Predicting the effects of hardwood competition on red pine seedling growth[1]

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Pin cherry (*Prunus pensylvanica* L.f.) and striped maple (*Acer pensylvanicum* L.) are potentially important competitors of red pine (*Pinus resinosa* Ait.) planted on recently clear-cut hardwood sites. By experimentally manipulating initial competitor densities on 2.0-m^2 plots, we were able to quantify and compare the effects of competitor species on red pine seedlings 2 years after planting on two sites in western Maine. Various measures of competitor biomass and leaf area index (LAI) were highly correlated; thus, we used LAI to quantify competitor abundance. On the site with poorer growth for both competitors and red pine, the only red pine variable significantly correlated with competitor LAI was specific leaf area (SLA) of current needles. On the site with better growth for all species, various measures of red pine biomass as well as diameter at ground level and SLA were significantly correlated with competitor LAI. Seedling height was not significantly correlated with competitor LAI at either site. Although there were no significant differences between competitor species in terms of their effect per unit of LAI, pin cherry tended to achieve much higher LAI (and biomass) than did striped maple and thus had a greater negative impact on red pine seedling growth. We conclude that general predictions of the early effects of competition under field conditions are possible, but that the strength of the relationships may be influenced by the extent to which microsite factors and site characteristics are incorporated.

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Le cerisier de Pennsylvanie (*Prunus pensylvanica* L.f.) et l'érable de Pennsylvanie (*Acer pensylvanicum* L.) sont des espèces compétitives potentiellement importantes dans le cas du pin rouge (*Pinus resinosa* Ait.) planté sur des sites feuillus récemment coupés à blanc. En modifiant expérimentalement la densité des espèces compétitives à l'intérieur de parcelles de 2,0 m^2, nous avons pu quantifier et comparer l'effet des espèces compétitives sur des semis de pin rouge plantés depuis 2 ans sur deux sites dans l'ouest du Maine. Diverses mesures de biomasse des espèces compétitives et d'indices de superficie foliaire étaient fortement corrélés. Par conséquent, nous avons utilisé l'indice de superficie foliaire pour quantifier l'abondance des espèces compétitives. Sur le site où la croissance des deux espèces compétitives et du pin rouge était faible, la seule variable du pin rouge significativement corrélée avec l'indice de superficie foliaire des espèces compétitives était la superficie foliaire spécifique des aiguilles de l'année en cours. Sur le site où toutes les essences avaient une meilleure croissance, plusieurs mesures de biomasse du pin rouge, ainsi que le diamètre au niveau du sol et la superficie foliaire spécifique, étaient significativement corrélés avec l'indice de superficie foliaire des espèces compétitives. La hauteur des semis n'était pas significativement corrélée avec l'indice de superficie foliaire des espèces compétitives sur aucun des sites. Même s'il n'y avait pas de différence significative entre les espèces compétitives quant à leur effet par unité de l'indice de superficie foliaire, le cerisier de Pennsylvanie avait tendance à atteindre un indice de superficie foliaire, et une biomasse, beaucoup plus élevés que l'érable de Pennsylvanie et avait par conséquent un impact plus grand sur la croissance des semis de pin rouge. Nous arrivons à la conclusion qu'il est possible de faire des prédictions générales sur les effets à court terme de la compétition au champ. Par contre, la justesse des prédictions peut varier dans la mesure où l'on tient compte des facteurs liés aux microsites et des caractéristiques du site.

[Traduit par la rédaction]

Introduction

There is an extensive literature documenting the effects of competitors on commercially important tree species in North America (e.g., bibliography by Stewart *et al.* 1984). However, controlling competition can be expensive, especially because it is a cost that often occurs early in the rotation, and thus must be carried through to final harvest. Furthermore, if control involves herbicides, it may meet resistance from the public. Thus, it is important to quantify the effects of competition over space and time if foresters are going to make informed decisions about the location and timing of competition control.

