Critical period of interspecific competition for northern conifers associated with herbaceous vegetation[1]

Robert G. Wagner, Gina H. Mohammed, and Thomas L. Noland

Abstract: Using critical-period analysis, we examined the temporal effects of interspecific competition from herbaceous vegetation on seedlings of jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), and black spruce (*Picea mariana* (Mill.) BSP) during the first 5 years after planting. The critical period is the time period during stand development when interspecific competition reduces tree growth. We found both similarities and differences in responses among tree species. Gains in stem volume index associated with increasing duration of vegetation control (expressed by weed-free curves) differed among species. In contrast, declines in stem volume index with increasing duration of competition after planting (expressed by weed-infested curves) were equal among species. Critical periods for stem volume index were shorter for shade-intolerant jack and red pine (1 and 2 years after planting) than for more shade-tolerant white pine and black spruce (1–3 years for spruce and 1–4 years for white pine). Intolerant species had greater absolute stem volume growth, but smaller relative declines from continuous association with herbaceous vegetation (85, 81, 78, and 67% for white pine, black spruce, red pine, and jack pine, respectively). Herbaceous vegetation did not affect survival and had a variable influence on height growth of all species.

Résumé : Les auteurs ont examiné, à l'aide de l'analyse de la période critique, les effets temporels de la concurrence interspécifique de la végétation herbacée sur les semis du pin gris (*Pinus banksiana* Lamb.), du pin rouge (*Pinus resinosa* Ait.), du pin blanc (*Pinus strobus* L.) et de l'épinette noire (*Picea mariana* (Mill.) BSP), durant les cinq premières années qui ont suivi la plantation. La période critique est une période, au cours de l'évolution du peuplement, durant laquelle la concurrence interspécifique réduit la croissance de l'arbre. Les auteurs ont trouvé des ressemblances et des différences quant à la réponse des différentes espèces d'arbres. L'indice du volume de la tige a enregistré, chez les différentes espèces, différents gains avec l'augmentation de la durée du contrôle de la végétation, exprimée par les courbes d'absence de mauvaises herbes. Par contraste, la diminution de l'indice du volume de la tige avec l'augmentation de la durée de compétition après la plantation, exprimée par les courbes d'infestation par les mauvaises herbes, était égale chez les différentes espèces. La période critique pour l'indice du volume de la tige était plus courte chez les pins gris et rouge, intolérants à l'ombre, (1 et 2 ans après la plantation) que chez le pin blanc et l'épinette noire, plus tolérants à l'ombre, (1–3 ans pour l'épinette et 1–4 ans pour le pin blanc). Les espèces intolérantes présentaient une plus forte croissance absolue du volume de la tige, mais une diminution relative du même indice plus faible, résultant d'une association continue avec la végétation herbacée (85, 81, 78 et 67% pour le pin blanc, l'épinette noire, le pin rouge et le pin gris, respectivement). La végétation herbacée n'a pas affecté la survie des espèces et son influence sur leur croissance en hauteur était variable.

[Traduit par la Rédaction]

Introduction

Optimizing vegetation-management strategies in young forest plantations requires an understanding of how the temporal effects of interspecific competition affect seedling survival and growth. Most research on interspecific competition in forest plantations, however, has focused on the effects of density or other spatial factors (Stewart et al. 1984; Walstad and Kuch 1987). Efforts to develop competition indices for young trees also have not adequately accounted for the temporal effects of surrounding vegetation (Burton 1993; Wagner 1993).

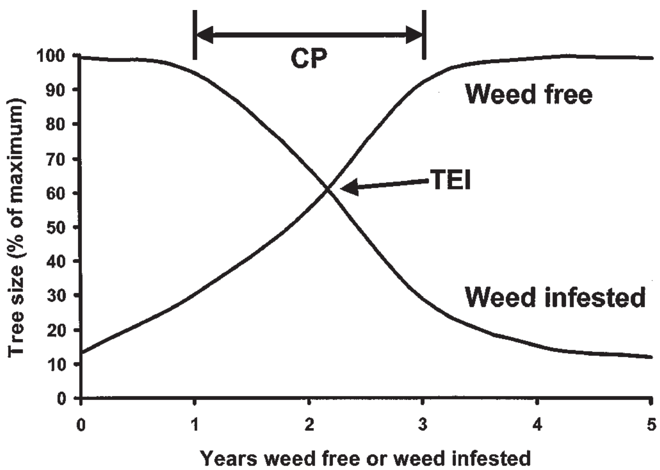
The critical-period concept, first developed in agriculture in the late 1960s (Zimdahl 1988), defines the time period during crop development when interspecific competition occurs between weed and crop plants. In practical terms, the critical period (CP) defines when during crop development weeds must be controlled to prevent significant losses in crop yield. Recent work in agriculture has focused on developing the CP for a wide range of agricultural crops (Weaver and Tan 1983; Weaver 1984; Zimdahl 1988; Hall et al. 1992;

Received August 24, 1998. Accepted March 20, 1999.

R.G. Wagner.[2] Department of Forest Ecosystem Science, 5755 Nutting Hall, University of Maine, Orono, ME 04469–5755, U.S.A. e-mail: Bob_Wagner@umenfa.maine.edu
G.H. Mohammed and T.L. Noland. Ontario Forest Research Institute, 1235 Queen Street East, Sault Ste. Marie, ON P6A 2E5, Canada.

[1]Main Agricultural and Forestry Experiment Station External Publication 2349.
[2]Corresponding author.

