Effects of competition from young northern hardwoods on red pine seedling growth, nutrient use efficiency, and leaf morphology

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ABSTRACT

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    The effects of competition from three northern hardwood tree species on red pine (*Pinus resinosa* **Ait.**) seedlings were examined on two clear-cut sites in western Maine. We examined how planted red pine seedlings altered their nutrient use efficiency and shoot morphology under **changing** environmental conditions and how these changes related to their ability to tolerate competition. A **three-**factor experimental design was used to determine the effects of species of competitors and their abundance as well as fertilization on red pine seedling growth, nutrient use efficiency, and leaf morphology. The competitors were striped maple (***Acerpensyfvanicum*** L.), red maple (*Acer rubrum* L.), and pin cherry (***Prunus pensylvanica*** L.) established at two densities (high and zero) with two levels of fertilization (0 and 224 g m^{-2} of 10-10-10 NPK commercial fertilizer). Nitrogen and phosphorus use efficiencies were calculated as total aboveground biomass divided by total nutrient content. Specific leaf area $(cm^2 g^{-1})$, leaf area ratio $(cm^2 g^{-1})$, and total leaf area (cm*) were measured for all red pine seedlings. Plots were harvested at two time periods, when pine seedlings were 2 years old (1989) and 3 years old (1990). Total biomass, annual production, and leaf area index $(m^2$ leaf area m^{-2} ground surface area) were calculated for competitors on each plot.

    Red pine seedlings had higher specific leaf area, leaf area ratio, and nitrogen use efficiency on competitor plots than on plots free of competition, suggesting a phenotypic response to resource depletion of light and nutrients by competitors. Fertilization decreased growth of red pine seedlings and decreased nitrogen use efficiency. Red pine total leaf area and biomass were lower on the competitor plots. Higher competitor biomass, leaf area index, and nutrient uptake explained the lower growth of red pine seedlings on competition plots. Pin cherry was the most significant competitor with striped maple being intermediate; red maple had the least effect on pine seedling growth. The results of this study indicate that the growth of red pine seedlings was governed by the availability of resources as influenced by the competitor species, the efficiency of nutrient use, and the ability of red pine to adjust its growth pattern in response to resource availability.

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INTRODUCTION

Competition among plants can be an important factor influencing succes sional patterns and diversity (Huston, 1979; Tilman, 1987b; Huston an Smith, 1987; Tilman, 1988) as well as productivity of species (Stewart et al 1984; Ross and Walstad, 1986). Despite the importance of competition, th mechanisms of interaction are often unknown (Schoener, 1983; Tilman 1987c). There is also uncertainty about whether apparent differences in com petitive abilities are related simply to biomass of different species or som inherent variations in ability (Goldberg and Werner, 1983; Goldberg and Fleetwood, 1987; Goldberg, 1990) and whether such abilities are constan under different levels of resource availability (Tilman, 1987a; Thompson 1987; Thompson and Grime, 1987; Smith and Huston, 1989). Goldber; (1990) has emphasized that competition must be examined in terms of botl the resource exploitation ability of some plants and the ability to tolerate lov levels of resource availability.

Disturbance, such as commercial clear-cutting, often causes some increas in ecosystem-level nutrient availability (Matson and Vitousek, 198 1; Vitou sek, 1985). Typically this increase in nutrient availability is relatively brie and declines in 2-5 years due to uptake of nutrients by vegetative regrowtl and leaching losses (Vitousek and Reiners, 1975; Hornbeck and Kropelin 1982; Hornbeck et al., 1990). Differences in the efficiencies of nutrient up take and use of resources by woody species in response to heterogeneous re source availability should affect the outcome of competition during the early stages of succession.

The efficiency with which a plant obtains or uses a unit of nutrient to pro duce biomass (nutrient use efficiency) should be somehow related to the abil ity of an individual plant to respond to fluctuating resource levels and to the distribution of species among habitats with varying resource availability. For a variety of species, nutrient use efficiency increases as nutrient availability decreases (Gray and Schlesinger, 1983; Shaver and Melillo, 1984; Birk and Vitousek, 1986; Lajtha and Klein, 1988). Species may also adjust to environ mental conditions by altering morphological characteristics. Increases in spe cific leaf area (SLA) (the amount of leaf area per gram leaf dry weight) in response to shade have been shown for a number of tree species (Kozlowski et al., 1991). SLA is affected by many environmental variables, including light quality and quantity, nutrient availability, and suboptimal temperatures (Poorter, 1989). Leaf area ratio (LAR), the relative amount of biomass a plant invests in leaf area, varies widely between species and depends on en vironmental conditions such as light and N supply (McDonald, 1989). Con sequently, a plant with relatively low photosynthetic rate could still be effi cient at gaining'a unit of carbon per unit N if it were efficient at producing

leaf area under conditions of N limitations (Chapin, 1987; Sage and Pearcy, 1987).

Conifers have evolved a pattern of nutrient utilization different from most hardwood species. Conifers have less than half the annual nutrient requirement of most hardwoods (Lassoie et al., 1985) because they retain numerous age classes of foliage and thus have lower nutrient demands for foliage replacement. They also have the capacity to internally redistribute a significant proportion of their annual nutrient requirement from older tissue (Jonasson, 1989, Chapin et al., 1990). These traits may assist conifers to tolerate competition from faster growing hardwoods. If conifers are able to internally utilize nutrients more efficiently as soil nutrient pools are depleted by hardwood competitors, then they may be able to adjust to and tolerate lower levels of soil nutrients.

On sites previously occupied by northern hardwoods, large industrial landowners often plant conifers after clear-cutting because these species are preferred for pulp and paper products (Maass, 1990). We propose that planted red pine (*Pinus resinosa* Ait.) seedlings alter their nutrient use efficiency and/ or shoot morphology under changing environmental conditions, and that these changes enhance their ability to tolerate competition from the hardwoods that soon dominate sites after clear-cutting. This study was designed to examine the competitive effects of three northern hardwood species (striped maple (*Acer pensylvanicum* L.), red maple (*Acer rubrum* L.), and pin cherry (*Prunus pensylvanica* L.)) on planted red pine seedlings. In addition, this study tested whether red pine seedlings respond to competitive environments by changing physiological and morphological attributes to cope with diminishing resources. This research was repeated at two sites to gain some insight as to how consistent results might be over space.