Current research is focusing on ways to accurately assess the degree of competition under field conditions. One fundamental question concerns what to measure on commercially important species to determine the degree to which they are experiencing competition. Recent work suggests that traditional measures such as height growth may not be best for early detection of competition effects (Brand 1990; Eissenstat and Mitchell 1983; Haywood 1986; Morris *et al.* 1990; Tappeiner *et al.* 1987). Another question concerns how to measure the competitors themselves to determine their potential for reducing growth of desired species over time and among sites. Although some distant-dependent, angular approaches have been tried (e.g., Rejmanek and Messina 1989), there is hope that less time demanding measures may be equally good at predicting growth of seedlings (MacDonald *et al.* 1990). There is also the question of how competition may affect growth under different site conditions (Cole and Newton 1987; Glover *et al.* 1989) and with different crop species (Goldberg 1990; Morris *et al.* 1990).

The purpose of this research was to investigate some of these questions with respect to red pine (*Pinus resinosa* Ait.) seedlings planted in Maine clearcuts formerly occupied by

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mixtures of hardwood species. Some of the highest quality sites in Maine are occupied by hardwood stands with varying inclusions of conifers. However, many of these stands are of low quality, having been selectively harvested many times in the last 100 years or more. Consequently, private industrial landowners increasingly clear-cut such stands (a practice made more feasible in recent years by the increase in biomass markets and the development of mechanized harvesting) and plant conifers. Although black spruce (*Picea mariana* (Mill.) B.S.P.) is the most commonly planted species in Maine (Maass 1990), red pine is probably the most commonly planted species on high quality hardwood sites. In Michigan, red pine planted on northern hardwood sites produced more volume than sugar maple (*Acer saccharum* Marsh.) stands (Frederick and Coffman 1978). However, if competition was not controlled early, red pine volumes were reduced by as much as 35% over the life of the plantation (Coffman 1989). Our objectives in this study were to (*i*) quantify the relationship of competition intensity to red pine seedling growth 2 years after planting, (*ii*) determine how, or if, competitor species influenced the relationship, (*iii*) investigate how various measures of competitor abundance and red pine seedling growth affected the ability to predict competition effects, and (*iv*) determine if results were comparable on two sites.

Site descriptions

Two sites were chosen from among those on Scott Paper Company land that were clear-cut with whole-tree (aboveground) harvesting during the fall–winter prior to the initiation of this study in May 1988. Although one of our objectives was to look at how different sites might affect our results, we could not do a study of many sites. To avoid large (from a management perspective) differences in sites, we chose sites that were (*i*) located in the same geographic area (approximately 29 km apart in western Maine), (*ii*) both scheduled to be planted with red pine, (*iii*) previously occupied by predominantly hardwood stands, and (*iv*) similar enough to support the same potential competitors. However, the sites were different in soil type and elevation, two factors we assumed could affect competitive relationships.

One site was on the southeast slope of Mount Abraham, approximately 9 km west of Kingfield, Maine, at 44°58′20″N and 70°19′35″W. Elevation ranged from 425 to 455 m over the 20-ha clearcut. Soils were in the Saddleback series (classified as Humic Lithic Cryorthods), which are typically thin, well-drained glacial tills occurring on mountain slopes (Soil Conservation Service, 1989, unpublished report).

The other site was on the south slope of Fletcher Mountain, approximately 5 km southwest of Bingham, Maine, at 45°02′22″N and 69°56′30″W. Elevation ranged from 245 to 305 m over the 40-ha clearcut. Soils were in the Berkshire series (classified as Typic Haplorthods), which are typically deep, well-drained to poorly drained glacial tills derived from shale and schist (Rourke *et al.* 1978; Arno *et al.* 1972).

Methods

Field

Although field studies of competition abound, many suffer from experimental design problems (Underwood 1986). In particular, it is common to compare species growth where competitors are abundant with growth in areas where competitors are absent. Such an approach is subject to the criticism that any observed differences in growth could be due as much to the factor(s) that caused the competitor to be absent or less abundant as they could to the effect of competition itself (Underwood 1986). On the other hand, experiments under highly controlled greenhouse or garden conditions may bear little resemblance to actual field conditions.