Fig. 1. Hypothetical relationship between years weed-free or weed-infested for 5 years after planting and percent of maximum tree size. The weed-free curve defines the length of time vegetation control must be maintained after planting to achieve maximum tree size. The weed-infested curve defines how tree size decreases with increasing numbers of years after planting before vegetation control is initiated. The critical period (CP) defines when vegetation control must be used (years 1–3 in example) to avoid reductions in tree size. The time of equal interference (TEI) defines where the influence of interspecific competition on tree size is equal under both the weed-free and weed-infested treatment regimes.



van Acker et al. 1993; Woolley et al. 1993; Singh et al. 1996).

The CP has been identified as an important component of integrated weed management for agriculture (Swanton and Weise 1991). Development of integrated forest vegetation management strategies also will require better identification of the site and vegetation conditions that are likely to benefit most from control measures (Wagner 1994). Identifying the conditions likely to benefit most from treatment is important for minimizing management interventions and more cost effectively prescribing vegetation control treatments.

The CP is composed of two components (Weaver and Tan 1983). The first, described by a weed-free curve, is the length of time weed control efforts must be maintained after crop establishment to prevent yield loss. The second component, described by a weed-infested curve, is the length of time weeds can remain in a crop before they interfere with crop growth and reduce yield. The CP is determined by the linear distance between the points where yield declines significantly on the weed-infested curve and yield levels off on the weed-free curve (Fig. 1). In practical terms, it is the time period between the point when interspecific competition begins to reduce crop yield and the point when additional vegetation control no longer increases crop yield. The point of intersection between weed-free and weed-infested curves identifies the time of equal interference (TEI) where yield loss from interspecific competition is equal under both temporal regimes (Cousens 1988; Singh et al. 1996). Wagner et al. (1996) describe the range of hypothetical outcomes possible for these relationships.

Critical-period research to date has focused almost exclusively on annual cropping systems. We found no work specifically identifying critical periods for forest stands. There have, however, been limited efforts to inadvertently quantify the weed-free (Lanini and Radosevich 1986; Newton and Preest 1988; Lauer et al. 1993) and weed-infested (Duba et al. 1985) components in separate studies with forest trees.

Our objective was to identify and compare the CP of herbaceous vegetation control for planted jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), and black spruce (*Picea mariana* (Mill.) BSP), during the first 5 years after planting. These four conifer species were selected because they vary widely in shade tolerance, occupy a range of ecological roles in forest succession and have considerable economic importance in the region.

Tolerance is defined as the relative capacity of a tree species to compete under low light and high root competition (Daniel et al. 1979). Jack pine, red pine, eastern white pine, and black spruce are rated as very intolerant, intolerant, intermediate, and tolerant, respectively. Jack pine and red pine are early successional species, while white pine and black spruce tend to be associated with later successional stages (Johnson 1994). We hypothesized that intolerant conifer species would have a higher growth rate and benefit more from early control of herbaceous vegetation than more tolerant species.

Methods

Study site

A site with sandy-textured soil in the Great Lakes – St. Lawrence forest type was selected 50 km north of Sault Ste. Marie, Ont., Canada. The site was clearcut harvested during 1987–1989. In July 1991, shortly before the site was selected for study, a Donaren disk trencher created trenches 1.5 m wide and 2–3 m apart.

Shortly after site preparation, herbaceous vegetation dominated by bracken fern (*Pteridium aquilinum* (L.) Kuhn), false melic grass (*Schizachne purpurascens* (Torrey) Swallen), rough mountain rice grass (*Oryzopsis asperifolia* Michaux), violets (*Viola* spp.), and low sweet blueberry (*Vaccinium angustifolium* Ait.) rapidly occupied the site. Low densities of trembling aspen (*Populus tremuloides* Michx.) from root suckers also were present.

Experimental design

Jack pine, red pine, eastern white pine, and black spruce seedlings were planted in a randomized complete block, split-plot design with 10 treatments and 4 blocks (replications) on the site. Each main plot is 28 × 28 m (0.0784 ha) in size and divided into four 14 × 14 m subplots to which each conifer species was randomly assigned. Thirty trees (five rows of six trees) of each species were planted on 2 × 2 m spacing in each subplot. A total of 1200 seedlings of each species (4800 total) were planted at the start of the experiment. A 2 m wide buffer, without planted trees, was placed around each subplot. To ensure that the seedlings were associated with a maximum abundance of herbaceous vegetation from the start of the experiment, all trees were planted in the undisturbed areas between the trenches, rather than on the inside edge of trenches as is the usual practice.

Planting stock of each species was obtained for the seed zone from local nurseries and planted with shovels in mid-May 1992. Stock types obtained for each species were jack pine, container, multipot 67 with 57 cm^3 volume (height 10.7 cm, stem diameter 3.1 mm); red pine, 2+0 medium bare-root (height 9.2 cm, stem diameter 4.3 mm); white pine, G (greenhouse transplant) +1.5 medium bare-root (height 9.5 cm, stem diameter 4.9 mm); and black spruce, G+2 medium bare-root (height 29.3 cm, stem diameter 5.2 mm). These stock types are typical of those used for these species when planted on similar sites in Ontario.

Vegetation treatments

Herbaceous vegetation (grasses, ferns, and forbs) was controlled in a sequential pattern on each main plot for the first 5 years after tree planting to provide tree responses for the two components of the critical-period analysis (Fig. 1). Ten vegetation treatments were used: no vegetation control; annual vegetation control; 1, 2, 3, and 4 years of consecutive control after planting; and waiting 1, 2, 3, and 4 years after planting before annual control was initiated.

