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Growth in Relation to Canopy Light Interception in a Red Pine (Pinus resinosa) Thinning Study

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ABSTRACT. Growth data from the most recent 5 years of a 40-year thinning study in an even-aged red pine (*Pinus resinosa*) forest in Cutfoot Sioux Experimental Forest, Minnesota, were used with intercepted photosynthetically active radiation (IPAR) data to determine the relationship between light interception and growth for a range of stand densities. Stand basal area (BA) growth was proportional to the amount of light intercepted within the stand (P = 0.06, r^2 = 0.73), and individual tree growth was inversely related to the amount of light intercepted by the canopy (P = 0.08, r^2 = 0.69). Stand growth efficiency (*SGE* = ratio of 5-year plot BA growth to plot median %IPAR) was only weakly correlated with stand density ($P \gg 0.10$, r = 0.31). The rate of change in stand growth efficiency may be a good indicator of change in forest condition over a range of stand densities. FOR. SCI. 38(1):199–202.

AS ENVIRONMENTAL ISSUES REACH GLOBAL SCALE, we seek ecological indicators for use in monitoring vegetation over large geographic areas. Indicators of condition must be based on sound ecological theory, and apply to different scales, from plot to forest and larger units of landscape. Stand growth efficiency (*SGE* = growth per unit of intercepted photosynthetically active radiation) may serve as a useful indicator of forest condition.

We know that growth varies among individual trees and between stands. For example, old forests grow more slowly than young forests, because of increased maintenance respiration (Larcher 1983). Also, self-shading and competition among plants often make light a limiting resource (Norman and Jarvis 1974). Other environmental factors limit the extent to which a dense canopy can be maintained. In all cases, the upper limit of the photosynthetic rate is determined by the amount of visible radiation or photosynthetically active radiation (PAR, 400–700nm) utilized by photosynthetic pigments (Pearcy et al. 1987). Furthermore, the degree to which canopies intercept light over a year is related to aboveground net primary productivity (Running et al. 1989).

In this paper, basal area growth data from the most recent 5 years of a 40-year thinning study were compared to the amount of visible light intercepted by the tree canopies over a range of stand densities in a red pine (*Pinus resinosa*) forest in north central Minnesota. We asked the basic questions: (1) To what extent does thinning of a forest affect the relationship between light interception and growth, and (2) how do individual trees respond as light becomes more limiting? If we can define the rate of change in *SGE* in forests of variable stocking, then changes in *SGE* may serve as a useful indicator of variation in environmental stress or cost of maintenance.

STUDY AREA

The study site is located on the Cutfoot Sioux Experimental Forest within the Chippewa National Forest, MN, and is a test of growing stock levels in red pine (Study #49-76, USDA Forest Service, Grand Rapids, MN). In 1990, the stand was 119 years old, with a light-to-medium density understory composed predominantly of green alder (*Alnus crispa*), hazel (*Corylus cornuta* and *Corylus americana*), willow (Salix spp.), blueberry (*Vaccinium augustifolium*), and bracken fern (*Pteridium aquilinum*). Terrain is generally flat and the soils are sandy; major soil series are Menahga and Graycalm. The red pine site index is medium quality 15.2 m at 50 years (Buckman 1962). The stand has been described as healthy, with no obvious signs of damage from insects, disease, weather, or fire (Barse, personal communication).

METHODS

In 1949, five thinning treatments corresponding to nominal levels of residual basal area (14, 18, 23, 28, and 32 m^2 ha-1 BA) were applied to the stand. Each treatment was replicated three times in 1-ha units, and three 0.08 ha plots were established within each unit. Thinning treatments have been repeated six times since 1949. There has been no mortality in the study plots since 1984, and at the time of the most recent thinning (1984), the two lowest basal area treatments were not thinned because of the small numbers of residual trees.

Tree diameter at breast height (dbh) has been measured at regular intervals on all trees within the 0.08 ha plots. Table 1 summarizes the measurements taken in 1984 (after treatment) and in 1989 on three plots within one replicate of each treatment.

