Critical period of interspecific competition for four northern conifers: 10-year growth response and associated vegetation dynamics[1]

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Abstract: The influence of the timing and duration of interspecific competition on planted jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), and black spruce (*Picea mariana* (Mill.) BSP) was assessed using 10-year growth responses in a northern Ontario experiment. Stand volume was 117%, 208%, 224%, and 343% higher for jack pine, red pine, white pine, and black spruce, respectively, with 5 years of vegetation control than with no vegetation control. Stand volume increased linearly with number of years of vegetation control, and the slope of the relationship varied among conifer species. Change-point regression analysis was used to derive segmented weed-free and weed-infested curves, and to simultaneously estimate key critical-period parameters. Weed-free and weed-infested curves in the 10th year were similar to those derived in year 5, indicating that the patterns established during the first few years after planting were relatively robust for the first decade. The critical-period was 2 and 3 years after planting for jack pine and red pine, respectively, and occupied most of the 5-year period for white pine and black spruce. Principal components analysis of the vegetation community indicated that repeated herbicide applications caused differential shifts in the relative abundance of shrub, fern, and moss species through the 10th year. Species richness, however, was not substantially different between the untreated control and the most intensive treatments. Difference modeling was used to quantify how annual volume increment during the first decade varied with time, conifer species, cover of woody and herbaceous vegetation, and stage of development.

Résumé : L'influence du moment et de la durée de la compétition interspécifique sur des plants de pin gris (*Pinus banksiana* Lamb.), de pin rouge (*Pinus resinosa* Ait.), de pin blanc (*Pinus strobus* L.) et d'épinette noire (*Picea mariana* (Mill.) BSP) a été évaluée à partir des réactions en croissance après 10 ans d'une expérience menée dans le nord de l'Ontario. Le volume des peuplements ayant fait l'objet d'un contrôle de la végétation pendant 5 ans était respectivement 117 %, 208 %, 224 % et 343 % plus élevé pour le pin gris, le pin rouge, le pin blanc et l'épinette noire que celui des peuplements où la végétation n'avait pas été contrôlée. Le volume des peuplements a augmenté linéairement avec le nombre d'années de contrôle de la végétation et la pente de la relation a varié selon l'espèce de conifère. Une analyse de régression segmentée a été utilisée pour déterminer les segments de la courbe qui sont affectés ou non par la compétition et pour estimer simultanément les paramètres clés de la période critique. Les segments de courbe affectés ou non par la compétition à la dixième année sont identiques à ceux calculés à la cinquième année, ce qui indique que les patrons de réaction établis au cours des premières années après la plantation sont relativement fiables pendant la première décennie. La période critique est survenue respectivement 2 et 3 ans après la plantation pour le pin gris et le pin rouge et a occupé une grande partie de la période de 5 ans pour le pin blanc et l'épinette noire. Une analyse en composantes principales de la communauté végétale a indiqué que des applications répétées d'herbicide ont causé des changements différents de l'abondance relative des arbustes, des fougères et des mousses au cours de la période de 10 ans. Toutefois, la richesse en espèces n'est pas substantiellement différente entre les placettes non traitées et les traitements les plus intenses. Une équation différentielle a été utilisée pour quantifier la variation de l'accroissement annuel en volume au cours de la première décennie en fonction du temps, de l'espèce de conifère, du couvert de végétation ligneuse et herbacée et du stade de développement.

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Introduction

Substantial increases in wood volume production from managing competing forest vegetation have been demonstrated for a wide variety of forest types and conditions in the longest-term studies from around the world (Wagner et al. 2006). While yield gains from 30% to 500% have been commonly demonstrated from effective vegetation control,

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the optimal timing and duration of vegetation control required to achieve desired rates of stand growth have not been identified. Knowing the best timing and minimum duration of vegetation control needed to achieve maximum yields can help forest managers reduce treatment costs, unnecessary herbicide use, variation in treatment success, and any negative ecological effects associated with vegetation control. Identifying the optimal timing and duration of vegetation control requires knowing when interspecific competition from early-successional vegetation influences the growth of young forest stands.