The treatment sequence began immediately after the trees were planted in June 1992. Vegetation was controlled using a broadcast application (by backpack sprayer) of glyphosate herbicide (Vision®) at 2 kg/ha of active ingredient in 93 L/ha water. Applications were made at the beginning of each growing season when vegetation had developed sufficient leaf area to receive the herbicide (generally the second or third week of June). All aspen on the plots was removed in 1992 by treating them with the same glyphosate mixture and manually cutting the stems several weeks after treatment. Because conifers are susceptible to injury from glyphosate at this time of year, all trees were protected with paper cups or plastic bags during herbicide application.

Variables measured

In October of each year, the survival and growth (height and ground-line stem diameter) of all trees were recorded. Stem volume index (stem diameter^2 × height) and height/stem diameter ratio (H/D) were calculated using height and stem diameter measurements from each tree.

Composition and abundance of all herbaceous vegetation in the 28 × 28 m main plots were collected between late August and early September of each year. Species and percent cover (ocularly estimated to the nearest 5%) were recorded for each plant species on six 1-m^2 (0.5 × 2 m) plots that were systematically located with a random start from the corner of each main plot.

Analytical approach

Mean tree survival and growth were examined for each species among the 10 treatments using a ANOVA and Waller – Duncan Bayes means separation test (k ratio = 100). Mean responses for seedlings in each subplot (experimental unit) were used for all analyses. All tree variables were tested for normality and homogeneous variances. Natural logarithmic transformation of stem diameter, stem volume index (SVI), and H/D was used for correction. Tree height did not require transformation. An arcsine transformation was used for percent survival.

Based on the analysis of treatment effects, SVI was identified as among the most responsive variables to treatment. In addition, stem volume is a variable of particular interest to forest managers. Therefore, SVI was used to develop the weed-free and weed-infested curves for each tree species.

Nonlinear regression analysis was used to derive the weed-free and weed-infested curves for the SVI of each tree species. Each equation was estimated using the means from 24 subplots (6 treatments × 4 replications). The number of trees per subplot averaged 22, 20, 26, and 25 for jack pine, red pine, white pine, and black spruce, respectively, in year 5.

Cousens (1988) suggests use of Gompertz equation and a rectangular hyperbola for critical-period analyses. Hall et al. (1992) and Singh et al. (1996) found a logistic function to provide the best fit. We found a logistic function generally provided the best fit for weed-free curves and a negative exponential function the best fit for weed-infested curves. After deriving the best regression equations for weed-free and weed-infested curves, the TEI was calculated for each species by identifying the time where SVI was equal for both functions.

Because similar negative exponential functions were found for the weed-infested curves of each conifer species, we compared the slopes of the equations to determine whether they were different among species. A full model (separate equations for each species) was compared with a reduced model (one equation with separate intercepts for each species and the same slope for all species) using an F test. The F statistic was calculated using the ratio of the difference between the residual sum of squares for the reduced and full models to the residual sum of squares for the full model divided by the appropriate degrees of freedom (Seber 1977). The P value was calculated as a percentile of the F distribution with the respective degrees of freedom.

Using orthogonal contrasts, the CP for each tree species was determined based on where along the weed-free and weed-infested curves there was a difference ($P < 0.05$) in SVI from 5 years weed-free and 0 years weed-infested, respectively. We considered approaches for deriving the CP used by other authors (Cousens 1988; Hall et al. 1992; Singh et al. 1996). Although confidence intervals or derivatives of the regression models can be used to derive a more precise fractional year where the CP might be established, the nature of vegetation management in the perennial forest system we examined is generally restricted to vegetation control activities during individual growing seasons. We felt, therefore, that estimating the CP based on integer years was a more appropriate approach.

As the rate of stem volume growth over the 5-year treatment period likely provides among the better indications of longer term trends in tree growth, we modeled the growth in SVI over the 5 years. Regression models for SVI of each species on each treatment and replication over the 5 years were developed using surviving trees (average of 22, 20, 26, and 25 for jack pine, red pine, white pine, and black spruce, respectively) from the original 30 that were planted in each subplot. We found a log–linear model provided a robust linear model of SVI growth across treatments and tree species. The slope values derived from this analysis were subjected to ANOVA and Waller – Duncan Bayes means separation test (k ratio = 100) to quantify different growth trends among the treatments.

Results

Patterns of herbaceous vegetation development

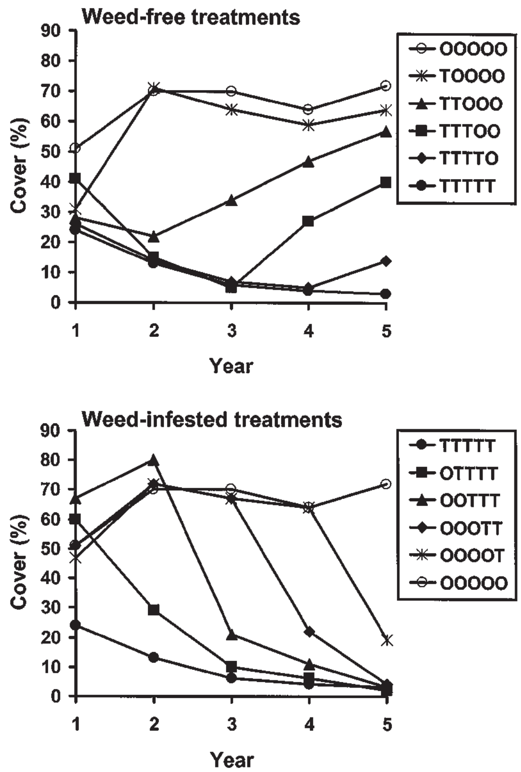
Since glyphosate is not soil active, herbaceous vegetation was able to recover in the year following each herbicide application. The sequence of treatments provided varying patterns of disturbance and recovery of herbaceous vegetation during the 5 years of study (Fig. 2), thus differing patterns of exposure to interspecific competition for all conifer seedlings. Cover of herbaceous vegetation achieved a maximum of 70% without vegetation control and repeated control achieved minimum cover values of less than 5%.

