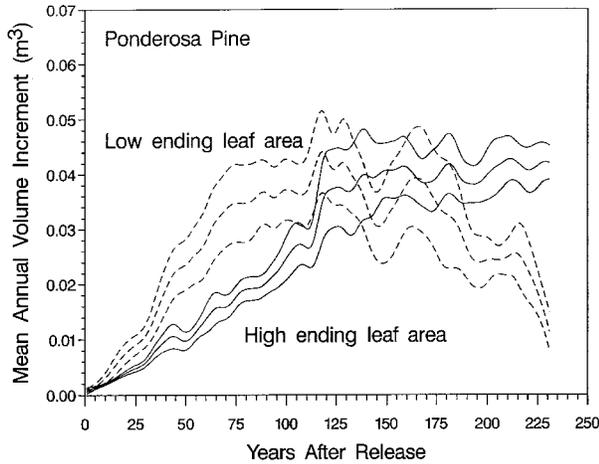
Figure 6. Mean annual volume increment over the life of ponderosa pine trees having the four highest ending leaf areas (> 700 m^2) or the five lowest ending leaf areas (< 300 m^2) and volume growth rates (< 0.02 m^3). Measurements were made annually, and growth patterns for trees differing in establishment or growth release dates were combined by beginning with the year at which growth first started to increase. The middle line is the mean of four (high) or five (low) trees in each group, and the upper and lower lines represent ± 1 standard error. For graphic purposes only, the ponderosa pine data were smoothed with a 20-year smoothing spline. Although the two groups had different growth patterns, annual variability made the differences hard to observe graphically.
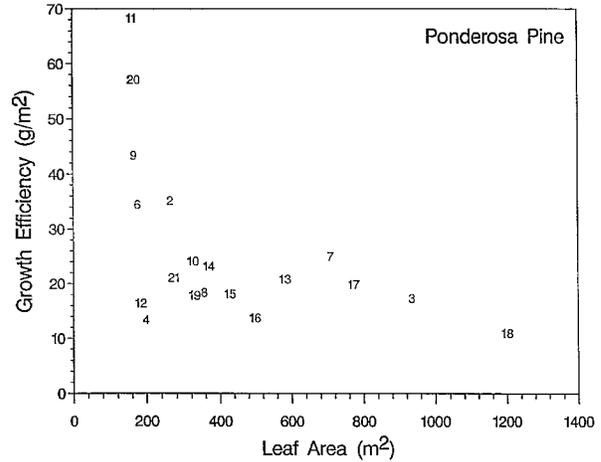
Figure 8. Growth efficiency (mean annual bole dry matter increase per unit leaf area) for ponderosa pine in relation to leaf area.

exhibited a high growth rate throughout their life. It is unlikely that trees much smaller in diameter than 75 cm acquire old-growth crown features, perhaps because they simply cannot persist long enough with slow growth rates. Additional observations of growth rates in old stands are needed to determine more about the full range of growth rates that can lead to old-growth conditions.

As commonly observed in other studies on radial increment growth, there is a strong volume growth response in ponderosa pine to short-term signals, presumably climatic, that affect all trees at once, resulting in simultaneous decreases or increases in growth in given years or somewhat longer time periods. Although the decadal time steps for growth measurements in lodgepole pine are inadequate to test for similar synchrony in this species, observation of tree rings in this and other studies suggest that the year-to-year variation in diameter or volume growth is lower in most subalpine tree species, including lodgepole pine. Presumably this difference between ponderosa pine and lodgepole pine is related to variability in rainfall and soil water availability in ponderosa pine stands, whereas lodgepole pine and other subalpine species normally experience complete soil water recharge from snowmelt at the beginning of each growing season and respond only weakly if at all to precipitation during the growing season. Stable isotope analyses of carbon in cellulose-nitrate extracts of annual rings could help determine the role of drought in affecting tree growth patterns.