The critical period (CP) of weed control, first developed in agriculture during the late 1960s to help farmers optimize weed control strategies in agricultural crops (Nieto et al. 1968; Zimdahl 1988), can be applied to forest systems to quantify the temporal influence of interspecific competition in young stands. The CP is the time period during crop development when interspecific competition from weeds must be controlled to prevent significant yield losses. Critical periods have been established for a wide range of agricultural crops (Zimdahl 1988). The CP for vegetable crops generally starts some weeks after emergence and ends sometime during the first half of the growing period (Hewson and Roberts 1973; Hall et al. 1992; Woolley et al. 1993). CP studies have been recently expanded to include management of forest vegetation (Wagner et al. 1996, 1999; Adams et al. 2003; Vegetation Management Research Cooperative 2005), and are important to developing strategies for integrated forest vegetation management (Wagner 1994).

The CP has two components (Weaver and Tan 1983). The first, described by a weed-free curve, is the length of time that 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 that 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. 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. Wagner et al. (1996) describe the range of hypothetical outcomes possible for these relationships.

This study reports the 10-year results of a critical-period study for four conifer species (jack pine, red pine, eastern white pine, and black spruce) in northern Ontario. Earlier results from this study were previously reported based on 3- and 5-year responses (Wagner et al. 1996, 1999). Since it is vital that determination of the CP for forest systems be based on long-term yield gains, we calculated the CP of vegetation control during the first 5 years after planting using volume production during the first decade of plantation development. In addition, we examined vegetation dynamics resulting from various timings and durations of annual herbicide (glyphosate) treatment, and quantified the relationship between stand growth and the abundance of various vegetation components during the first decade of stand development.

Methods

Study site and experimental design

The study site is located in the Great Lakes – St. Lawrence forest type (Rowe 1972) about 44 km northeast of Sault Sainte Marie, Ontario, Canada (46°49′05.7″N, 83°58′04.6″W). The site was clear-cut 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. The soil is uniform and sandy textured. 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.

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 m × 28 m (0.078 ha) in size and divided into four 14 m × 14 m subplots, to which each conifer species was randomly assigned. Thirty trees (5 rows of 6 trees) of each species were planted on 2 m × 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 typically done. Details about the planting stock used for each tree species are described in Wagner et al. (1999).

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 weed-free and weed-infested curves used in a CP analysis. 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 a.e. (acid equivalent)·ha^{-1} in 93 L·ha^{-1} water. Applications were made at the beginning of each growing season when vegetation had developed sufficient leaf area to receive the herbicide (generally 2nd to 3rd week of June). All aspen on the plots were 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 that time of year, all trees were protected with paper cups or plastic bags during herbicide application.

Variables measured

Tree size (height and root-collar stem diameter) was measured immediately after planting in spring 1992. At the end of each growing season (October) for the first 5 years after planting (1992–1996) and in the 10th year (2001), the survival and growth (height and root-collar stem diameter) of all trees was measured. Height and stem diameter from each year were used to calculate stem volume (using a cone volume equation) and height/diameter ratio (HDR). In cases where trees had multiple stems, the diameter and height of the largest stem were used.

Vegetation cover for each plant species in the 28 m × 28 m main plots was estimated between late August and early September each year from 1992 to 1996 and in 2001. For the 1992–1996 samples, percent cover was visually estimated to the nearest 5% on six 1 m^2 (0.5 m × 2 m) plots that were systematically located with a random start from the corner of each main plot. Because of the larger size of the planted trees and vegetation in 2001, cover was visually estimated to the nearest 5% on three 4 m^2 circular plots (1.13 m radius) that were systematically located in each subplot (12 sample plots per main plot). Species were identified according to Newmaster et al. (1998).

Analytical approach

All analyses conducted in this study used the open source statistical environment, R (R Development Core Team 2005).

Tenth-year growth response

We calculated the survival rate, height, stem diameter at root collar, mean stem volume of live trees (using a cone volume equation), rate of multileadering, HDR, and stand volume per hectare in each subplot for each tree species for the 10th-year measurements. Each variable was compared among treatments using a quadratic response-surface, mixed-effects model that accommodated the split-plot experimental design. ANOVA was used to examine the effect of tree species, number of years of vegetation control, whether the control was early (immediately after planting) or late (one or more years after planting), and the various interactions for each variable. Prior to analysis, residuals from the model for each variable were examined for homoskedasticity and normality using diagnostic graphs. Results indicated that diagnostics were satisfactory for height, diameter, and survival, but that tree volume, stand volume, and HDR showed heteroskedasticity and non-normality within the residuals. Weighted regression was used to correct the problem for these variables, which proved satisfactory upon examination of subsequent diagnostics.