METHODS

This research was conducted at two clear-cut sites approximately 29 km apart in western Maine. Both sites supported similar early successional species and were planted with red pine seedlings from the same seed source. However, they differed with respect to soils and elevation (see below). The sites were chosen from among those clear-cut using whole-tree harvesting techniques by Scott Paper Company in late fall of 1987. Each site was formerly occupied by hardwoods and was planted with red pine by Scott Paper Company in May-June 1988.

Site descriptions

Mt. Abraham
The first site was located approximately 9 km west of Kingfield, Maine, on the southeast slope of Mt. Abraham, 44°58′20″N latitude, 70" 19′35″W lon-

gitude, along an elevational gradient of 425-455 m. The total area harvester
was approximately 20 ha. Soils in this area are classified as Humic Lithic
Cryorthods (Soil Conservation Service, unpublished report, 1989), in the
Saddleback-Mahoosuc-Sisk association. The Saddleback series, which dom
inates the study area, consists of shallow, well-drained soils that formed on a
thin veneer of glacial till.

Fletcher Mt.

The second site was located about 5 km west of Bingham, Maine, on the
southwest slope of Fletcher Mt., $45°02'22''N$ latitude, $69°56'30''W$ longi-
tude, along an elevational gradient of 245-305 m. Soils in this area are Typic
Haplorthods in the Berkshire-Peru-Leicester association (Arno et al., 1972)
The soils on Fletcher Mountain are classified as Berkshire very stony loam
and are derived from glacial till of shale and schist. The size of the harvested
area on Fletcher Mt. was about 40 ha.

The closest weather station to Fletcher Mt. and Mt. Abraham is Rangeley,
Maine (44" 58'N latitude, $70°$ 39'W longitude), approximately 24 km from
Mt. Abraham, at 466 m elevation. Average annual minimum and maximum
temperatures are 3.3 $°C$ and $9.7°$ C, respectively. Mean temperature is about
20°C in July and about ─ 9° C in January. The average annual precipitation,
including the amount received as snowfall, is about 102 cm. Precipitation is
distributed fairly evenly among the seasons (NOAA, 1987) .

Soil sampling

To assess the site quality of the hardwood sites after the clear-cutting, 36
soil samples were collected within the clear-cut area at the Fletcher Mt. site
and 32 soil samples at the Mt. Abraham site in July, 1988 and 1989. Samples
came from four randomly located positions in each block (described below)
at each site. Soil samples were collected to a 15 cm depth using a 2.5 cm di-
ameter soil sampling tube. Samples were not differentiated by horizon. Twelve
cores were taken within a 20 cm radius and cornposited for each sample. De-
terminations of soil pH in water, organic matter content, extractable P, ex-
changeable base cations (Mg, Ca, K), and extractable NO_3 and NH_4 were
made by the Plant and Soil Analysis Laboratory at the University of Maine.
Extractable Ca, K, Mg, and P (1 N ammonium acetate, pH 3.0) were ana-
lyzed by inductively coupled plasma emission spectrometry (ICP). NH_4 in
soil was extracted in I N KCl and analyzed on an ammonia analyzer. NO_3
was extracted in deionized water and analyzed on an ion chromatograph .

Competitor species

Three hardwood species were chosen as potential competitors of red pine
seedlings based on their natural occurrence in the northern hardwood region

(White, 199 1). Red maple, striped maple, and pin cherry, are among the fast growing, early successional species common on disturbed sites throughout the Northeast (Bormann and Likens, 1979). In high-density stands, pin cherry grows rapidly, with early canopy closure (high leaf area index) and high net annual production and nutrient accumulation (Marks, 1974). The buried seed strategy of pin cherry depends on prolonged dormancy and accumulation of seeds in the soil, and has an important advantage of seed being in situ prior to disturbance. Striped maple and red maple not only produce abundant wind-dispersed seeds but sprout prolifically (Burns and Honkala, 1990b), which enables them to establish quickly after large-scale disturbances such as commercial clear-cuts. Red maple's indeterminate growth period is not long in comparison with pin cherry, whose extension growth is rapid and continues for more than 90 days (Marks, 1975), whereas striped maple typically ends its extension growth a few weeks prior to pin cherry's (Bicknell, 1982).

Experimental design

The experimental design at Mt. Abraham was a 2 x 2 x 2 factorial with two competitors (pin cherry and striped maple), at two densities (0, weeded; high, unweeded), and two levels (0 and 224 g m^{-2}) of NPK fertilizer applied as commercial 10-10-l 0, OSMOCOTE, with a release time of 3 months. This design included eight replicates of each treatment combination established in blocks. At Fletcher Mt. a $3 \times 2 \times 2$ factorial design was implemented with three competitors (pin cherry, striped maple, and red maple), at two densities (0, high), and two levels (0 and 224 g m^{-2}) of commercial IO-10– 10 NPK fertilizer. Sites where stump sprouts occurred were excluded from the selection of red maple plots. This design included nine replicates (blocks) of each treatment combination.

At each site, the clear-cut area was subdivided into blocks representing equal width strips across the clear-cuts. Within each block a point was randomly located from which the nearest eight areas of high (more than 75% of maximum) density of each competitor were chosen. One 2.0 m^2 circular plot was established in each area. Four of the eight plots per species were randomly chosen as high-density plots and four were chosen as zero-density plots. NPK fertilizer was applied to two randomly selected red pine seedling plots per block (one zero density, one high density) in May 1989, immediately after snow melt. In June 1988, one 6-month-old containerized red pine seedling was planted in each plot. At the time of planting, the height and diameter at ground level of each red pine seedling were measured. These measurements were used in subsequent statistical analysis as covariates to remove any influence of initial size of seedlings on their final size. After planting the pine seedlings, high-density competitor plots were weeded to remove all species except the competitor. Zero-density competitor plots were weeded of all species.

