

Twenty-four Years of Ponderosa Pine Growth in Relation to Canopy Leaf Area and Understory Competition

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ABSTRACT. With data from a long-term experiment in which initial stocking of trees and understory vegetation were controlled, we tested the hypothesis that stand growth is directly correlated with the development of the forest canopy; e.g., growth is proportional to canopy leaf area. The hypothesis was generally supported. Stands of ponderosa pine without understory vegetation more rapidly developed canopy leaf area than stands with an understory. At very low leaf area indices, wood production per unit of leaf area was more efficient, particularly in stands where the understory vegetation had been removed. Once the leaf area index exceeded 2.0, however, the efficiency of wood production remained stable and was comparable for stands with and without understory vegetation. FOR. SCI. 33(2):538-547.

ADDITIONAL KEY WORDS. *Pinus ponderosa*, sapwood area, water use.

SILVICULTURISTS HAVE LONG ATTEMPTED to increase stand growth by reducing stocking levels and by improving the availability of soil resources. Ecologists have suggested that silvicultural treatments might be more appropriately evaluated if stands were compared at equivalent canopy densities rather than at equivalent ages (Miller 1981, Waring 1983). Canopies may be compared on the basis of their projected leaf area or on the amount of solar radiation they absorb (Waring 1983).

We were able to evaluate the effect of stocking control and removal of understory vegetation on the growth of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) at equivalent canopy densities by analyzing data collected over 24 years (Barrett 1982). Changes in canopy density were expressed as projected surface area of foliage (m^2 foliage/ m^2 ground). This leaf area index (LAI) was estimated by a linear correlation with sapwood basal area (Waring and others 1982), which could be applied because only a few trees had died in the course of 24 years, and the remaining trees had yet to form a significant amount of heartwood.

Study Area

The study area is in the USDA Forest Service Pringle Falls Experimental Forest (43°N, 121°W, 1,350 m above sea level), about 60 km southwest of Bend, Oregon. The experimental site is an east-facing slope that receives

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about 60 cm of precipitation annually, 85% of which falls between October and April. From January to March, the snowpack is about 60 cm deep (Franklin and Dyrness 1973).

The 30 rectangular 0.08-ha plots, each surrounded by a 10-m buffer strip, were established in 1957. At initiation of the experiment, the selected stand contained old-growth ponderosa pine (about 50/ha) growing above 40- to 70-year-old suppressed trees (about 17,000/ha) (Barrett 1982). These younger trees in the understory averaged 5.0 cm diameter and 2.5 m height. Trees on the site are projected to reach 24 m in height at 100 years (Barrett 1982).

Ground vegetation consisted mainly of bitterbrush (*Purshia tridentata* [Pursh] D.C.), varnish-leaf ceanothus (*Ceanothus velutinus* Dougl. ex Hook.), and green-leaf manzanita (*Arctostaphylos patula* Greene). Soils developed from dacite pumice extend to a depth of 80 cm, where a buried soil profile can be found in an older ash layer (Barrett 1982).

Methods

In 1958, all of the old-growth pines were removed, and five stocking levels, each replicated six times, were established in the understory. Tree densities for the five levels were 2,470, 1,235, 618, 309, and 153 trees/ha. All treatments were randomized and extended into the surrounding buffer strips. Within each stocking treatment, half of the plots were kept clear of understory vegetation by herbicides and mechanical means for the duration of the experiment. Beginning in the fall of 1959, and during every fourth growing season thereafter until 1979, diameter at breast height (dbh), total height, and height to the base of the live crown were measured on all trees (Barrett 1982).

In the summer of 1983, we measured dbh and height of all trees to the base of the live crown. In addition, we measured total height of at least 12 trees per plot at the two lower stocking densities and of at least 25 percent of the trees at higher densities.

ESTIMATING LEAF AREA

Leaf area of ponderosa pine was estimated with the assumption that it has a linear relationship with sapwood cross-sectional area at the base of the live crown, where a square centimeter of sapwood supports 0.25 m² leaf area (Waring et al. 1982, Larsson et al. 1983). Taper in the sapwood area between breast height and the base of the live crown was predicted from a relationship with breast-height diameter, tree height, and distance from the crown base to the treetop ($r^2 = 0.97$, $P < 0.001$) that was developed from data collected from 120 trees (Cochran 1979).