PAR transmittance through the overstory red pine canopy was measured under clear sky conditions between 1230 and 1500 solar time on May 30–31, 1990, on a grid of 16 sample stations within each 0.08 ha plot. A portable integrating radiometer (the 80-sensor Sunfleck Ceptometer, Decagon Devices, Inc., Pullman, WA) was used. At each station, 30 Ceptometer readings (each reading is the average of the 80 sensor values) were taken while holding the instrument horizontal and rotating in a circle. This procedure effectively sampled approximately 4m^2 per station, or about 8% of each 0.08-ha plot.

Additional measurements of incident PAR were made at sample stations in large clearings (>220m^2) and canopy gaps (16–20m^2) before and after measurements were made under the canopy on each plot. Preliminary analyses (not shown) revealed that the measurements made in the smaller canopy gaps near solar noon were consistently 6% less than the large clearing measurements. In the few cases where small canopy gaps had to be used, we adjusted these measured values accordingly.

STATISTICAL ANALYSES

The following procedure was used to estimate intercepted photosynthetically active radiation (%IPAR) for each 0.08 ha plot. First, canopy transmittance was estimated at each below-canopy station on each plot as the ratio of the station average PAR to the average of the incident PAR taken immediately before and after the plot measurements. Distributions of these values were positively skewed because of canopy gaps, and so a logarithmic

TABLE 1.

Summary of measurements in each study stand of red pine. The treatment means are listed to the right of the third plot value (e.g., for 148/136 in the "No. trees" column, the treatment mean is 136 trees/ha).

	1984		1989	1984–1989		1990			
Treatment (m^2/ha)	No. trees (no./ha)	Basal area (m^2/ha)	Basal area (m^2/ha)	Basal area growth (m^2/ha)	Mean tree growth (m^2/tree)	%IPAR	LAI[1]	Stand GE (m^2/ha/IPAR)	Tree GE (m^2/tree/IPAR)
13.8	124	16.3	18.0	1.7	0.014	66.1	2.2	2.58	0.021
	136	17.5	19.4	1.9	0.014	52.0	1.5	3.71	0.027
	148/136	17.1/17.0	19.1/18.8	2.0/1.9	0.013/0.014	63.9/60.7	2.0/1.9	3.11/3.13	0.021/0.023
18.4	173	21.3	23.7	2.3	0.014	72.9	2.6	3.21	0.019
	148	20.6	22.6	2.0	0.013	74.4	2.7	2.67	0.018
	185/169	21.8/21.2	24.3/23.5	2.5/2.3	0.014/0.014	56.7/68.0	1.7/2.3	4.49/3.46	0.024/0.020
23.0	247	22.4	24.9	2.5	0.010	70.6	2.5	3.56	0.014
	222	23.4	25.6	2.2	0.010	73.2	2.6	3.02	0.014
	185/218	22.8/22.9	25.2/25.2	2.4/2.4	0.013/0.011	77.6/73.8	3.0/2.7	3.14/3.24	0.017/0.015
27.5	334	28.1	30.5	2.4	0.007	72.4	2.6	3.32	0.010
	321	27.7	29.5	1.8	0.006	68.1	2.3	2.60	0.008
	272/309	26.7/27.5	28.8/29.6	2.1/2.1	0.008/0.007	80.0/73.5	3.2/2.7	2.63/2.85	0.010/0.009
32.1	395	31.7	34.9	3.2	0.008	82.9	3.8	3.81	0.010
	334	32.1	34.2	2.2	0.006	82.0	3.4	2.63	0.008
	346/358	32.3/32.0	34.7/34.6	2.4/2.6	0.007	77.4/80.8	3.0/3.4	3.08/3.17	0.009/0.009

[1] LAI estimated from canopy transmittance using Beer-Lambert Law and assumed extinction coefficient of 0.52. The growth data used in Table 1 was provided by the USDA Forest Service, North Central Forest Experiment Station's Silvicultural Project (NC-4101) in Grand Rapids, MN.

transformation was applied prior to finding the mean value for each plot. The antilogarithm was then subtracted from unity to estimate plot %IPAR. This estimate of median %IPAR ignores reflectance from the top of the forest canopy, and canopy absorption of PAR reflected from the ground. Total reflectance (visible and near-infrared) for conifer canopies is approximately 10%, mostly in the near infra-red region of the light spectrum (Knipling 1970, Gates et al. 1965). Reflectance and canopy absorption of light reflected from the ground are probably small, and they tend to cancel one another in this analysis. We performed a regression of %IPAR on the 1989 residual basal area per plot.