Subsequent weeding was done at 2- to 3-week intervals throughout each grow-
ing season. By early, frequent weeding, the removed plants were very small,
thus minimizing disturbance to the plots. This weeding procedure main-
tained high-density plots as monocultures with respect to competitor species.
All vegetation in a 1 .O m buffer zone was clipped as necessary to keep it the
same height as the competitors to prevent outside vegetation from shading
the seedlings in excess of what was provided by the competitors. This experi-
mental approach follows guidelines suggested by Goldberg and Werner
(1983). Photosynthetically active radiation (PAR, 400-700 nm range) un-
der the hardwood canopies was measured with a portable light meter (Sun-
fleck Ceptometer, Decagon Devices, Pullman, WA, USA). Two perpendicu-
lar measurements were taken at the height of the terminal shoot of individual
pine seedlings to quantify the seedling's light environment. Two additional
measurements were taken in the open to quantify full incident PAR. Samples
were obtained on a clear day between 11:00 and 14:00 h solar time in late July
prior to the final harvest (1990). Percent sunlight available to individual
seedlings was calculated as: (PAR under canopy/ PAR open) $\times 100$.

Growth and nutrient use efficiency

Half of the treatment plots were harvested in the second growing season
(1989) and the remaining treatment plots were harvested in 1990. To allow
the pine seedlings to acclimate, no seedlings were harvested at the end of the
first growing season (1988). To determine total aboveground biomass and
nutrient use efficiencies, all red pine seedlings were separated into current
needles, older needles, and stems. Plant components were dried at 70°C for
48 h prior to weighing. Two seedlings per treatment combination from adja-
cent blocks were ground in a Wiley Mill to pass a 20-mesh screen and then
pooled by tissue type (current needles, older needles, and stems) to reduce
the total number of nutrient analyses. Plant tissue samples were analyzed by
the Plant and Soil Analysis Laboratory at the University of Maine for total N
and P content per component. Total N of plant tissue was determined by block
digestion using a sulfuric acid-hydrogen peroxide solution for total Kjeldahl
N and analyzed on a Wescan ammonia analyzer. To determine total P, ground
plant tissue samples were dry ashed at 550°C for 5-6 h and dissolved in 50%
HCl. Total P was analyzed by inductively coupled plasma emission spectrom-
etry (ICP). Precision and accuracy for the tissue nutrient analysis were all
within $\pm 5\%$.

Nutrient use efficiency for the red pine seedlings was calculated as total
biomass produced per total amount of nutrient in the biomass. This calcula-
tion of nutrient use efficiency differs from Ingestad's (1979b) and Agren's
(1983) concept of nitrogen productivity in that relative growth rate was not
calculated. However, growth of all seedlings for the first 6 months before

planting was maintained at optimum greenhouse conditions and analysis of covariance was used to account for initial height or diameter differences at the time of planting. In addition, maximum pine seedling age at the final harvest was 3 years old, and seedlings had not yet had a major turnover in foliar tissue. Thus, whole plant (aboveground) nutrient use efficiency seemed most appropriate. To determine biomass and annual production of the hardwood competitors, plants were separated into foliage, current twigs, and older twigs. Plant components were dried at 70°C for 48 h prior to weighing. Annual production of the hardwoods was estimated by summing total foliage, current twigs, and stem biomass increment per plot.

Specific leaf area

In both years (1989 and 1990), approximately 20 needles per age class (current and older) were randomly selected from each harvested red pine seedling to estimate leaf area per seedling. Needles were subsequently frozen to preserve until processing to reduce the amount of needle shrinkage. For hardwood competitors, about 20 leaves per plot were selected to estimate leaf area for each competitor plot using a leaf area/mass relationship. Leaves were pressed in a plant press immediately after harvest to preserve until measurements could be taken. Projected leaf area was measured using a video camera coupled to a computer image processing system (Decagon, DIAS II, 1989).

Statistical analysis

To determine differences in soil characteristics, a two-factor analysis of variance was used to compare sites and time periods. Where analysis of variance was significant, a Tukey's Studentized Range test was used to separate means (Dixon et al., 1990). A three-factor analysis of covariance was used to test for significant differences in biomass, nutrient use efficiency, and specific leaf area of red pine seedlings among species of competitors, density of competitors, and nutrient amendment. The covariate was either initial height or diameter of the red pine seedlings. Analysis of covariance requires satisfying the assumptions of homogeneity of variance and equality of slopes (Hicks, 1973). These assumptions were tested and decisions about valid statistical methodology were based on their results. The two possible covariates were initially tested by analysis of covariance (BMDP2V) for all response variables. Where covariates were significant they were included in the model; otherwise they were excluded (Dixon et al., 1990). In no case was initial pine seedling diameter significant in the covariance analysis. To determine differences in growth and leaf area index (LAI) of the competitors, a two-factor analysis of variance was used to compare species and nutrient amendment.

Where analysis of variance was significant, a Tukey's Studentized Range test was used to separate means (Dixon et al., 1990).

RESULTS

Soil   characteristics

All nutrients, including extractable N, had higher values on Mt. Abraham, except for extractable P in 1989 (Table 1). Soil ammonium was higher the first summer (1988) after the clear-cut than the second summer (1989) for both Mt. Abraham and Fletcher Mt. (Table 1).

Red pine seedling growth

In 1989, total biomass of red pine seedlings was significantly affected by species ($P = 0.007$), weeding ($P < 0.0001$), fertilization ($P = 0.010$), species by weeding ($P = 0.003$), and weeding by fertilizer ($P = 0.020$) interaction at Fletcher Mt. Fertilization significantly reduced total biomass of red pine seedlings on weeded plots but had no effect on unweeded plots (Fig. 1). The competitive effects are much greater on the unfertilized plots than the fertilized plots for the maples but similar for pin cherry. The greatest reductions in biomass occurred in the fertilized pin cherry plots (Fig. 1). At Mt. Abraham, species   ($P = 0.0005$),   weeding ($P = 0.000\ 1$), and species by weeding ($P = 0.004$) interaction significantly affected red pine seedling total biomass. As expected, there were no significant differences between species on the weeded plots; however, on the unweeded plots, pin cherry significantly reduced pine total biomass while striped maple did not (Fig. 1).

In 1990, total biomass of red pine seedlings was significantly affected by weeding ($P = 0.002$) , fertilization ($P = 0.026$), and species by weeding ($P = 0.001$) interaction at Fletcher Mt. Pin cherry competitors significantly reduced pine total biomass by about 60% compared with weeded plots but there were no reductions in pine total biomass on the unweeded maple plots. On the weeded pin cherry and striped maple plots, fertilization reduced total pine biomass (Fig. 2). On Mt. Abraham, total biomass of red pine seedlings was significantly affected by species ($P = 0.00\ 1$) and weeding ($P = 0.000\ 1$), and species by weeding interaction ($P = 0.0\ 19$).