Tree size and survival response

Fifth-year survival was not reduced ($P = 0.24$) by herbaceous vegetation for any of the conifer species (Table 1). Survival averaged 66, 72, 85, and 82% for red pine, jack pine, white pine, and black spruce, respectively, across treatments.

Tree height among treatments was variable (Table 1) but revealed minor increases for red pine ($P = 0.002$), white pine ($P = 0.001$), and spruce ($P = 0.0002$) with increasing duration of vegetation control. Jack pine (165 cm) was taller

Fig. 2. Patterns of herbaceous vegetation cover resulting from treatments used to produce the weed-free and weed-infested curves. The sequence of herbaceous vegetation removal each year was coded as follows: T, herbicide treated; O, untreated.



(P < 0.05) than spruce (111 cm). Red pine (96 cm) and white pine (95 cm) were not different (P > 0.05), but smaller (P < 0.05) than jack pine and spruce.

Stem diameter and SVI were the most responsive variables to treatment (Table 1), decreasing substantially (P < 0.0001) when all conifer species were associated with herbaceous vegetation for increasing periods of time. Association with herbaceous vegetation for 5 years (OOOOO) reduced SVI of white pine, black spruce, red pine, and jack pine by 85, 81, 78, and 67%, respectively, relative to plots with five continuous years of vegetation control (TTTTT).

The H/D decreased (P < 0.0001) with increasing years of vegetation control for all species (Table 1). The H/D after 5 continuous years of vegetation control (TTTTT) was 26, 26, 29, and 32 for white pine, red pine, jack pine, and black spruce, respectively. Without vegetation control (OOOOO), H/D increased to 46, 40, 55, and 55 for white pine, red pine, jack pine, and black spruce, respectively.

Weed-free and weed-infested curves

The weed-free and weed-infested curves for SVI are shown in Fig. 3. The R^2 for the weed-free curves ranged from 0.55 to 0.76 (Table 2). The weed-free curves were best described using a logistic function (except for white pine which was linear) and were more varied among conifers, suggesting a species-specific response to increasing duration of vegetation control. The R^2 for weed-infested curves ranged from 0.53 to 0.88. The slopes of the negative-exponential, weed-infested curves were equal (P = 0.21) for all conifer species, indicating the same rate of decline in stem volume for every year of delay in controlling herbaceous vegetation after planting.

Despite differences in the weed-free and weed-infested curves, the TEI occurred between 1 and 2 years for all species. Solving for the equations in Table 2, the TEI was 1.36, 1.73, 1.94, and 1.81 for jack pine, red pine, white pine, and black spruce, respectively.

Critical periods

Results from the orthogonal contrasts of SVI for the treatments revealed different CPs among conifer species (Fig. 3). Jack and red pine had the shortest CP, occurring during the first and second years after planting. Black spruce had a CP from 1 to 3 years after planting. White pine benefitted most from an increasing duration of vegetation control, having a linear weed-free curve and the longest CP among species, ranging from 1 to 4 years.

Stem volume growth

Analysis of slope coefficients for log–linear models of SVI growth over the 5 years revealed that all four conifer species had different ($P \leq 0.05$) growth rates (Table 3). However, similar groupings of slope values among treatments indicated that competition from herbaceous vegetation had similar effects among conifer species. Three general groupings of treatments emerged from this analysis. Treatments TTOOO, TTTOO, TTTTO, TTTTT, and OTTTT had the steepest slopes and were generally not different (P > 0.05), indicating that 2 or 3 years of treatments in earlier years produced stem volume growth rates equal to that of treatments with 4 or 5 years of continuous treatments. Lower growth rates were produced by treatments TOOOO, OOOTT, and OOTTT, and they were not generally different (P > 0.05) from one another, suggesting that a single treatment immediately after planting produced a response equal to 2 or 3 years of control when delayed. Treatments OOOOO and OOOOT produced the lowest growth rates.

Discussion

Competition from herbaceous vegetation had strong influences on stem diameter, SVI, and H/D of all conifer species during the first 5 years after planting. However, height growth was less sensitive, and survival was not affected. Insensitivity of height growth relative to diameter growth has been generally observed in other studies (Zedaker et al. 1987). Increases in stem diameter with decreasing vegetation abundance, and the insensitivity of height growth relative to diameter, have been documented in other studies with these tree species (Morris et al.1990; Brand 1991; MacDonald and Weetman 1993). The H/D values have generally been found to increase when tree seedlings are shaded by neighboring plants (Cole and Newton 1987; Lieffers and Stadt 1994).

We found both similarities and differences among tree species in their response to interspecific competition from herbaceous vegetation based on their tolerance rating. The absolute rate of stem volume growth decreased with increasing tolerance (jack pine > red pine > white pine > black spruce). Differences associated with tolerance also were observed in the shape of the weed-free curves, length of the CP,

Table 1. Fifth-year survival, height, stem diameter, stem volume index, and height/diameter ratio for jack pine, red pine, white pine, and black spruce under 10 patterns of herbaceous vegetation removal.