In 1981, we confirmed that less than 3% of the total wood cross-section at breast height consisted of heartwood by coring 10 trees in the 2,470/ha and 153/ha stocking treatments. This knowledge allowed us to estimate the leaf area of all trees from diameter measurements and knowledge of bark thickness for each year from the time treatments began in 1959 until 1979. In calculating leaf area, we accounted for additional formation of heartwood with data from the sampling of wood cores in 1983.

ESTIMATING GROWTH

Tree volume was calculated for each tree from an equation developed especially for the study area (DeMars and Barrett, USDA Forest Service, Forest Sciences Laboratory, Bend, OR, unpublished). Growth was determined by taking the differences between all consecutive measurements and interpo-

lating values for the periods between measurements. Tree height, required to estimate volume, was not measured on all trees in 1983; therefore, specific height equations had to be developed for each combination of stocking and controlled and uncontrolled understory vegetation. The equations, which were based on measurements from 35 to 175 trees, explained between 70 and 85% of the variation in height ($P < 0.001$).

Growth in wood biomass was determined for each plot by multiplying volume growth by wood specific gravity. The latter value, estimated from core samples taken at breast height from 5 to 19 trees per plot, depending on stocking, ranged from 260 to 310 kg/m³. To estimate how much stemwood was produced per unit of foliage, we divided the increment in volume or biomass by the estimated leaf area of each tree. Average growth efficiency was determined for each plot. Stand stem growth was calculated by summing the growth of individual trees in a given plot, then converting the value to growth per hectare.

To remove heteroscedasticity and make the relationships easier to analyze statistically, the reciprocal of growth efficiency was regressed against *LAI*. This transformation gave a linear relationship with correlation coefficients above 0.77. The analyses were performed on the complete 24-year data set ($n = 90$) and again on all but the last 4-year period ($n = 75$). In this way, the estimates of growth and canopy development made with equations derived from earlier measurements could be compared with values from the last sampling.

To account for possible growth differences associated with tree size, we added information about mean stem biomass and mean leaf area per tree. Because *LAI* was important in predicting growth efficiency, we examined the rate of increase in *LAI* as a function of current *LAI*.

The accuracy of predicted changes in leaf area, as well as growth efficiency and stand growth, was assessed: first, by comparing the coefficients of the relationships generated from the entire study with those derived without the last set of measurements and, second, by comparing projected values with values taken during the last measurement period. Stand growth was predicted in two ways: by calculating continuous accumulation as the product of predicted *LAI* and predicted growth efficiency, and by describing growth as a function of *LAI*.

Results

Over the 24 years of the experiment, diameter increased 71% (5 cm) on trees growing at the highest stocking level and 171% (12 cm) on trees growing at the lowest stocking level. With control of understory vegetation, mean diameter at the highest stocking level increased 63% (5 cm) and at the lowest stocking level 300% (24 cm).

Basal area increased from 5.1 to 31.5 m²/ha at the highest level and from 0.35 to 8.8 m²/ha at the lowest level over the same period. With no understory, it increased from 3.8 to 33.59 m²/ha and from 0.35 to 12.9 m²/ha at the two stocking extremes.

Tree growth efficiency decreased rapidly as the canopy developed (Figure 1). The main effect of understory removal was expressed at low leaf area indices. For example, at *LAI* 1.0, understory removal increased growth per unit of leaf area 30% over that for plots with an understory.

Although the relationship between growth efficiency and canopy leaf area differed significantly (Table 1, $P < 0.01$) among some 4-year measurement