Because much of the literature uses LAI in the growth efficiency index, we also calculated plot mean projected leaf area index (LAIs) for comparison (Table 1). The average canopy transmittance was converted to LAI using the Beer-Lambert Law, by assuming the extinction coefficient of 0.52 for ponderosa pine forests applied to the similar structure of red pine (Pierce and Running 1988).

Stand growth efficiency (*SGE*) was estimated by the ratio of 5-year plot basal area growth (1984–1989) to plot median %IPAR. Tree growth efficiency (*TGE*) was estimated by dividing mean tree basal area growth by plot median %IPAR. Normally, growth efficiency would be estimated by using PAR measurements taken during the growth period, rather than at the end, as in this study. Since leaf area tends to increase over time following thinning, later measurement will tend to underestimate efficiency. But assuming that differences in IPAR among treatments in 1990 reflect the same relative differences that existed earlier, comparisons of efficiency among treatments are valid.

The effects of thinning on the relationship between growth and light absorption were estimated using simple linear regressions of basal area growth per stand and per tree on %IPAR. Other comparisons among treatments utilized a one-way analysis of variance, assuming a completely random design.

RESULTS

Treatment mean BA growth increased with residual basal area ($P > 0.10$, $r^2 = 0.50$) from 1.9, 2.3, 2.4, 2.1, to 2.6 m^2/ha (Table 1). The trend of increasing BA growth with increasing density is a typical result in thinning experiments where upper canopy trees are removed (Assmann 1970). The apparently low BA growth observed for the second-highest density is difficult to explain and will affect the later analyses of growth efficiency.

Treatment median %IPAR increased with 1989 residual basal area ($P < 0.01$, $r^2 = 0.91$) and was 60.7, 68.0, 73.8, 73.5, and 80.8 from the lowest to highest density, respectively (Table 1). Basal area growth increased with %IPAR ($P = 0.06$, $r^2 = 0.73$), on a per-treatment basis. Mean tree growth per treatment decreased with increasing %IPAR ($P = 0.08$, $r^2 = 0.69$).

Although BA growth was linearly related to %IPAR, mean *SGE* was not different among treatments. Mean *SGE* for low to high stand densities were 3.13, 3.46, 3.24, 2.85, and 3.17 m^2/ha, and only weakly correlated ($P \gg 0.01$, $r = 0.31$) with residual BA.

DISCUSSION

The increase in stand basal area growth with increasing %IPAR for the five treatments matched findings of others, with the assumption that %IPAR and canopy leaf area are directly related at low LAIs (Russell et al. 1989, Marshall and Waring 1986, Pierce and Running 1988). We know that BA growth responds to certain thinning treatments (Oren et al. 1987). It is interesting that 5 years after thinning, there were still differences in median %IPAR among treatments. These differences are more likely due to canopy gaps that have not filled in yet. We would expect that all treatments will approach the same value of %IPAR eventually, except for the extremely low density treatments.

The decrease in mean tree growth observed with increasing %IPAR supports conclusions by Waring et al. (1981) that growth of individual trees and net assimilation rate decrease as the competing canopy increases. The average tree is under more stress due to competition, and grows slower, at higher %IPAR for the stand (Ford 1975).

The lack of significant effect of stand density on stand growth efficiency suggests SGE may be more suitable than TGE as an indicator of forest condition, because SGE would allow us to compare forests with various stand densities without the need for stratification by stand density.

Stand growth is usually related to LAI in the literature (Oren et al. 1987, Mitchell et al. 1983), but we think stand growth related to %IPAR is more relevant. The use of %IPAR eliminates the need to measure additional variables, and develop models for those variables (e.g., extinction coefficients, sapwood basal area) to estimate LAI (Marshall and Waring 1986). In addition, %IPAR takes physiological processes into account. For example, the LAIs of 6 and 12 only potentially intercept a 4% difference in PAR (Pierce and Running 1988). This helps explain why photosynthetic uptake is similar for thinned and unthinned forests if the initial LAI is high. The relationship of LAI to IPAR varies with species, so if we are interested in the comparison of SGE for different species, it is reasonable to use IPAR rather than LAI in the calculation of SGE.

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