To take advantage of some experimental control while still operating under "natural" conditions, we followed a design suggested by Goldberg and Werner (1983). This first involved finding areas (≥ 2.0 m^2) throughout each clearcut dominated by each of the competitor species in this study (pin cherry (*Prunus pensylvanica* L.f.) and striped maple (*Acer pensylvanicum* L.)) during May and early June of 1988. These two species were chosen because they are common components of the early successional community on hardwood sites (Bicknell 1982; Marks 1974) and were present throughout our study areas. After finding 30 such areas for each species at each site, 2.0-m^2 circular plots were established and all individuals except those of the competitor species were removed. We then weeded each plot to a randomly chosen density between 10 and 100% of its original density. To ensure that a wide range of densities resulted, three plots were assigned to each of ten 10% density-reduction intervals between 10 and 100%. Three completely weeded plots for each species–site combination were randomly chosen from plots that had been established in the same way at the same time and on the same sites, but which were part of a different study. This gave us 33 plots initially for each competitor species at each site; as a result of mortality, we ended up with 27–31 plots per competitor species–site combination. The randomization of density reduction avoided confounding the effects of microsites and competitor density, but did not eliminate the effects of either. Plots were not greatly disturbed by the weeding or density reduction because the removed plants were typically very small (≤ 5 cm tall). Plot size was based on (*i*) a desire to minimize the effects of roots from plants outside the plot (most plants near the plots were small and not of sprout origin), (*ii*) the assumption that over the course of the study most shading would come from plants within the plots, and (*iii*) logistical constraints due to the time it took to weed these plots, which influenced the number of plots that could be included in the study. However, it should be noted that this plot size is not necessarily the optimum.

Following plot selection, one 6-month-old, containerized red pine seedling was planted at the center of each plot in June 1988. Diameter at the root collar and height were recorded at time of planting. During the 1988 and 1989 growing seasons, plots were hand weeded at 2–3 week intervals to keep the plots free of any species other than the competitor species. Almost all weeded material came from small (≤ 5 cm tall), new germinants. Sprouting from previously weeded stems was rare, presumably because of their small size at the time of the first weeding and the frequent weeding thereafter. When necessary, areas outside the plot were also weeded or clipped to avoid any shading from vegetation taller than that inside the plots.

At the end of the growing season in 1989, all vegetation in each plot was clipped at ground level to determine various growth parameters. After determining red pine seedling diameter at the root collar and height, plants were separated into the following components: (*i*) new needles (formed in the current year), (*ii*) 2-year-old needles, and (*iii*) woody tissue (stems and branches). Components were dried at 70°C for 48 h prior to weighing. Approximately 20 needles per age-class were randomly selected from each red pine seedling prior to drying, and their projected leaf area was determined with a Decagon digital image analyzer. Needles were then dried and weighed to determine specific leaf area (SLA, $\mathrm{cm^2 \cdot g^{-1}}$) for each seedling; this could then be used to determine leaf area by age-class for each seedling. For hardwood competitors, approximately 20 leaves per plot were selected and pressed immediately to prevent their surface area from shrinking prior to measurement. They were then analyzed in the same way as the pine needles so that competitor leaf area index (LAI, $\mathrm{cm^2 \cdot cm^{-2}}$) could be determined for each plot. Competitor leaf weight and woody tissue weight were also measured in the same way as they were on the red pine seedlings.

Statistical analysis

Statistical analyses proceeded in a sequential fashion. First, Pearson correlation coefficients (r) among pine variables were determined to see the degree to which these growth measures were correlated and to provide an idea as to which ones might have similar relationships to competitor variables. This allowed us to reduce the number of regression equations generated and to make inferences about possible substitutes to facilitate field measurements. We then did the same thing for the competitor variables. Finally, we calculated Pearson correlation coefficients for all possible pairs of pine variables and competitor variables. As with the above, this served as a screening process and alerted us to possible problems with collinearity. Correlation coefficients were determined with BMDP8D (Dixon 1990).