Critical-period analysis

Appropriate methods for calculating the CP continue to be debated, and better methods are being sought (Cousens 1988; Hall et al. 1992; Singh et al. 1996; Knezevic et al. 2002). CP estimation for the 5th-year responses from this study (Wagner et al. 1999) used nonlinear regression analysis (negative exponential and logistic functions) to derive the weed-infested curve, weed-free curve, and time of equal interference (TEI). Orthogonal contrasts were used to statistically define the beginning and end of the CP along the curves.

Numerous other CP modeling strategies have been tried, including use of Gompertz and rectangular hyperbola curves. One approach has arbitrarily identified the CP as the location on the curve where a 2%, 5%, or 10% decline is observed (Hall et al. 1992; Singh et al. 1996). Alternatively, multiple range tests have been used to identify the times that are significantly different from the first or last measurements. This strategy was criticized by Cousens (1988), who noted that the CP should be dictated by biological rather than statistical considerations, and suggested that the response curves themselves should be used. Cousen's suggestion, however, still left open the problem of identifying the model form. Knezevic et al. (2002) provide the most recent review of alternative approaches and suggest that combinations of ANOVA and nonlinear regression should be used to derive CP components for agronomic crops.

A nonlinear model form is clearly needed where the quantities of interest (beginning of CP on the weed-infested curve, end of the CP on weed-free curve, and TEI) are expressed directly as parameters in the model, and where estimation takes advantage of the underlying structure of the data. In addition, the model would need to: (1) simultaneously fit the weed-free and weed-infested curves, (2) explicitly parameterize any departures from a norm, and (3) constrain the weed-free and weed-infested curves to the temporal bounds of the experiment.

To accomplish this modeling objective, we developed a new approach using a simultaneous change-point regression with maximum likelihood estimation. Maximum likelihood estimates have desirable properties, such as asymptotic efficiency and asymptotic normality (Casella and Berger 1990). Simultaneous three-segment regressions were fit to the stand volume per hectare variable for the weed-free and weed-infested curves using the following:

$$y = \begin{cases} y_2 & x \geq x_{f2} \text{ and weed-free} \\ y_1 + \left(\dfrac{x - x_{f1}}{x_{f2} - x_{f1}}\right)(y_2 - y_1) & x_{f1} \leq x < x_{f2} \text{ and weed-free} \\ y_1 & x < x_{f1} \text{ and weed-free} \end{cases}$$

$$y = \begin{cases} y_1 & x \geq x_{i2} \text{ and weed-infested} \\ y_1 + \left(\dfrac{x_{i2} - x}{x_{i2} - x_{i1}}\right)(y_2 - y_1) & x_{f1} \leq x < x_{i2} \text{ and weed-infested} \\ y_2 & x < x_{i1} \text{ and weed-infested} \end{cases}$$

where y is the 10-year volume, y_1 is the 10-year volume for the 5 years weed-infested treatment, y_2 is the 10-year volume for the 5 years weed-free treatment, x is the number of years of treatment (either weed-free or weed-infested), x_{i1} is the point on the weed-infested curve where volume growth decreases, x_{i2} is the point on the weed-infested curve where volume growth stops decreasing, and x_{f1} and x_{f2} are points on the weed-free curve where volume growth starts and stops increasing, respectively (Fig. 1). To permit direct estimation of the CP quantities of interest, the following substitutions were made for x_{f2} and x_{i2}:

$$x_{\mathrm{f2}} = x_{\mathrm{il}} + c$$

$$x_{\mathrm{i2}} = \frac{t(x_{\mathrm{f1}} - x_{\mathrm{f2}}) + x_{\mathrm{il}}(t - x_{\mathrm{fl}})}{t - x_{\mathrm{f2}}}$$

where c is the CP and t is the TEI.

Maximum likelihood estimation involved maximizing the joint probability density function for the observations conditional on the model. This process required computing prediction residuals for all observations (weed-free and weed-infested) within a tree species as a function of the predictor (time) and response (stand volume per hectare) variables, and the unknown parameters y_1, y_2, x_{f1}, x_{i1}, c, and t, based on the model form above. A residual-generating function, simply the difference between the observation and prediction, was embedded within a normal probability density function with zero mean, and standard deviation included as another parameter. The natural logs of these probabilities were then summed, as an objective function, which was then maximized using the Nelder–Mead algorithm to produce parameter estimates for all seven parameters (the six above and the standard deviation of the residuals) and a Hessian matrix. The residuals were then extracted to construct model diagnostics, which indicated that the necessary assumptions, viz., that the residuals were normally distributed and had constant variance, were satisfied. The Hessian was inverted to obtain approximate standard errors for the parameter estimates.