Height and diameter

In 1989, height growth of pine seedlings was significantly reduced by fertilization and diameter growth was significantly affected by species and weeding on both Fletcher Mt. and Mt. Abraham. In 1990, height growth was significantly affected by species ($P = 0.004$) and weeding ($P = 0.002$) on Mt.

TABLE I

Soil analysis from Fletcher Mt. ($n = 36$) and Mt. Abraham ($n = 32$) in July 1988 and 1989. Average values of soil characteristics in columns followed by different letters are significantly different ($P < 0.01$)

| Soil parameters	pH	OM%	CEC (meq per 100 g)	Exchangeable cation (kg ha-')			Extractable (kg ha-')			Total Kjeldahl nitrogen (kg ha-')	% Base saturation
				K	Mg	Ca	P	NO_3	NH_4		
July 1988											
Fletcher Mt.	4.7a	13.91a	3.68a	167.0a	81.7a	464a	4.95a	5.40a	56.66a	-	34.70a
Mt. Abraham	4.5b	21.98b	6.09c	260.6b	194.4b	1365b	8.98c	21.94d	138.2b	-	50.08c
July 1989											
Fletcher Mt.	4.7a	15.09a	4.22b	167.0a	104.7a	645a	4.81b	6.63b	3.81c	4363a	43.1 lb
Mt. Abraham	4.5b	25.33b	7.73c	264.8b	220.0b	1801b	4.07a	21.21c	11.04d	10154b	58.97c
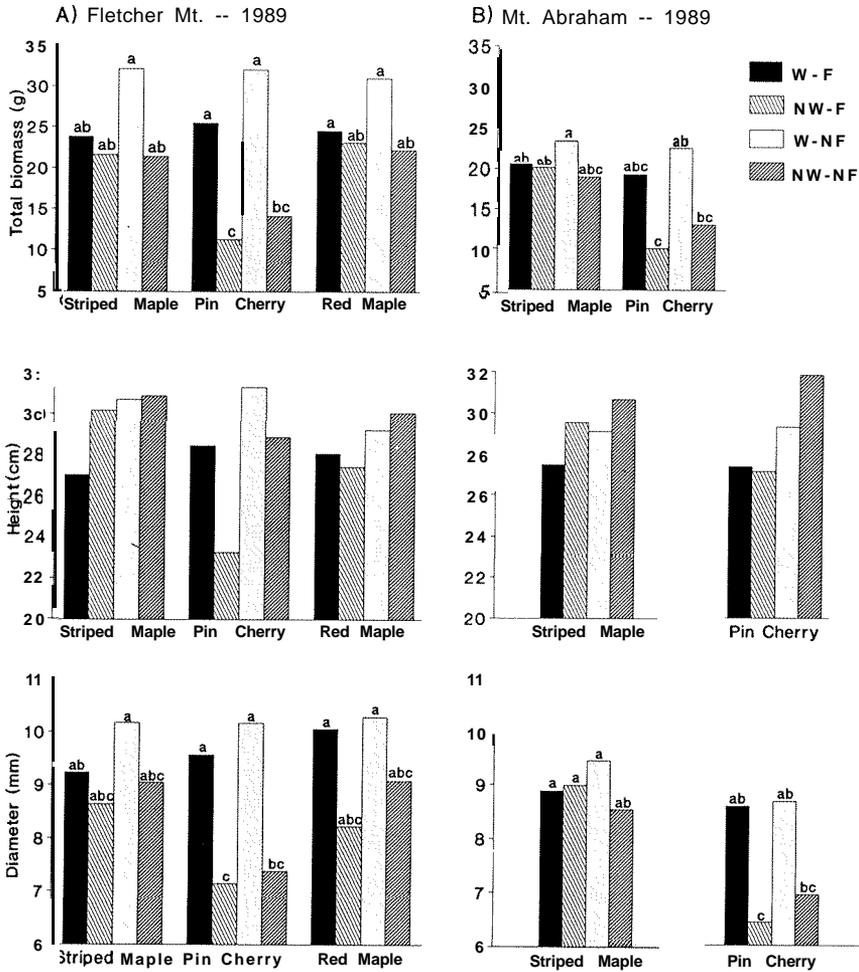
Fig. 1. Effects of competitor species, weeding, and fertilization on total biomass, height, and diameter of red pine seedlings harvested in 1989 from Fletcher Mt. and Mt. Abraham. W-F, weeded, fertilized; NW-F, unweeded, fertilized; W-NF, weeded, unfertilized; NW-NF, unweeded, unfertilized. Means within a graph followed by different letters are significantly different according to the Tukey's Studentized Range Method (Dixon et al., 1990).