Herbaceous vegetation control treatment	Survival (%)	Height (cm)	Stem diameter (mm)	Stem volume index (cm^3)	Height/diameter ratio
Jack pine					
OOOOO	74*a*	164.6*abcd*	30.7*e*	1871.8*c*	55.0*a*
TOOOO	78*a*	179.6*abc*	37.7*cd*	3095.9*bc*	49.2*b*
TTOOO	64*a*	190.3*a*	50.5*ab*	5364.3*a*	38.4*c*
TTTOO	77*a*	181.4*ab*	53.5*a*	5498.7*a*	34.3*d*
TTTTO	76*a*	170.5*abc*	57.9*a*	6084.8*a*	29.8*f*
TTTTT	79*a*	164.9*abcd*	57.3*a*	5735.7*a*	29.1*f*
OTTTT	60*a*	153.8*cd*	51.4*ab*	4504.3*ab*	30.2*ef*
OOTTT	72*a*	141.7*d*	43.1*bc*	3002.1*bc*	33.2*de*
OOOTT	76*a*	154.5*cd*	41.1*c*	2992.1*bc*	38.1*c*
OOOOT	67*a*	156.2*bcd*	34.1*de*	2303.8*c*	47.0*b*
Red pine					
OOOOO	53*a*	76.6*c*	19.5*e*	400.1*d*	39.8*a*
TOOOO	73*a*	88.5*bc*	22.3*de*	585.4*cd*	40.5*a*
TTOOO	73*a*	108.3*a*	32.3*bc*	1385.8*ab*	34.2*b*
TTTOO	74*a*	114.9*a*	36.9*ab*	1911.2*a*	31.1*cd*
TTTTO	78*a*	111.1*a*	40.0*a*	2069.2*a*	27.8*ef*
TTTTT	62*a*	97.8*ab*	37.2*ab*	1792.8*ab*	26.1*f*
OTTTT	64*a*	99.0*ab*	36.5*ab*	1614.2*ab*	27.2*ef*
OOTTT	65*a*	87.7*bc*	18.9*bc*	969.0*bc*	28.9*de*
OOOTT	58*a*	84.8*bc*	26.4*cd*	735.8*c*	32.2*bc*
OOOOT	64*a*	88.6*bc*	22.9*de*	585.2*cd*	38.9*a*
White pine					
OOOOO	83*a*	82.0*cd*	17.9*h*	326.8*f*	46.1*a*
TOOOO	81*a*	96.8*abc*	26.3*ef*	799.9*de*	37.9*bc*
TTOOO	87*a*	108.4*a*	30.2*de*	1206.6*c*	36.9*c*
TTTOO	85*a*	107.0*a*	33.4*cd*	1442.9*bc*	33.1*d*
TTTTO	91*a*	97.0*abc*	38.6*ab*	1719.8*ab*	25.4*g*
TTTTT	87*a*	107.1*a*	42.3*a*	2129.5*a*	25.6*g*
OTTTT	88*a*	99.8*ab*	36.4*bc*	1651.7*ab*	27.6*fg*
OOTTT	77*a*	90.1*bcd*	30.9*d*	1065.3*cd*	29.2*ef*
OOOTT	80*a*	78.9*d*	25.6*f*	671.6*e*	31.1*de*
OOOOT	87*a*	85.8*bcd*	21.0*g*	472.0*f*	41.6*ab*
Black spruce					
OOOOO	83*a*	98.8*de*	18.6*f*	407.5*e*	54.6*a*
TOOOO	85*a*	111.8*bcd*	21.7*ef*	687.9*d*	53.9*a*
TTOOO	78*a*	119.3*ab*	29.6*bc*	1337.7*b*	42.7*bc*
TTTOO	80*a*	129.2*a*	33.8*ab*	1775.3*ab*	40.3*c*
TTTTO	76*a*	120.2*ab*	38.9*a*	2145.2*a*	32.2*e*
TTTTT	93*a*	120.2*ab*	38.7*a*	2118.0*a*	32.3*e*
OTTTT	79*a*	113.9*bc*	33.3*b*	1507.8*ab*	35.3*d*
OOTTT	76*a*	97.2*e*	28.7*c*	952.4*c*	36.0*d*
OOOTT	84*a*	97.6*e*	26.1*cd*	886.0*cd*	39.4*c*
OOOOT	82*a*	102.2*cde*	23.0*de*	687.2*d*	45.9*b*

Note: Sequence of herbaceous vegetation removal each year was coded as follows: T, herbicide treated; O, untreated. Values with different letters within a species and variable indicate a difference ($P \leq 0.05$) between treatments.

and relative gain in stem volume from repeated vegetation control. The weed-free curves for the more intolerant species (jack and red pine) had a steeper slope and quickly leveled off after 2 years of control. In contrast, the intermediate and tolerant species (white pine and black spruce) continued to increase in SVI with increasing years of vegetation control. This difference resulted in a shorter CP (1 and 2 years) for jack and red pine and a longer CP (1–3 or 4 years) for spruce and white pine. Therefore, the intolerant conifers required fewer years of vegetation control to achieve maximum size than the more tolerant conifers. Relative increases in SVI from continuous vegetation control also were greater for the tolerant (651% for white pine, 519% for black spruce) than intolerant conifers (448% for red pine, 306% for jack pine).

Fig. 3. Weed-free and weed-infested curves for jack pine, red pine, white pine, and black spruce based on 5-year SVI (cm^3). Equations for curves are shown in Table 2. Line indicated by CP is the critical period. The CP was determined by identifying which number of years weed free and weed infested were different ($P \leq 0.05$) from 5 years weed free and 0 years weed infested, respectively.