Once variables were chosen for regression analysis, we used scatterplots of pairs of variables to determine models that might fit the data. For generation and comparison of equations for different species–site combinations, we used BMDP1R (Dixon 1990). We used BMDPAR (Dixon 1990) for nonlinear models. Finally, for significant equations, we used an independent data set from the same site (but from a different study) and correlated actual values with those predicted by the models. The independent data came from plots that were weeded to exclude other species but did not have the density of competitor stems reduced. However, the range of LAI and competitor biomass was large and within the limits of values used in the generation of our regression equations. All analyses were conducted with a significance level of 0.05.

Results and discussion

Random weeding of plots to different initial densities gave a wide range of values for each competitor species at each site. However, species–site combinations gave quite different means. Pin cherry plots (mean = 545 g) had more than twice the biomass of striped maple plots (mean = 216 g) at Fletcher Mountain. Each species had only half as much biomass (pin cherry = 147 g; striped maple = 117 g) at Mount Abraham as at Fletcher Mountain. Correlations among total competitor biomass, LAI, leaf biomass, and stem biomass were all significant and high ($r = 0.86–0.99$), indicating that any of them could be used equally well to represent the degree of competition on a plot. We focused on LAI because of its potential ease of measurement under field conditions (Pierce and Running 1988) and its proven utility in other studies (MacDonald *et al.* 1990). Although Brand (1986*b*) did not find LAI necessary in his competition index, he did say that LAI was strongly correlated with brush cover (which was in his index) and thus did not explain any additional variability. Furthermore, because leaves provide shade, have a strong influence on transpiration, and contain much of a young plant's nutrients, there are strong biological reasons why LAI is a good choice for measuring competitors.

The red pine seedlings were very similar in height (means = 15.3–15.8 cm) and diameter (means = 3.0–3.2 mm) at root collar at the time of planting on all species–site combinations. This homogeneity of original heights and diameters may explain why they were not significantly correlated with final biomass for any of the species–site combinations and were seldom significantly correlated with other pine seedling variables. However, many of the seedling variables were significantly correlated, although the strengths of relationship were highly variable. Thus, choice of a variable to use for measuring growth response to competition was important.

We calculated the correlation coefficients between all pine seedling variables at time of harvest and competitor LAI. When calculating so many correlations, occasional spurious individual correlations are expected, so it is more appropriate to look for patterns than to rely on any one specific correlation. One obvious trend was that red pine seedling size was not significantly correlated with competitor LAI on either pin cherry or striped maple plots at Mount Abraham. In contrast, most red pine variables were significantly and negatively correlated with competitor LAI at Fletcher Mountain. An exception to these two generalizations was that SLA of new red pine needles was significantly and positively correlated ($r = 0.43–0.75$) with competitor LAI on all species–site combinations.

Height of red pine seedlings was never significantly correlated with competitor LAI. Although height is often measured by field foresters to assess competitive response, studies on a variety of coniferous species do not show a consistent height response to competition (Brand 1990; Eissenstat and Mitchell 1983; Gratkowski and Lauterbach 1974; Haywood 1986; Jaramillo 1988; Morris *et al.* 1990; Neary *et al.* 1990; Parker and Yoder-Williams 1989; Stone 1980; Tiarks and Haywood 1986). Several possible reasons exist for the lack of height response to competition at our sites. For example, perhaps the competition was not yet strong enough to influence height growth. Because shoot elongation in determinate species is very dependent on conditions of the previous year, height after two growing seasons would only reflect the 1st year's competition, which was not very great on either site (personal observation). It is also possible that carbon allocation to terminal-shoot elongation has high priority for these shade-intolerant seedlings (Daniel *et al.* 1979), and thus they allocate even scarce resources to height first. However, we do not have data to test the various possible explanations.