Abraham and by fertilization ($P = 0.018$) on Fletcher Mt. Species by weeding significantly interacted ($P = 0.018$) at the Fletcher Mt. site such that pine seedling diameter was only reduced by pin cherry competitors (Fig. 2). At Mt. Abraham, pine seedlings on weeded plots had lower diameter growth on pin cherry than striped maple plots (Fig. 2). Pine diameter growth on the unweeded, fertilized pin cherry plots was the lowest of all treatment combinations, similar to the results from Fletcher Mt. (Fig. 2).
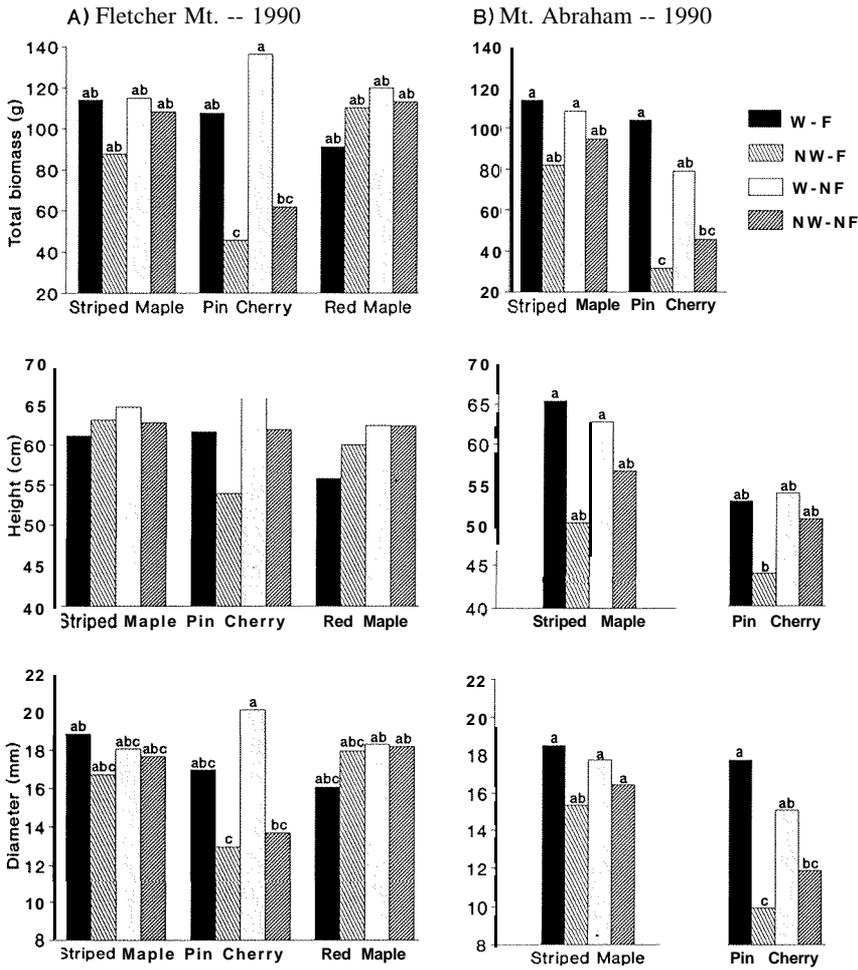
Fig. 2. Effects of competitor species, weeding, and fertilization on total biomass, height, and diameter of red pine seedlings harvested in 1990 from Fletcher Mt. and Mt. Abraham. W-F, weeded, fertilized; NW-F, unweeded, fertilized; W-NF, weeded, unfertilized; NW-NF, unweeded, unfertilized. Means within a graph followed by different letters are significantly different according to the Tukey's Studentized Range Method (Dixon et al., 1990).

Nutrient use efficiency of red pine seedlings

Species, weeding, fertilization, and species by fertilizer interaction significantly ($P < 0.00$ 1) affected red pine nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE) on Fletcher Mt. in 1989. NUE was greater on unweeded plots and unfertilized pin cherry plots (Fig. 3). PUE was inversely related to NUE with the unfertilized pin cherry plots having the lowest value for pine PUE whereas the fertilized red maple plots had the highest PUE (Fig.
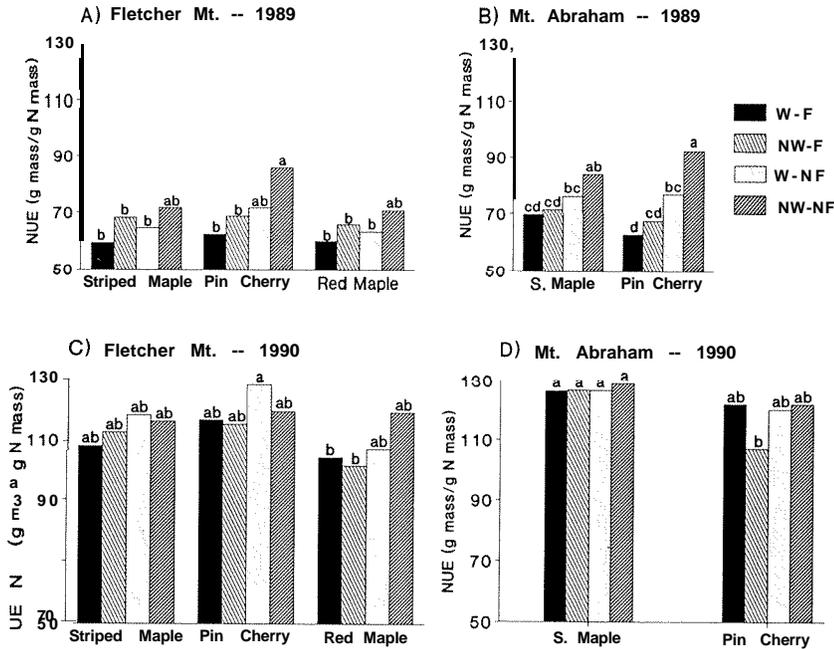
Fig. 3. Effects of competitor species, weeding, and fertilization on nitrogen use efficiency (NUE) of red pine seedlings harvested in 1989 and 1990 from Fletcher Mt. and Mt. Abraham. W-F, weeded, fertilized; NW-F, unweeded, fertilized; W-NF, weeded, unfertilized; NW-NF, unweeded, unfertilized. Means within a graph followed by different letters are significantly different according to the Tukey's Studentized Range Method (Dixon et al., 1990).

4). On Mt. Abraham, the unfertilized plots had higher NUE and lower PUE than fertilized plots in 1989 (Figs. 3 and 4). In addition, there was a significant increase in pine NUE and a decrease in PUE on unweeded, unfertilized pin cherry and striped maple plots.

Species ($P=0.001$) and fertilization ($P=0.000\ 1$) had a significant effect on red pine NUE and PUE on Fletcher Mt. in 1990. NUE and PUE were higher on unfertilized plots for both weeded and unweeded treatments (Figs. 3 and 4). Species ($P=0.0003$) and fertilization ($P=0.034$) had a significant effect on NUE and fertilization ($P<0.001$) had a significant effect on PUE at Mt. Abraham in 1990. There were no significant differences in NUE among the weeded plots in 1990. However, on the unweeded plots, pine NUE was significantly lower on the fertilized pin cherry plots than on the other treatment combinations (Fig. 3). NUE was the highest on the striped maple plots.