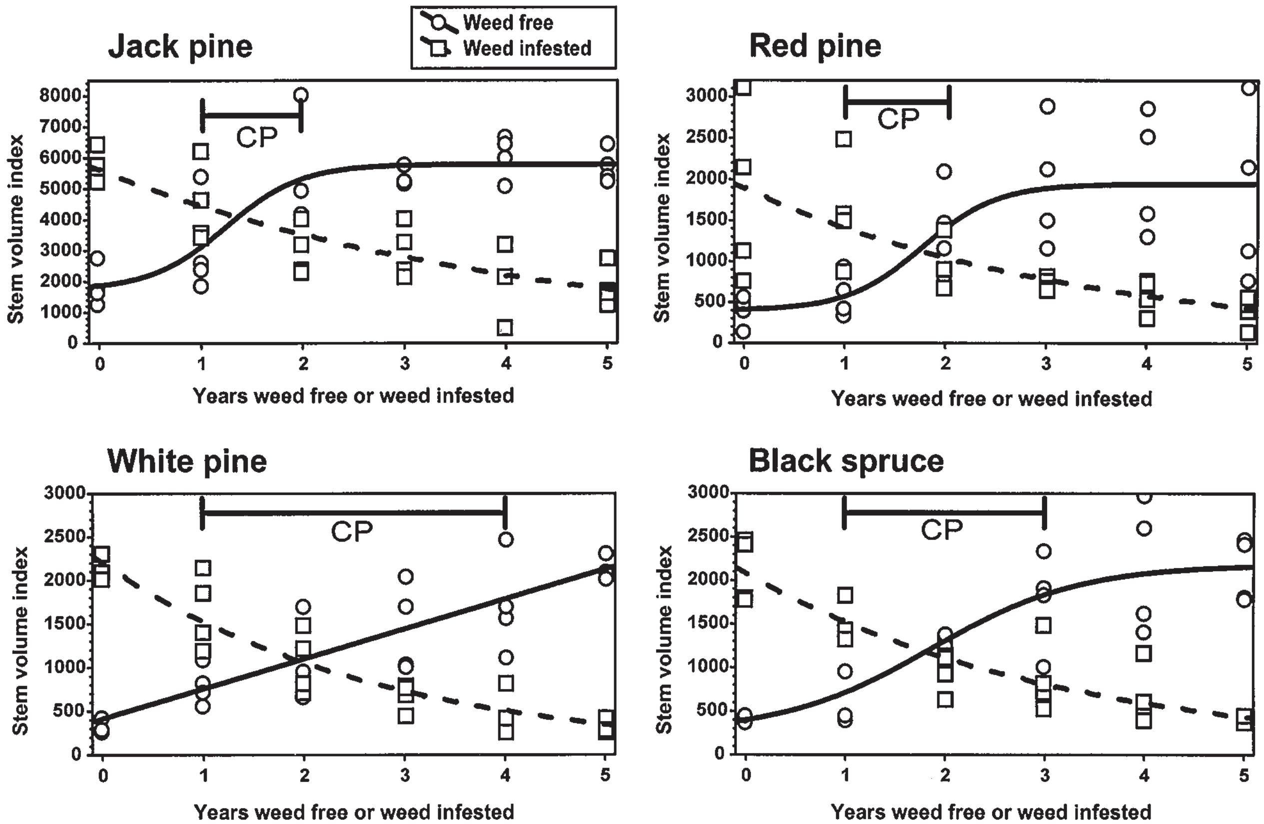


Table 2. Regression equations for weed-free and weed-infested curves for 5-year stem volume index for each conifer species.

Tree species	Relationship	Equation	MSE	R^2
Jack pine	Weed free	$SVI = 1732.7 + 4064.9/(1 + e^{-2.7(t-1.25)})$	1 097 233	0.72
	Weed infested	$SVI = 5617.7\ e^{-0.233}$	798 931	0.70
Red pine	Weed free	$SVI = 399.0 + 1542.7/(1 + e^{-2.69(t-1.77)})$	403 397	0.55
	Weed infested	$SVI = 1887.1\ e^{-0.296t}$	243 297	0.53
White pine	Weed free	$SVI = 413.1 + 343.1t$	125 474	0.75
	Weed infested	$SVI = 2196.9\ e^{-0.368t}$	62 006	0.88
Black spruce	Weed free	$SVI = 254.3 + 1925.5/(1 + e^{-1.34(t-1.87)})$	168 556	0.76
	Weed infested	$SVI = 2079.4\ e^{-0.315t}$	79 408	0.81

Note: The R^2 values for all nonlinear equations were estimated by 1 – (residual SS/corrected SS). The equations are plotted in Fig. 3. SVI, stem volume index (cm^3); t, years weed free or weed infested after planting.

The tolerant conifers in this study, therefore, appeared to be better able than the intolerant conifers to take advantage of the increased environmental resources or other conditions made available from the continuous removal of herbaceous vegetation. An alternative argument is that jack pine and red pine captured available site resources sooner than white pine and spruce, so did not benefit from continued vegetation control. By year 5 of this study, however, crown closure among the trees was a number of years away and substantial growing space was still available to be captured for jack and red pine on the site. It also could be argued that the smaller relative decline in SVI for intolerant conifer species (85, 81, 78, and 67% for white pine, black spruce, red pine, and jack pine, respectively) resulting from competition with herbaceous vegetation is indicative of greater competitiveness. In either case, results from this study suggest a differing ability among these four conifer species to respond to the environmental changes associated with controlling herbaceous vegetation.