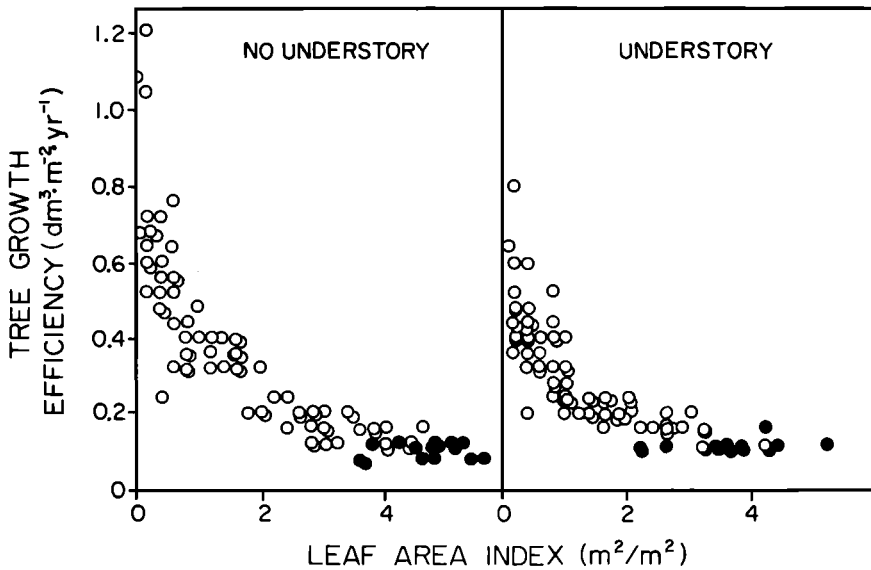


FIGURE 1. Average annual growth efficiency (stem volume produced/unit of foliage area) in relation to leaf area index (foliage area/ground area). Data are for measurements made at six 4-year intervals, the last shown by filled circles.

periods, there was no pattern (Figure 2); thus, pooling data for the entire 24-year period seemed justified (Figure 1).

Inclusion of the amount of leaf area per tree significantly reduced the amount of unexplained variation in the independent variable ($1/GE$, Table 1) in all eight equations. The greatest negative effect on growth appeared where understory vegetation was present. Leaf area and stem biomass were closely correlated because live crown ratios were similar among treatments (0.72–0.83). In such cases, both variables are functions of stem diameter.

The presence or absence of understory vegetation did not alter the slope of the relationship between the reciprocal of growth efficiency and LAI . The intercept was significantly lower, however, on plots without an understory, indicating that growth efficiency at low LAI was improved by understory removal (Table 1).

The relationship of LAI increase and current LAI can be described with a parabolic curve (Figure 3), because LAI increases over time in a form described by a sigmoid curve. The equations in Table 1 best fit the data up to LAI 2.0. Above LAI 2.0, plots varied considerably, probably indicating site differences in water availability rather than in stocking (Barrett 1970). When understory vegetation was removed, leaf area initially increased more rapidly than it did when the understory was present (Figure 3, Table 1). Relative changes in LAI for the entire data set can be described equally well by a peaking function (Jensen and Homeyer 1970):

$$\Delta LAI_i = \left[\left(e^{-\left| \frac{(LAI_i/LAI_m) - 1}{0.9} \right|^{3.0}} - 0.2167 \right) / 0.7813 \right] \Delta LAI_{\max}$$

where

ΔLAI_i = net annual increment of LAI at LAI_i ,

TABLE 1. Regression equations for predicting stemwood growth efficiency (GE), leaf area increment (ΔLAI), and stand stemwood growth (G_1 and G_2) as a function of stand LAI and mean tree leaf area (LA).

Dependent variable	Annual growth units	Understory vegetation	Intercept ^a	Independent variables			n	r ²
				LAI	LAI ²	LA		
1/GE	dm ³ /m ²	+	2.12***	1.39 ^{NS}			75	0.79
		-	1.19	1.50			75	0.87
		+	2.04**	1.61 ^{NS}			90	0.80
		-	1.05	1.67			90	0.87
1/GE	kg/m ²	+	7.16***	5.45 ^{NS}			75	0.77
		-	4.33	5.58			75	0.85
		+	7.18**	5.87 ^{NS}			90	0.77
		-	3.96	6.11			90	0.86
1/GE	dm ³ /m ²	+	3.06***	1.28 ^{NS}		0.02***	75	0.88
		-	2.29	1.45		0.01	75	0.91
		+	1.77***	1.36 ^{NS}		0.02***	90	0.90
		-	0.95	1.45		0.01	90	0.92
1/GE	kg/m ²	+	10.29***	4.98 ^{NS}		0.09***	75	0.85
		-	8.34	5.35		0.03	75	0.91
		+	6.06**	4.85 ^{NS}		0.09**	90	0.89
		-	3.61	5.35		0.04	90	0.90
ΔLAI	m ² /m ²	+	0.0002 ^{NS}	0.1649***	-0.0259***		75	0.83
		-	0.0012	0.2205	-0.0386		75	0.73
		+	0.0096 ^{NS}	0.1420***	-0.0187***		90	0.82
		-	0.2420	0.1706	-0.0256		90	0.69
G_1	m ³ /ha	+	0.41**	1.65 ^{NS}	-0.14 ^{NS}		75	0.94
		-	0.80	1.68	-0.17		75	0.91
		+	0.55**	1.38 ^{NS}	-0.08 ^{NS}		90	0.93
		-	0.93	1.49	-0.12		90	0.90
G_1	T/ha	+	0.11**	0.50 ^{NS}	-0.06 ^{NS}		75	0.90
		-	0.23	0.44	-0.04		75	0.91
		+	0.16**	0.39 ^{NS}	-0.02 ^{NS}		90	0.89
		-	0.27	0.37	-0.03		90	0.89
G_2	m ³ /ha	+	0.41***	1.93 ^{NS}	-0.20 ^{NS}	-0.008 ^{NS}	75	0.90
		-	0.76	1.92	-0.20	-0.005	75	0.93
		+	0.51***	1.73 ^{NS}	-0.14 ^{NS}	-0.008 ^{NS}	90	0.97
		-	0.87	1.71	-0.15	-0.006	90	0.94
G_2	T/ha	+	0.11***	0.60**	-0.08***	-0.003***	75	0.94
		-	0.22	0.50	-0.05	-0.001	75	0.92
		+	0.14***	0.50 ^{NS}	-0.04**	-0.003***	90	0.93
		-	0.26	0.43	-0.03	-0.001	90	0.92