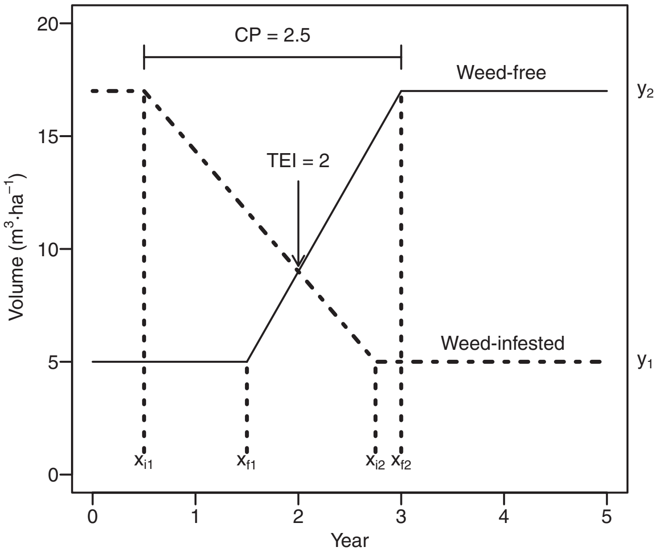
Parameter estimates from the final change-point models provided values for the start of the CP, length of the CP, and TEI, as well as estimates of the standard error for each parameter, for each of the four tree species.

Vegetation community dynamics

As indicated by analysis of Wagner et al. (1999), annual herbicide treatments applied during the first 5 years of the experiment had a dramatic effect on the cover of woody and herbaceous vegetation. The temporal differences in the cover of competing plant species produced substantial differences in the early growth of the four conifer species. The question of interest in year 10 was how the longer-term composition and abundance of the vegetation community was influenced by the variety of herbicide treatments that were applied during the first 5 years of the experiment.

In addition to examining total cover among the treatments for the first decade, we used principal components analysis (PCA) of species class coverage among the 10 treatments and four blocks. Ten species classes were used for this analysis based on common life form: conifer, hardwood, tall shrub, shrub, grass, forb, fern, sedge, lichens, and moss. We did not standardize the variables, because the units (percentage cover) are common to all classes. The analysis identified three components of particular interest: shrub, moss, and fern cover, which were examined further.

Fig. 1. Idealized example of simultaneous change-point regression used to describe weed-free and weed-infested curves with key components of the critical period. CP is the critical period (2.5 years long in example), TEI is the time of equal interference (occurring in year 2 in example), y_1 is the 10-year volume for the 5 years weed-infested treatment, y_2 is the 10-year volume for the 5 years weed-free treatment, x_{i1} is the point on the weed-infested curve where volume growth decreases, x_{i2} is the point on the weed-infested curve where volume growth stops decreasing, and x_{f1} and x_{f2} are the points on the weed-free curve where volume growth starts and stops increasing, respectively.



Tree growth versus vegetation abundance and composition

The final question of interest was how differences in the abundance and composition of the vegetation community produced by the 10 treatments over time specifically influenced stand volume growth during the first decade. Before conducting this analysis, bivariate correlation among six of the relevant species class variables (hardwood, tall shrub, shrub, herbaceous, conifer, and moss) was used to determine whether colinearity would complicate using any of them as predictors in a model. Results indicated that there was no correlation among the species class variables that might present a problem.

We used a difference modeling approach to examine how annual volume growth ($m^3 \cdot ha^{-1} \cdot year^{-1}$ at the subplot level) during the first 10 years was influenced by conifer species, age, annual cover for each of six vegetation classes (herbaceous, moss, hardwood, conifer, shrub, and tall shrub), and the interactions. Linear and quadratic terms for age were included to track changes in average annual growth. The initial model was limited by strong heteroskedasticity, non-normal residuals, and autocorrelation of residuals in time. To correct these problems, an alternative model was developed where the sum of vegetation cover was grouped into "woody" (hardwoods, tall shrubs, and shrubs) and "herbaceous" (grasses, ferns, forbs, and sedges) classes, and a growth period variable ("development") was added to separate volume growth occurring early (years 1–5) or later (years 6–10) in the decade. The resulting interaction term between the woody, herbaceous, and development variables permitted testing whether the influence of woody and herbaceous vegetation changed as a function of stand maturity. The assumptions necessary for fitting this model form were satisfied.