Although we identify these differences as being correlated with species tolerance, we only had a single conifer species representing each point on this gradient. Multiple species representing these characteristics would be required to more confidently associate these observed patterns with tolerance or ecological role. These results, however, provide an initial basis for discussion. It also should be noted that the results

Table 3. Mean slope coefficients from log-linear regression models of SVI for 5 years after planting for each vegetation treatment sequence (T, herbicide treated; O, untreated) and conifer species.

Treatment	Jack pine	Red pine	White pine	Black spruce
OOOOO	1.445*c*	0.986*f*	0.893*e*	0.758*e*
TOOOO	1.524*bc*	1.103*ef*	1.087*c*	0.809*e*
TTOOO	1.747*a*	1.325*abc*	1.220*b*	0.941*cd*
TTTOO	1.745*a*	1.421*ab*	1.264*ab*	1.065*ab*
TTTTO	1.798*a*	1.431*a*	1.244*ab*	1.151*a*
TTTTT	1.752*a*	1.337*abc*	1.345*a*	1.088*ab*
OTTTT	1.733*a*	1.303*bc*	1.259*ab*	1.028*bc*
OOTTT	1.608*b*	1.229*cd*	1.086*c*	0.918*d*
OOOTT	1.587*b*	1.160*de*	1.018*cd*	0.842*de*
OOOOT	1.494*bc*	1.141*de*	0.958*de*	0.765*e*

Note: Means are average slopes from models developed separately for each replication ($n = 4$). Different letters next to each slope within a species indicate a significant difference ($P \leq 0.05$).

from this study apply to the specific conditions encountered on one site. Responses may, of course, vary depending on the temporal pattern of invasion by herbaceous vegetation after logging and site preparation, as well as any other site differences that alter competitive interactions between conifers and herbaceous vegetation.

Despite these differences among species, several similarities in response also were identified. Negative exponential functions best described the weed-infested curves and the slope of these curves was the same for all species. Similar weed-infested curves indicated that the relative declines in stem volume growth under interspecific competition with herbaceous vegetation were similar among the conifer species over time.

Although the weed-free curves differed among species, it did not substantially alter the TEI, which occurred between 1 and 2 years for all species. The TEI is the time where the amount of tree growth resulting from vegetation control since planting is equal to the tree growth obtained from starting continuous vegetation control from that point through the fifth year (Cousens 1988). The fact that the TEI occurred between years 1 and 2 indicates that a single year of vegetation control before the TEI produced a SVI equal to that produced by approximately 2 years of vegetation control after the TEI. Subtracting the TEI from 5 years (the full period examined) and dividing this value by the TEI provided a precise measure of this ratio for each species. This ratio was 2.68, 1.89, 1.59, and 1.76 for jack pine, red pine, white pine, and black spruce, respectively. For example, 2.68 years of vegetation control were required after the TEI to yield the same SVI for jack pine after 5 years as 1 year of control before the TEI. The value of earlier vegetation control on longer term growth also was corroborated by the SVI growth rate analysis (Table 3).

Since survival was unresponsive and height growth only slightly responsive to competition from herbaceous vegetation, no CP was identified for these variables for any species. Wood and Mitchell (1995) showed that increases in height growth following vegetation control can often be delayed for several years after increases in stem diameter growth are observed. Therefore, critical periods for height growth may develop with time.

Our analysis of SVI slope values over the 5 years suggests the degree to which the pattern of vegetation control is likely to influence tree growth over the longer term. These results indicate a greater long-term benefit if effective vegetation control is applied immediately after planting than more intensively in later years. Wood and von Althen (1993) also found that controlling vegetation in the year of planting enhanced diameter growth of white and black spruce more than waiting until the year after planting. A study with Norway spruce (*Picea abies* (L.) Karst.) found greatest growth when vegetation was controlled during site preparation, with substantial decreases occurring as the interval between planting and competition release increased (Lund-Høie 1984).

It may have been possible to demonstrate statistically that the left side of critical period occurred at year 0 or immediately after planting (Fig. 3). Unfortunately, we were only able to reduce vegetation cover in the year of planting to about 25% (Fig. 2). An unusual June frost top killed the bracken fern on the study site, allowing it to escape herbicide exposure and rapidly recover the first growing season. This level of competition may have been sufficient to produce no difference in SVI between treatments TTTTT and OTTTT for all conifer species (Tables 1 and 3). Based on the relative importance of early vegetation control indicated in this and other studies, as well as the greater opportunities for intensive vegetation control just before planting, forest managers are probably best advised to consider the functional CP to begin the year of planting.

Early size differences produced by herbaceous vegetation control can have significant long-term consequences for stand development. For example, Lauer et al. (1993) found that herbaceous vegetation control applied in the first and second year after planting nearly doubled wood volume gains in loblolly pine (*Pinus taeda* L.) at age 9 relative to trees that had only received vegetation control in the first year. This effect was consistent over a range of sites across the southern United States. Continued monitoring of this study will help determine whether patterns of vegetation control during the first 5 years after planting can significantly alter longer term stand dynamics in northern forest ecosystems.

Acknowledgments

This research was supported by the Vegetation Management Alternatives Program (VMAP) in the Ontario Ministry of Natural Resources. John Winters and Ago Lehela (Ontario Forest Research Institute) provided excellent field support. Stephanie Arnold (University of Maine) and Dr. Michael Ter-Mikaelian (Ontario Forest Research Institute) provided support with the statistical analysis.

References

Brand, D.G. 1991. The establishment of boreal and sub-boreal conifer plantations: an integrated analysis of environmental conditions and seedling growth. For. Sci. **37**: 68–100.