^a Significant differences between treatments with (+) and without (-) understory vegetation are indicated: **0.01, ***0.001, NS not significant at 0.05. Regressions are derived from analyses of 6, or all measurement periods using the total 24-year data set (n = 90), and from analyses of the same data set but without the last period (n = 75).

Note: Adjusted r² is reported for multiple linear regression models with variables included in the equations at significance level 0.01. G_1 and G_2 refer, respectively, to equations with and without the variable mean tree leaf area.

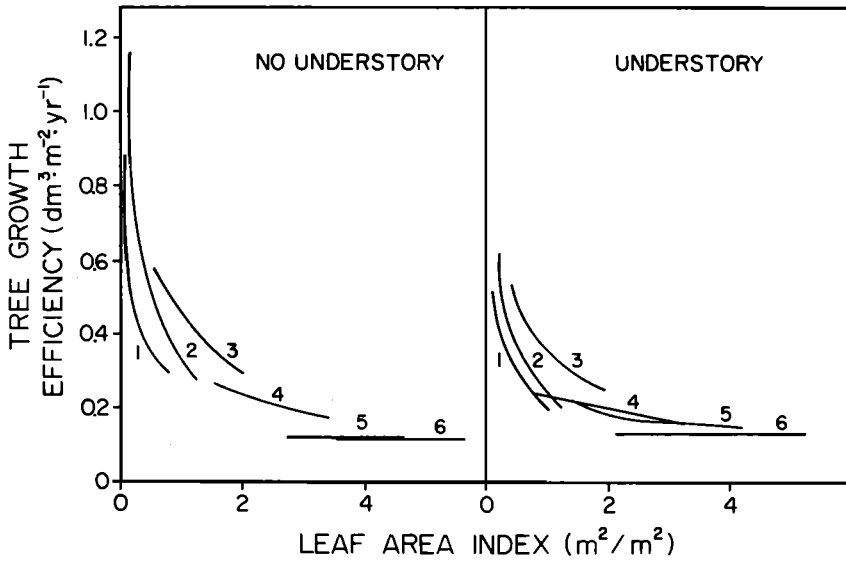


FIGURE 2. Least squares fit of average annual growth efficiency (stem volume produced/unit of foliage area) in relation to leaf area index (foliage area/ground area). Data taken at six 4-year intervals are shown by separate lines numbered sequentially.

ΔLAI_{max} = maximum rate of LAI accumulation, and
 LAI_m = LAI at ΔLAI_{max} .

With an understory, $r^2 = 0.81$; with no understory, $r^2 = 0.69$.

Predicted change in LAI during the last 4-year period was within 30% of measured values for plots without an understory and within 45% of those with an understory. Much of the error may reflect real variation from plot to plot (Figure 3). Predictions of growth efficiency in units of volume or biomass were within 20 and 30%, respectively, of measured values, and estimates of leaf area within 15%.