Leaf area of red pine seedlings

In 1989, SLA of current needles was significantly higher on plots where competitors were present on both sites (Table 2). LAR was significantly af-
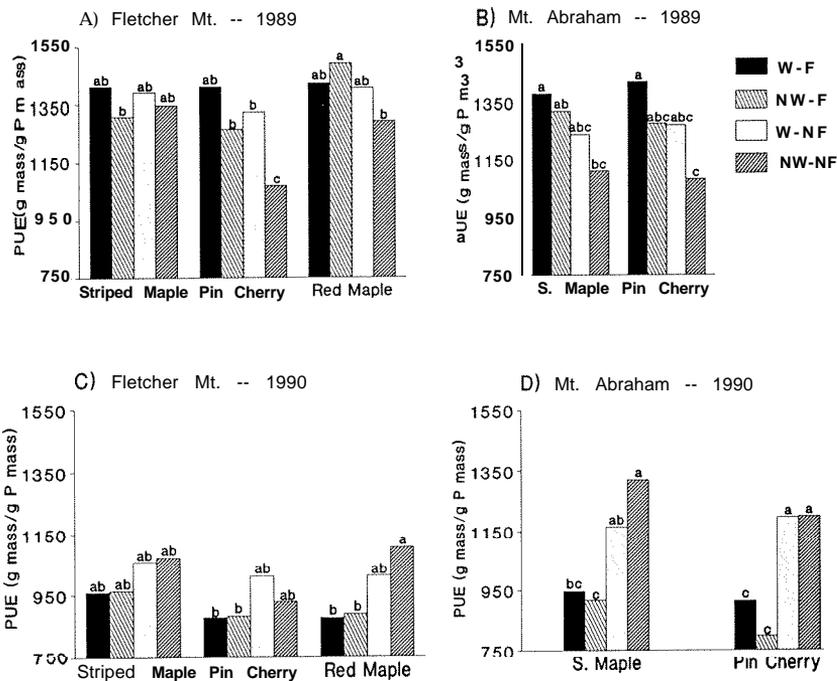
Fig. 4. Effects of competitor species, weeding, and fertilization on phosphorus use efficiency (PUE) of red pine seedlings harvested in 1989 and 1990 from Fletcher Mt. and Mt. Abraham. W-F, weeded, fertilized; NW-F, unweeded, fertilized; W-NF, weeded, unfertilized; NW-NF, unweeded, unfertilized. Means within a graph followed by different letters are significantly different according to the Tukey's Studentized Range Method (Dixon et al., 1990).

fected by species ($P=0.019$), weeding ($P< 0.001$), and fertilization ($P=0.020$), species by weeding ($P= 0.006$), and weeding by fertilization ($P=0.049$) interaction on Fletcher Mt. On Mt. Abraham, LAR was significantly affected by species ($P= 0.035$), weeding ($P= 0.031$), and fertilization ($P= 0.003$). LAR was higher, but total leaf area was lower, on the unweeded plots at both sites (Table 2). LAR was higher on the unfertilized plots than on fertilized plots for all competitor species except striped maple on Fletcher Mt. (Table 2).

In 1990, red pine seedlings in plots with pin cherry had the highest SLA of both current and older needles (Table 3). As in 1989, SLA was greater on the unweeded plots than on plots with no competition (Table 3). The pine seedlings with the highest LAR occurred on unweeded pin cherry plots at both sites (Table 3). Total leaf area was greatest for pine seedlings on the weeded plots with seedlings on the unfertilized pin cherry plots on Fletcher Mt. having the highest total leaf area (Table 3).

TABLE 2

Average values for specific leaf area (cm* g^{-1}) of current (SLA^1) and older (SLA^2) needles, total leaf area (LA) (cm*), and leaf area ratio (LAR) of red pine seedlings harvested in 1989 from Fletcher Mt. and Mt. Abraham. SM, striped maple; PC, pin cherry; RM, red maple

Species-treatment	Fletcher Mt.				Mount Abraham			
	SLA'	SLA^2	LA	LAR	SLA'	SLA^2	LA	LAR
Weeded								
SM-Fertilized	66.53	11.02	1217.7abc	51.86	69.57b	61.28	1031.4ab	55.07b
SM-Unfertilized	68.42	64.90	1647.9a	51.13	75.06ab	57.17	1285.2a	55.38ab
PC-Fertilized	68.32	78.27	1334.0ab	51.76	71.62b	67.02	1039.0ab	53.16b
PC-Unfertilized	71.59	72.03	1638.5a	53.38	76.05ab	61.94	1235.4a	55.37ab
RM-Fertilized	65.98	62.70	1254.6abc	48.94				
RM-Unfertilized	67.31	61.20	1590.6a	52.07	-	-	-	-
Unweeded								
SM-Fertilized	91.94	72.62	1223.2abc	59.30	74.35ab	66.47	1055.6ab	52.47b
SM-Unfertilized	78.93	65.94	1238.4abc	59.93	77.72ab	67.06	1035.2ab	55.32ab
PC-Fertilized	93.81	69.70	655.37c	53.38	90.36a	60.67	556.02b	55.35ab
PC-Unfertilized	77.28	71.42	781.31bc	62.59	88.48a	71.19	818.32ab	62.25a
RM-Fertilized	70.15	66.09	1187.2abc	51.63	-	-		
RM-Unfertilized	75.27	61.68	1140.1abc	52.93		-	-	-

Values in columns followed by different letters are significantly different ($P < 0.05$) according to Tukey's Studentized Range Method (Dixon et al., 1980).

TABLE 3

Average values for specific leaf area (cm^2 g^{-1}) of current (SLA') and older (SLA^2) needles, total leaf area (L.4) (cm^2), and leaf area ratio (LAR) of red pine seedlings harvested in 1990 from Fletcher Mt. and Mt. Abraham. SM, striped maple; PC, pin cherry; RM, red maple