Given the above, we looked at two forms of relationships between competitor LAI and pine seedling variables to determine if species or site differences existed. We chose SLA of new needles as one response variable and compared regression equations across all four species–site combinations. The other response variable was red pine seedling biomass (but only for Fletcher Mountain) because it was one of the most negatively correlated ($r = -0.61$ to -0.74) variables with competitor LAI.

A total of 110 cases were available for testing the relationship of LAI and SLA (one case with an SLA 50% greater than the next highest SLA was excluded because it was so inconsistent with the other 110 values). A comparison of slopes and intercepts across the four species–site combinations indicated that there were no significant differences, and residuals showed no patterns so the four data sets were combined (Table 1). The resulting equation (Fig. 1) was highly significant ($p < 0.001$) but the r^2 was relatively low (0.32). The positive relationship with competitor LAI could indicate a phenotypic response (more foliage surface area per unit of leaf biomass) to the shade provided by competitors. Brand (1986*a*) also found that SLA was a good indicator of competitive stress.

The relationship between LAI and pine seedling biomass at Fletcher Mountain involved 57 cases. The regression line for competitor LAI and red pine seedling biomass was best described by a nonlinear model ($Y = ae^{bX}$), which we chose because it gave a random distribution of residuals (linear models tended to underestimate seedling biomass at low competitor LAI), could be transformed ($\ln(Y) = a + bX$) and thus used to compare between data sets, and had a better fit (larger r^2 and smaller standard error) than a straight line. However, other forms, such as the hyperbolic model ($Y = a/[1 + bX]$) used by Goldberg and Fleetwood (1987), gave equally good results. There were no statistically significant differences with

TABLE 1. Analysis of variance of regression between pine seedling SLA and competitor LAI for four species–site data sets

	df	MS	F	p	r^2	SEE	df	MS	F	p	r^2	SEE
	Mount Abraham						**Fletcher Mountain**					
Pin cherry plots												
Regression	1	672.46	5.29	0.03	0.18	11.28	1	3431.00	29.61	0.000	0.52	10.77
Residual	24	127.24					27	115.89				
Striped maple plots												
Regression	1	577.50	6.22	0.02	0.19	9.64	1	786.61	6.57	0.017	0.21	10.94
Residual	26	92.90					25	119.69				
Comparison of regressions over groups with residuals within groups												
Regression	6	92.86	0.82	0.56								
Residuals	102	113.63										
Combined plots (n = 110)												
Regression	1	5785.79	51.44	0.00	0.32	10.61						
Residual	108	112.48										

NOTE: Because the intercepts and slopes of the four equations were not significantly different, the data sets were combined. df, Degrees of freedom; MS, mean square; p, probability; SEE, standard error of estimate.