Results

Tenth-year survival and growth

Mean survival was 69%, 62%, 75%, and 71% for jack pine, red pine, white pine, and black spruce, respectively, across treatments (calculated from Table 1). Survival declined an additional 3% for jack pine, 4% for red pine, 10% for white pine, and 11% for black spruce relative to the 5th-year measurement. Results from the response surface analysis indicated that survival in year 10 was not affected by the number of years of vegetation control ($p = 0.282$) or whether the treatments were delayed after planting ($p = 0.370$), but did differ among conifer species ($p = 0.003$) (Table 2).

In contrast with results from the 5th year, tree height in the 10th year increased with increasing numbers of years of vegetation control ($p < 0.001$) and if the treatments were applied earlier rather than later ($p = 0.012$). Jack pine (401 cm) and red pine (328 cm) were taller than white pine (209 cm) and black spruce (258 cm) ($p < 0.001$). The relatively short stature of white pine was likely due to infections by white pine weevil (*Pissodes strobi* Peck) and white pine blister rust (*Cronartium ribicola*) that were observed to cause poor health in many of the surviving trees. An ANOVA on rates of multiple leaders indicated that black spruce had the highest rate of multiple leadering (35%) followed by white pine (13%) ($p < 0.001$). The proportion of multiple leaders increased with longer periods of vegetation control ($p < 0.001$) for black spruce. Multiple leaders were found on about half of the spruce with 4 or 5 years of vegetation control compared with only 8% for spruce on untreated plots. Multiple leadering was evident in only 1% of jack pine and 3% of red pine.

Stem diameter and volume continued to be the most sensitive variables to levels of vegetation control. Stem diameter was 39%, 56%, 66%, and 76% larger for jack pine, red pine, white pine, and black spruce, respectively, with 5 continuous years of vegetation control than with no vegetation control (Table 1). Individual tree volume was more responsive, with 99%, 210%, 227%, and 289% higher volumes for jack pine, red pine, white pine, and black spruce, respectively, with 5 years of vegetation control than no vegetation control. Results from the ANOVA (Table 2) indicated that both stem diameter and individual tree volume varied by conifer species ($p < 0.001$) and were influenced primarily by the number of years of vegetation control ($p < 0.001$) rather than whether the timing of application was earlier or later ($p = 0.808$). The shape of the effect for years of vegetation control was quadratic for both stem diameter ($p < 0.001$) and volume ($p = 0.033$).

The HDR also was sensitive to the treatments, decreasing quadratically as the number of years of vegetation control increased ($p < 0.001$). HDR values were highest for black spruce (likely related to multileadering), similar for jack and red pine, and lowest for white pine (likely due to weevil infection) ($p < 0.001$). The timing of vegetation control also was important ($p < 0.001$), indicating that lower HDR values were produced with delayed vegetation control.

By combining the stem volume of individual trees with survival, we examined the influence of the treatments on total stand volume, which provides the most useful response variable for assessing growth and yield effects. Total stem volume production varied among conifer species ($p < 0.001$) with highest productivity for jack pine, less for red pine, and least for white pine and black spruce (Tables 1 and 2). Stand volume was 117%, 208%, 224%, and 343% higher for jack pine, red pine, white pine, and black spruce, respectively, with 5 years of vegetation control than with no vegetation control (Table 1). Stand volume increased linearly with number of years of vegetation control ($p < 0.001$) and the slope of the relationship varied by species ($p < 0.001$). Stand volume was not affected by timing of herbicide application ($p = 0.993$).

Critical period

Results from the change-point regression of 10-year stand volume produced a set of segmented, linear weed-free and weed-infested "curves" for each conifer species (Fig. 2). Parameter estimates derived from the models provided quantitative estimates for the start of the CP, length of CP, and TEI, as well as estimates of the standard error for each parameter (Table 3).