Species-treatment	Fletcher Mountain				Mount Abraham			
	SLA'	SLA^2	LA	LAR	SLA'	SLA^2	LA	LAR
Weeded								
SM-Fertilized	96.14b	72.33ab	6457.8ab	57.23	97.51ab	78.04b	6526.8a	58.51ab
SM-Unfertilized	91.18b	77.73ab	6400.2ab	56.37	93.33b	81.27b	6216.1a	56.99ab
PC-Fertilized	104.87ab	76.16ab	6778.2ab	63.06	95.91ab	83.00b	6218.4a	60.13ab
PC-Unfertilized	98.04ab	79.58ab	8134.1a	60.40	93.00b	81.63b	4630.3abc	58.70ab
RM-Fertilized	90.55b	72.33ab	5093. 1abc	55.95				
RM-Unfertilized	97.06b	70.44b	7050.8ab	58.69				
Unweeded								
SM-Fertilized	102.37ab	77.36ab	5116.6abc	59.36	100.95ab	83.47b	5006.9ab	58.81ab
SM-Unfertilized	96.36b	78.00ab	6300.9ab	59.44	87.25b	77.52b	5133.3ab	53.94b
PC-Fertilized	120.32a	90.17a	2871.2c	63.76	111.96a	102.1 la	2075.4c	63.81ab
PC-Unfertilized	112.24ab	87.25ab	3967.5bc	63.10	110.70a	92.8 lab	3015.4bc	66.17a
RM-Fertilized	98.43ab	71.94ab	6500.9ab	58.96		-		
RM-Unfertilized	99.08ab	74.78ab	6590.2ab	59.96	-			-

Values in columns followed by different letters are significantly different ($P < 0.05$) according to Tukey's Studentized Range Method (Dixon et al., 1990).

TABLE 4

Average values for total aboveground biomass (g per plot), annual production (g per plot), leaf area index ($m^2 m^{-2}$) of hardwood competitors on Fletcher Mt. and Mt. Abraham plots harvested in 1989. SM, striped maple; PC, pin cherry; RM, red maple

Species-treatment	1989			1990			
	Total biomass'	Annual production	Leaf area index*	Total biomass	Annual production	Leaf area index*	% PAR
Fletcher Mt.							
SM-Fertilized	293.22ab	265.01ab	1.09ab	390.94a	231.47a	0.94b	83.95a
SM-Unfertilized	189.74a	167.63a	0.68ab	258.15a	169.79a	0.87a	90.87a
PC-Fertilized	1314.94c	1149.90c	3.39c	2624.17c	1525.68c	4.38c	23.27c
PC-Unfertilized	677.00b	581.98b	1.73b	1427.25b	862.70b	2.47b	55.72b
RM-Fertilized	203.25a	183.32a	0.30a	182.74a	133.90a	0.58a	84.30a
RM-Unfertilized	243.54a	219.77a	0.69ab	181.30a	123.42a	0.41a	95.09a
Mt. Abraham							
SM-Fertilized	56.38a	47.08a	0.22a	160.83ab	106.07ab	0.52ab	81.89a
SM-Unfertilized	192.80ab	162.00a	0.69ab	81.83a	48.89a	0.26ab	92.26a
PC-Fertilized	389.66b	358.36b	1.51c	1124.13c	583.30c	1.70b	39.30b
PC-Unfertilized	3 12.9 lab	264.99ab	0.98bc	516.48bc	308.30bc	1.14bc	56.05ab

Within a site, values in columns followed by different letters are significantly different ($P < 0.05$) according to Tukey's Studentized Range Method (Dixon et al., 1990).
'Denotes variables with unequal variance that could not be corrected with a logarithmic or square root transformation.
*Denotes variable with a square root transformation in the analysis of variance table to correct for unequal variance.

Growth of hardwood competitors

In 1989 and 1990, there was a significant difference among competitors in total aboveground biomass, annual production and LAI on both sites. Pin cherry consistently had greater biomass than either striped maple or red maple on Fletcher Mt. (Table 4). In 1989, pin cherry on fertilized plots had twice the aboveground biomass of pin cherry on unfertilized plots and more than three times the biomass of the other two species (Table 4). In addition, pin cherry LAI on fertilized plots was three times that of the other species (Table 4). In 1990, total aboveground biomass of pin cherry on fertilized plots was almost twice that of pin cherry on unfertilized plots. Striped maple biomass was only 15% of the pin cherry biomass on fertilized plots but more than twice that of red maple (Table 4). Annual production of pin cherry was significantly higher than the other species on both sites as well.

In general, total aboveground biomass, annual production, and LAI were higher on Fletcher Mt. than on Mt. Abraham. For example, total biomass of pin cherry and striped maple was two to three times higher on Fletcher Mt.

than on Mt. Abraham in 1990 (Table 4). Percent PAR available to red pine seedlings was significantly lower under pin cherry than either striped maple or red maple canopies (Table 4).

DISCUSSION

Destructive sampling for biomass determinations is not always possible because it is costly, time consuming, and destroys the sampled seedlings. Thus, simpler measurements such as height and diameter, have been used to determine the success and growth of planted seedlings. However, only diameter growth was consistently suppressed by competitors at both sites in both years. Many other studies have demonstrated that height is not a reliable measure of competitor influence (Zutter et al., 1986a; Brand and Janas, 1988; Brand, 1990; Morris et al., 1990). For example, Strothman (1967) found that dry matter production was the single most useful measure of growth response of red pine seedlings to removal of competition from dense beaked hazel (*Corylus conuta* Marsh.), whereas differences in height were small and non-significant. In contrast, root collar diameter proved to be a reliable estimator of total seedling dry weight for black spruce (*Picea mariana* B.S.P.) and jack pine (*Pinus banksiana* Lamb.) on a variety of sites (Morris et al., 1990).

Increased nutrient use efficiency, SLA, and LAR may alleviate some of the stress effects due to reduced resources but does not prevent growth reductions. Coleman and Bazzaz (1992) observed a similar response in *Abutilon theophrasti* Medic., a C_3 annual, which responded to low nutrient availability by increasing the efficiency of leaf area production per unit N. They found that although photosynthetic nitrogen use efficiency (PNUE) increased with decreased nutrient availability, the increase in PNUE did not account for the effects of nutrients on growth. However, they did suggest that if *A. theophrasti* did not increase its PNUE then growth reductions due to N limitations would have been more extensive. In another study, Nambiar (1990) reported that weeds severely reduced N uptake by radiata pine (*Pinus radiata* (D. Don)) trees through direct competition for N. This in turn decreased tree growth despite the increased NUE of pines.