Data presented here are not adequate to characterize reasons for the differences in growth patterns. It is likely, however, that the wide range of growth patterns and abrupt changes in growth rates for some of the trees are the result of several factors, including competition for limited resources, lightning strikes, pathogens and possibly genetic differences (Waring 1987). Based on the limited growth data, I conclude that lodgepole pine trees growing slowly late in their life had gradually decreasing growth rates over a period of many decades, and that continued declines in growth could be expected. The high and increasing growth rates for lodgepole pine trees
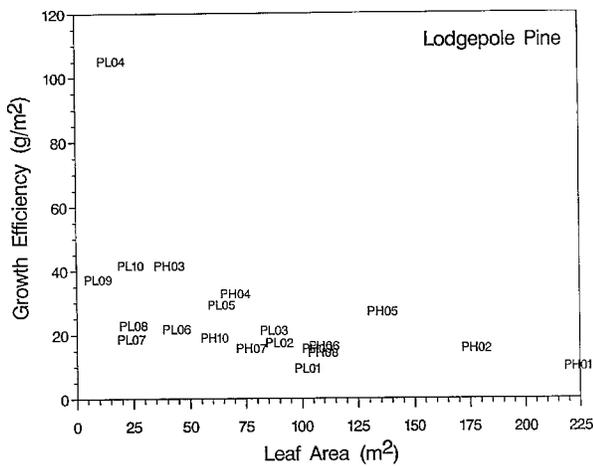
Figure 7. Growth efficiency (mean annual bole dry matter increase per unit leaf area) for lodgepole pine in relation to leaf area.

crown changes characterizing old-growth trees are related to height or resource conditions (e.g., hydraulic effects, nutrients, soil water availability), reaching a large size early may tend to hasten the development of structural features characteristic of old-growth trees.

It should be cautioned, however, that the patterns of growth observed may not be the only ones leading to the old-growth condition. In the ponderosa pine study, for example, trees were selected to have diameters fairly close to 75 cm. Other trees in the stand were larger, and it is possible that some of these trees

with high leaf areas (Figure 5) suggest that in some trees, the potential for growth increases with age. It should be noted, however, that precipitation during the last decade was the highest on record, and growth of most lodgepole pine trees reflected this increase in water availability. The apparent response to water may have reflected less evaporative demand, less cavitation, and greater availability of nitrogen in surface soil horizons rather than greater availability of water in soil (R.H. Waring, personal communication).

The response of ponderosa pine is not as clear. Although growth declined in many trees, the pattern of decline often included a fairly brief period of rapid decrease in growth followed by relatively stable growth at the new rate for as much as seven decades (Figure 1). Mortality in both species may be related to some specific disturbance, such as a lightning strike or insect or disease attack, or maybe several disturbances, which causes death over a short time period rather than by slow attrition over decades as might occur in lodgepole pine. Attrition may predispose the trees to disturbance effects, however.

Declining growth efficiencies with increasing tree leaf area (Figures 7 and 8) may be the result of increased self-shading (most trees were clearly dominants compared with their neighbors). But higher growth rates for these trees than for their counterparts with lower leaf areas (Figures 3 and 4) suggest that high leaf areas still conferred an advantage on these trees. Adjusting for projected versus total leaf area, the growth rates observed in this study for old lodgepole pine trees are similar at equivalent leaf areas to those found by Long and Smith (1990) for stands 70–120 years old. In general, growth efficiencies have been shown to decline with increasing leaf areas, and this decline is associated with several factors, including shading of foliage and a decline in the ratio of photosynthetic surface to respiring tissue (Kaufmann and Ryan 1986, Roberts and Long 1992). Ryan and Waring (1992) concluded, however, that low net primary production in old lodgepole pine stands could not be explained by higher maintenance respiration. Yoder et al. (1994) suggested that reduced photosynthesis in foliage from old trees may be related to reduced hydraulic conductance in the vascular system.

The preponderance of growth efficiencies below 100 g m^{-2} in the majority of trees (Figures 7 and 8) suggests that almost all trees had lost their resistance to insect and disease attacks (Waring and Pitman 1985). Nonetheless, some of these trees had persisted for many decades or for more than a century with low growth efficiencies, suggesting that defense mechanisms may be more effective in old trees than in younger trees with low growth efficiencies. The higher growth efficiencies observed at low leaf areas may reflect recent decreases in leaf areas not yet accompanied by reduced mean annual growth over the 10 or 5 year period (see especially lodgepole pine tree PL04 in Figure 7). However, more analyses are required to determine why growth efficiencies vary so widely at low leaf areas.

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