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can J. For. Res. **23**: 2141–2152.

Cole, E.C., and. Newton, M. 1987. Fifth-year response of Douglas-fir to crowding and nonconiferous competition. Can. J. For. Res. **17**: 181–186.

Cousens, R. 1988. Misinterpretations of results in weed research through inappropriate use of statistics. Weed Res. **28**: 281–289.

Daniel, T.W., Helms, J.A., and Baker, F.S. 1979. Principles of silviculture. McGraw-Hill Book Co., New York.

Duba, S.E., Nelson, L.R., and Gjerstad, D.H. 1985. Interaction of genotype and vegetation control on loblolly pine seedling performance. *In* Proceedings of the 3rd Biennial Southern Silviculture Research Conference, 7–8 Nov. 1984, Atlanta, Ga. *Edited by* E. Shoulders. USDA For. Serv. Gen. Tech. Rep. SO-54. pp. 305–308.

Hall, M.R., Swanton, C.J., and Anderson, G.W. 1992. The critical period of weed control in grain corn (*Zea mays*). Weed Sci. **40**: 441–447.

Johnson, J.E. 1994. The Lake States region. *In* Regional silviculture of the United States. *Edited by* J.W. Barrett. John Wiley & Sons, Inc., New York. pp. 81–127.

Lanini, W.T., and Radosevich, S.R. 1986. Response of three conifer species to site preparation and shrub control. For. Sci. **32**: 61–77.

Lauer, D.K., Glover, G.R., and Gjerstad, D.H. 1993. Comparison of duration and method of herbaceous weed control on loblolly pine response through midrotation. Can J. For. Res. **23**: 2116–2125.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. **24**: 1193–1198.

Lund-Høie, K. 1984. Growth responses of Norway spruce (*Picea abies* L.) to different vegetation management programmes—preliminary results. Aspects Appl. Biol. **5**: 127–133.

MacDonald, G.B., and Weetman, G.F. 1993. Functional growth analysis of conifer seedling responses to competing vegetation. For. Chron. **69**: 64–68.

Morris, D.M., MacDonald, B., and McClain, K.M. 1990. Evaluation of morphological attributes as response variables to perennial competition for 4-year-old black spruce and jack pine seedlings. Can. J. For. Res. **20**: 1696–1703.

Newton, M., and Preest, D.S. 1988. Growth and water relations of Douglas-fir (*Pseudotsuga menziesii*) seedlings under different weed control regimes. Weed Sci. **36**: 653–662.

Seber, G.A.F. 1977. Linear regression analysis. John Wiley and Sons, Inc., New York.

Singh, M., Saxena, M.C., Abu-Irmaileh, B.E., Al-Thahabi, S.A., and Haddad, N.I. 1996. Estimation of critical period of weed control. Weed Sci. **44**: 273–283.

Stewart, R.E., Gross, L.L., and Honkala, B.H. 1984. Effects of competing vegetation on forest trees: a bibliography with abstracts. USDA For. Serv. Gen. Tech. Rep. WO-43.

Swanton, C.J., and Weise, S.F. 1991. Integrated weed management: the rationale and approach. Weed Technol. **5**: 657–63.

van Acker, R.C., Swanton, C.J., and Weise, S.F. 1993. The critical period of weed control in soybean [*Glycine max.* (L.) Merr.]. Weed Sci. **41**: 194–200.

Wagner, R.G. 1993. Research directions to advance forest vegetation management in North America. Can. J. For. Res. **23**: 2317–2327.

Wagner, R.G. 1994. Toward integrated forest vegetation management. J. For. **92**(11): 26–30.

Wagner, R.G., Noland, T.L., and Mohammed, G.H. 1996. Timing and duration of herbaceous vegetation control around four northern coniferous species. N.Z. J. For. Sci. **26**: 39–52.

Walstad, J.D., and Kuch, P.J. 1987. Vegetation management for conifer production. John Wiley & Sons, Inc., New York.

Weaver, S.E. 1984. Critical period of weed competition in three vegetable crops in relation to management practices. Weed Res. **24**: 317–325.

Weaver, S.E., and Tan, C.S. 1983. Critical period of weed interference in transplanted tomatoes (*Lycopersicon esculentum*): growth analysis. Weed Sci. **31**: 476–481.

Wood, J.E., and Mitchell, E.G. 1995. Silvicultural treatments for black spruce establishment in boreal Ontario: effect of weed control, stock type, and planting season. Canadian Forest Service, Sault Ste. Marie, Ont. North. Ont. Develop. Agree. Tech. Note.

Wood, J.E., and von Althen, F.W. 1993. Establishment of white spruce and black spruce in boreal Ontario: effects of chemical site-preparation and post-planting weed control. For. Chron. **69**: 554–560.

Woolley, B.L., Michaels, T.E., Hall, M.R., and Swanton, C.J. 1993. The critical period of weed control in white beans (*Phaseolus vulgaris*). Weed Sci. **41**: 180–184.

Zimdahl, R.L. 1988. The concept and application of the weed-free period. *In* Weed management in agroecosytems: ecological approaches. *Edited by* M.A. Altieri and M. Liebman. CRC Press, Inc., Boca Raton, Fla. pp. 145–155.

Zedaker, S.M., Burkhart, H.E., and Stage, A.R. 1987. General principles and patterns of conifer growth and yield. *In* Forest vegetation management for conifer production. *Edited by* J.D. Walstad and P.J. Kuch. John Wiley & Sons, Inc., New York. pp. 203–241.