Many studies have shown that trees alter various developmental characteristics such as SLA and LAR in response to resource availability. For example, Kolb and Steiner (1990) found that shading significantly increased LAR of northern red oak *(Quercus rubra* L.) seedlings whereas root competition from grasses decreased LAR. A specific environmental variable may increase or decrease SLA depending on the species studied (see Dijkstra (1989) for review). In this study, an increase in SLA occurred on competition plots with the highest competitor LAI and the most shading. Increases in SLA and LAR under competition may have buffered some of the decreases in growth that would have been observed without a phenotypic adjustment. However, total

red pine leaf area and biomass were significantly reduced on plots with the highest competitor biomass and LAI. Other studies have shown varying results. Bazzaz et al. (1989) found that competition tended to increase SLA for *Abutilon,* but attributed the reduced performance of *Abutilon* in competition to an initial decrease in LAR. Zutter et al. (1986b) reported that competition resulted in higher SLA of loblolly pine seedlings but less aboveground biomass, leaf area, and diameter growth. However, Colbert et al. (1990) found no significant differences in SLA of 4-year-old loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii)* due to fertilization or weed control.

Canopy LAI has been used to assess competitive ability of plants in other studies (Caldwell, 1987; Barnes et al., 1990; White and Elliott, 1992). The relative differences among competitor species in canopy LAI may explain differences in the red pine seedling growth. Fertilized pin cherry plots on Fletcher Mt. had an average LAI of 3.39 in 1989 and 4.38 in 1990. In both years, total biomass of red pine seedlings was lower on these plots than on any other plots. Thus, competition for light may have been an important mechanism reducing red pine growth and limiting NUE. Light levels measured in July 1990 under pin cherry canopies averaged about 23% and 56% of full sunlight for fertilized and unfertilized plots, respectively.

Weeding significantly affected nutrient use efficiencies in 1989, but the use efficiencies were significantly higher on competition plots than on weeded plots. However, there were no significant differences in nutrient use efficiencies due to weeding in 1990 when shading from competitors was highest. The high shading in 1990 could have limited the increase in NUE that would have been observed due to decreased nutrient availability caused by competitor nutrient uptake. In a greenhouse study, Elliott and White (1992) observed a significant reduction in nutrient use efficiencies under low light levels (27% of full greenhouse light). Perhaps light levels under canopies of pin cherry did not reduce sunlight in 1989 to the extent and duration of that observed in the greenhouse study, but by July of 1990 the pin cherry canopies were reducing light close to the greenhouse low light level. NUE increased on all treatment combinations from 1989 to 1990, an increase over time that has been noted in slash pine plantations (Gholz and Fisher, 1985).

Overall, fertilization decreased growth and NUE of pine seedlings in 1989. Although pine seedling biomass was lower on fertilized plots than unfertilized plots, pin cherry biomass and annual production increased in response to fertilization. In addition, pin cherry accumulated 1.9 and 1.7 times more N in its new growth on fertilized plots than on unfertilized plots in 1989 and 1990, respectively. Pin cherry also had six times more N in annual growth than either striped maple or red maple. Higher competitor biomass, LAI, and nutrient uptake would explain the lower red pine biomass on fertilized plots with competitors present, but pine seedling growth was also suppressed on weeded plots due to fertilization in both years, except on Mt. Abraham in 1990.

Although most studies have found an increase in conifer growth after fertilization, a few studies have found that conifer growth decreased (Brand, 1990, Brand and Janas, 1988). For example, Brand and Janas (1988) noted a slight growth depression in white pine and white spruce seedlings with fertilizer application. They attributed this growth depression to induced changes in osmotic potential of soil moisture. However, depression of growth due to osmotic water stress seems unlikely since NPK was applied at a relatively low application rate (224 g m^{-2}) and in a slow release form (OSMOCOTE). Other possible explanations are that NPK fertilization imposed an N/P imbalance (Ingestad, 1979a,b; Radwan and Shumway, 1983; Timmer and Armstrong, 1987), or that mycorrhizal associations of red pine seedlings decreased with fertilization (Menge et al., 1977; Van den Driessche, 1983; Ekwebelam and Reid, 1983; MacFall et al., 1991). However, because belowground biomass was not measured in our study, it is difficult to determine why fertilization depressed red pine seedling growth above ground on weeded plots.

The growth of red pine seedlings was the result of (a) availability of resources influenced by the competitor species, (b) the efficiency of nutrient use, and (c) the ability of red pine to adjust its biomass allocation and growth pattern in response to resource availability. Although red pine seedlings exhibited phenotypic plasticity of nutrient use and leaf morphology, they could not compensate for the growth reductions caused by competition from faster growing species. However, the plasticity in nutrient use efficiency by red pine in competitive environments may alleviate some of the stress effects.

Growth of red pine seedlings was significantly reduced by competitors on both sites in both years. Pin cherry appeared to be a more important competitor than either striped maple or red maple due to its higher annual production and LAI. In our study, red maple was the least important competitor, contrary to expectation. However, we used seedlings instead of stump sprouts, which are the major form of red maple competition in some clear-cuts. Red maple stump sprouts can grow much faster than seedlings because they have an established root system, and, therefore, may be more competitive than our results suggest. Altered nutrient use efficiency and leaf morphology of the red pine seedlings did not prevent growth losses due to competition, but this phenotypic adjustment may buffer losses that would have otherwise been observed and may allow red pine seedlings to tolerate competitive environments for extended periods of time.

In conclusion, this study supports Goldberg's (1990) assertion that similar growth forms have similar competitive abilities, and that the apparent differences in competitive abilities are due primarily to differences in total biomass attained by individual species. Pin cherry exhibits traits that reduce the performance of red pine seedlings, such as high annual production and LAI. At the same time, red pine is exhibiting competitive tolerance traits by plasticity

of leaf morphology and nutrient use efficiency. Survival, tolerance, and phenotypic adjustment to diminishing resources may be red pine's measure of competitive ability. How long red pine seedlings can survive under dense pin cherry canopies is an important question yet to be answered. In this study, red pine seedlings in the most competitive environment (i.e. pin cherry, fertilized plots) increased total biomass in 1990 by approximately three times the amount of 1989 (Figs. I and 2). Thus, even in these environments red pine survives, grows, and tolerates competition. Although red pine is classified as an intolerant species (Burns and Honkala, 1990a) and removal of competition from light (Strothman, 1967) has increased red pine seedling growth, how long red pine can survive under competitive environments is unknown. Long-term studies examining competitive interactions are necessary to determine competitive outcomes. In natural populations, long-term competitive ability may be related to processes that structure the community, such as survival and tolerance mechanisms which may be important in predicting successional change.

ACKNOWLEDGMENTS

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