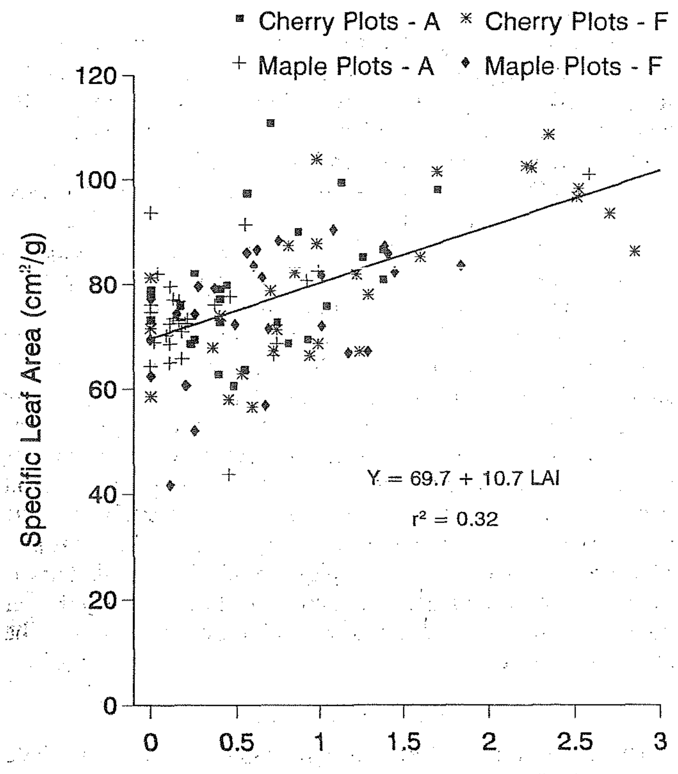

FIG. 1. Regression line of specific leaf area of red pine seedlings versus leaf area index of competitors on pin cherry plots and striped maple plots on Mount Abraham (A) and Fletcher Mountain (F).

respect to intercept and slope between the two competitor species, so the two data sets were combined (Table 2). The resulting equation (Fig. 2) had an r^2 of 0.53 and was highly significant ($p < 0.001$).

The independently derived values for pine seedling biomass and SLA of current needles were compared with those predicted from our regression equations. The correlation coefficient between observed and predicted was 0.65 ($n = 32$; $p < 0.001$) for the biomass model and thus seemed to be robust for these sites and species. However, correlation between observed and predicted was 0.25 ($n = 57$; $p = 0.064$) for the SLA model. Although this was not surprising given the low r^2 and high standard error of that model, it makes us less certain about the robustness of our SLA model.

We were unable to distinguish any differences in competitive effect between striped maple and pin cherry other than those due to LAI. This concurs with the prediction of Goldberg and Werner (1983), whose subsequent studies with herbaceous plants varied in terms of support for the hypothesis (Goldberg 1987; Goldberg and Fleetwood 1987). Although other studies have shown species differences in competitive effects (e.g., Cain 1988; Smith 1989; Warren *et al.* 1987), it is not clear whether those differences were due to variation in biomass among species or something else. However, it should be noted that our conclusion is dependent on regression lines not being statistically different, which in turn is related to the strength of the relationship, and thus to the confidence interval around the regression coefficients. In the case of predicting SLA, the relationship was weak, so it cannot be considered strong evidence supporting the lack of a species effect. The relationship for seedling biomass was higher, but still left 47% of the variation unexplained.

The results of this research suggest that the effects of competition were not consistent between our two sites, which other studies have also shown (Cole and Newton 1987; Eissenstat and Mitchell 1983; Glover *et al.* 1989; Sims and Mueller-Dombois 1968). This may have been due simply to the slower growth of species at Mount Abraham than at Fletcher Mountain. Competitors had about twice as much biomass on Fletcher Mountain plots used in this study, and red pine seedlings growing in completely weeded plots in a separate study had about one-third more biomass per seedling at Fletcher Mountain (Elliott 1991). With its higher elevation, shallower soil, and poorer drainage (personal observation), Mount Abraham is a harsher site for plant growth. Consequently, competitor leaf area and biomass may not have been large enough to significantly affect the light, nutrient, and water availability known to affect red pine growth (Alban 1971; Strothmann 1967; Wilde *et al.* 1968). However, the

TABLE 2. Analysis of variance of regression between ln(seedling biomass) and competitor LAI for pin cherry and striped maple plots at Fletcher Mountain

	df	MS	F	p	r^2	SEE	df	MS	F	p	r^2	SEE
			Pin cherry plots						**Striped maple plots**			
Fletcher Mountain plots												
Regression	1	3.25	46.77	0.00	0.63	0.26	1	1.48	15.65	0.00	0.39	0.31
Residual	28	0.07					25	0.10				
Comparison of regressions over groups with residuals within groups												
Regression	2	0.05	0.62	0.54								
Residuals	53	0.08										
Combined plots ($n = 57$)												
Regression	1	5.01	62.49	0.00	0.53	0.28						
Residual	55	0.08										

NOTE: Because the intercepts and slopes of the two equations were not significantly different, the data sets were combined. df, Degrees of freedom; MS, mean square; p, probability; SEE, standard error of estimate.