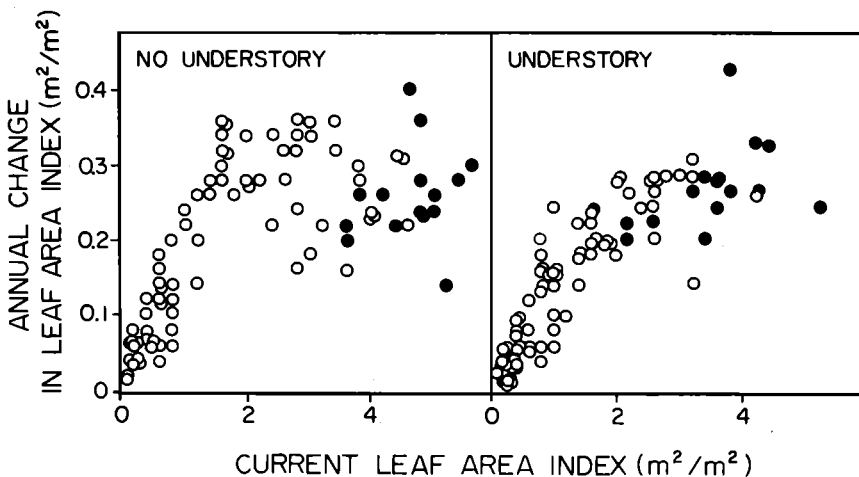


FIGURE 3. Annual change in the leaf area index (foliage area/ground area) in relation to the current leaf area index. Data are from measurements made at six 4-year intervals.

Production is a product of leaf area index and growth efficiency. The most rapid change in production occurred at the early periods because growth efficiency actually increased along with *LAI* (Figure 4). The rate of increase in production decreased and eventually stabilized as increasing *LAI* was balanced by a proportional decrease in growth efficiency (Figure 2). *LAI* appeared to be approaching maximum at the densest stocking levels, as shown by very slow increments in leaf area (Figure 3) and by the first signs of density-related mortality of smaller trees. Eventually, as the trees become larger, maintenance respiration is expected to further reduce growth rates (Whittaker 1975, Waring and Schlesinger 1985). Growth estimated as the product of *LAI* and growth efficiency was within 20 and 30%, respectively, of measured volume (Figure 4) or biomass increment, and when estimated as a function of stand leaf area was within 10% of the measured values (Table 1).

Discussion

The exponential decrease in growth efficiency observed with increasing *LAI* (Figures 1,2) is similar to that observed in lightly managed forests of *Pinus contorta* Dougl. (Mitchell et al. 1983), *Pinus sylvestris* L. (Waring 1985), and *Pseudotsuga menziesii* (Binkley and Reid 1984). In intensively managed forests of *Pseudotsuga* (Waring et al. 1981) and *Pinus ponderosa* (Larsson et al. 1983), where frequent thinning allows lower crowns to be maintained and to contribute substantially more to net carbon uptake (Helms 1971, Linder and Axelsson 1982), growth per unit leaf area decreases nearly linearly with increasing *LAI*.

The rapid decrease in growth efficiency observed between 0 and 2.0 *LAI* probably is not related to a comparable reduction in photosynthesis, al-

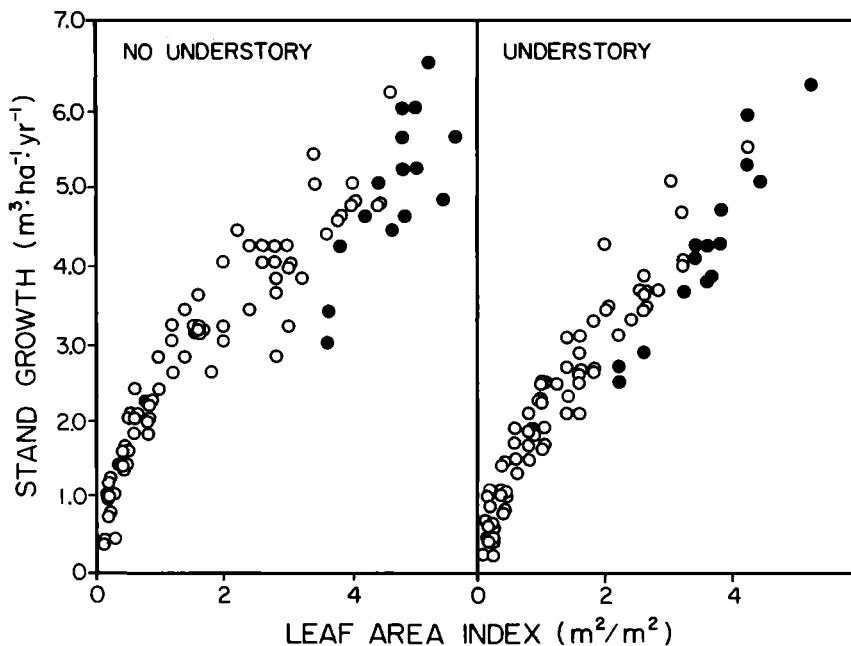


FIGURE 4. Average annual stand volume-growth in relation to leaf area index (foliage area/ground area). Data are from measurements made at six 4-year intervals.

though irradiance may be reduced by 40 to 50% in that range of canopy cover (Kira and Shidei 1967, Jarvis and Leverenz 1983). Once irradiance drops below 50% of that at the top of the canopy, shaded foliage is equally efficient over a broad range in *LAI* (Nygren and Kellomaki 1983). Even in a stand of *Picea abies* with *LAI* 11.6, for example, uptake by shaded foliage in the canopy accounted for 30% of the annual total (Schulze et al. 1977).

At comparable *LAI* below 1.5, plots with an understory used the available water more rapidly than plots without an understory. Although the transpiring surface of the understory vegetation was not determined, it used water equivalent to a pine canopy with *LAI* of 0.7 when it was fully developed (Figure 5). These findings help explain why growth efficiency among treatments differed only at low *LAI*. The increase in growth efficiency between the first and third periods at a comparable *LAI* of 1.0 (Figure 2) suggests, however, that roots did not fully reoccupy the coarse-textured pumice soil for 12 years (Hermann and Petersen 1969, Youngberg and Cochran 1982). Once they fully occupied the soil, the relative allocation of photosynthate to stems may also have increased.

A decrease in growth efficiency at a given *LAI* throughout the study was related to an increase in average tree leaf area (Table 1) and could be a result of leaf area accumulating faster than crowns expand. For example, trees on lightly stocked plots had 10 times the foliage but only 4 times the crown volume of trees growing at denser stocking with similar *LAI*. Such differences would permit trees at higher stocking levels to photosynthesize more efficiently than those growing at lower stocking because light would pene-

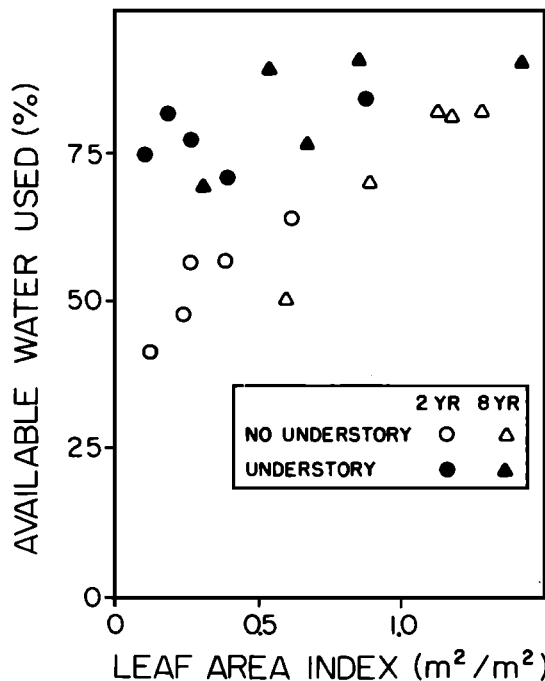


FIGURE 5. Percentage of available soil water used by the end of the growing season, as compared with water used by an adjacent uncut stand, in relation to the leaf area index (foliage area/ground area) of ponderosa pine plots with and without understory vegetation 2 and 8 years after initiation of the experiment (calculated from Barrett 1970).

trate more efficiently. In addition, a better ground cover provided by the distribution of a given *LAI* on more trees reduces the amount of light that is not intercepted and is unavailable for photosynthesis.

Once forests approach their maximum *LAI*, differences in growth efficiency are often between 75 and 85 g wood produced per square meter of foliage annually, even in contrasting environments where the amount of leaf area or duration of display differ considerably (Waring 1985, Waring and Schlesinger 1985). This study emphasizes the idea that the major effects of silvicultural treatments may be best assessed by comparing tree responses at a common, relatively low leaf area index (Waring 1983, 1985).

A temporary improvement in resource availability, such as that observed in this study, significantly increases the initial rate of canopy development (Miller 1981, Waring 1983). A sustained improvement in the availability of scarce resources, although economically often a questionable alternative, should increase the maximum leaf area, while maintaining high growth efficiency by shifting carbohydrate allocation away from roots (Waring and Schlesinger 1985).

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