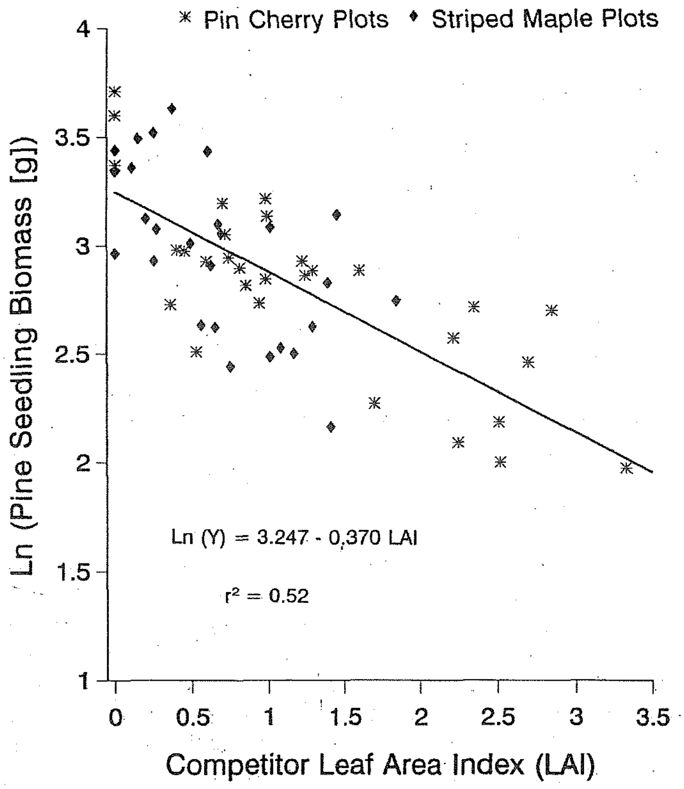

FIG. 2. Regression line of the natural log of red pine seedling biomass (aboveground) versus leaf area index of competitors on pin cherry plots and striped maple plots on Fletcher Mountain.

mean (0.76) and range (0.11–1.84) of striped maple LAI at Fletcher Mountain were very similar to the mean (0.72) and range (0.17–1.70) of pin cherry LAI at Mount Abraham, yet the correlation between competitor LAI and red pine seedling biomass was statistically insignificant at Mount Abraham, whereas it was significant at Fletcher Mountain. If relationships were consistent between sites and species, competition should have had a stronger effect on red pine growth in the Mount Abraham pin cherry plots. This difference between sites may be due to different ratios of available resources (e.g., light, nutrients, and water), which Tilman (1988) suggests could change the nature and outcome of competition between species. Alternatively, some factor such as temperature could have had a stronger effect on red pine growth at Mount Abraham than did the competitors, thus accounting for the lack of significant competition effects.

From a practical perspective, we suggest that competitor LAI and seedling root collar diameter may be useful variables for predicting early competitive effects. LAI can potentially be estimated readily by field instruments such as the Decagon sunfleck ceptometer (Pierce and Running 1988) and the Li-Cor LAI-2000 (Gower and Norman 1991). Although we used seedling biomass as a response variable at Fletcher Mountain, its high correlation (0.84) with root collar diameter suggests that the latter could be used for quick, nondestructive field surveys. The strength of relationships may be improved by incorporating microsite factors and site characteristics. When possible, studies should follow the plots for several years. Our study used data obtained 2 years after harvesting and planting because that is when many vegetation management decisions are made. However, the lack of significant correlations between competitors and red pine seedlings at Mount Abraham may be a reflection of the short duration (relative to observed growth rates) of this study. Finally, different plot sizes and (or) variable radius plots should be tested. This is especially important if relationships are to be followed over time because both competitors and crop species will be changing in size.

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