The weed-infested "curves" were continuously linear for the entire 5-year period for jack pine, red pine, and black spruce (Fig. 2). For white pine, however, the weed-infested "curve" was level from 0 to 1.8 years, declined abruptly, and was level through year 5. The weed-free "curves" were continuously linear for the entire 5 years for white pine and black spruce. For jack pine, however, the weed-free "curve" increased from year 0 and was flat after 2.6 years. The weed-free "curve" for red pine was level from 0 to 1 year, increased to 3.3 years, and then was flat through year 5.

The parameter estimates from these models indicated that the start of the CP was at the time of planting (when x_i is negative) for all conifers except white pine, whose CP began at 1.8 years (Table 3). The length of the CP (calculated as CP + x_i, if x_i is negative) was 2.6 years for jack pine, 3.3 years for red pine, 4.2 years for white pine, and 6.3 years (or the whole 5-year period) for black spruce. The TEI was 1.7, 2.0, 2.1, 2.9 years for jack pine, red pine, white pine, and black spruce, respectively.

Change points for the weed-free curves of white pine and black spruce, and the weed-infested curves of jack pine, red pine, and black spruce were estimated beyond the time range of the treatments and appear in the graphs as orphaned line segments at edges of the plotting area (Fig. 2). The presence of these orphaned line segments may reflect an inadequacy of the segmented regression model. However, a biological interpretation also may be possible. For example, the orphaned line segments on the right side of the weed-free curves suggest that additional yield gains may have been realized with additional years of vegetation control. Orphaned line segments on the right side of the weed-infested curve suggest that additional yield losses may have resulted from exposure to weeds beyond 5 years. The only explanation for orphaned line segments on the left side of the weed-infested

Table 1. Tenth-year survival, height, stem diameter at root collar, mean stem volume of live trees, stand volume per hectare, and height/diameter ratio (HDR) for jack pine, red pine, white pine, and black spruce under 10 patterns of herbaceous vegetation control during the first 5 years after tree planting.

Treatment	Survival (%)	Height (cm)	Root-collar diameter (mm)	Mean tree volume (cm^3)	Stand volume ($m^3 \cdot ha^{-1}$)	HDR
Jack pine						
0	68.3	370.1	77.1	8 347	8.9	49.1
1	76.6	411.7	92.7	13 060	15.1	45.9
12	59.2	445.3	107.5	18 159	16.1	42.2
123	70.8	417.0	110.7	17 973	19.5	37.9
1234	71.4	413.6	111.5	18 087	19.5	37.6
12345	75.8	410.3	107.0	16 571	19.3	39.0
2345	58.0	405.3	107.6	16 556	14.6	38.1
345	70.0	378.5	100.9	13 752	14.5	37.9
45	74.2	384.7	97.9	13 443	15.2	39.9
5	64.2	377.2	91.6	11 731	13.1	41.4
Red pine						
0	50.0	259.0	62.6	4 243	3.7	42.1
1	71.7	276.0	68.5	5 201	5.6	40.9
12	65.0	332.1	87.6	9 708	9.8	38.2
123	70.8	386.6	95.6	13 089	14.4	41.0
1234	73.3	382.2	99.3	13 749	15.5	38.9
12345	57.5	353.5	97.7	13 155	11.4	36.3
2345	62.2	363.4	96.6	12 713	12.1	38.1
345	60.8	329.5	90.1	9 798	9.1	36.7
45	51.7	298.1	81.1	7 641	6.1	36.7
5	58.3	302.9	81.6	7 732	7.2	37.5
White pine						
0	78.0	184.5	43.0	1 394	1.7	44.5
1	75.8	191.1	49.7	1 985	2.4	39.8
12	68.3	223.4	61.2	3 501	4.1	37.0
123	65.0	234.9	68.3	4 304	4.3	35.8
1234	85.0	202.7	61.5	3 041	3.9	34.4
12345	79.2	237.2	71.3	4 561	5.5	34.8
2345	79.9	227.5	68.4	4 279	5.3	34.4
345	69.0	208.5	66.3	3 754	4.1	32.4
45	70.0	183.8	55.4	2 341	2.4	34.1
5	76.7	191.4	53.3	2 410	3.0	36.3
Black spruce						
0	70.0	202.1	38.2	1 279	1.4	55.9
1	71.7	236.1	45.6	2 359	2.6	60.9
12	66.7	251.8	52.1	3 092	3.2	50.9
123	65.8	294.1	59.4	4 077	4.2	51.2
1234	67.5	276.4	60.7	3 912	4.2	47.5
12345	80.8	288.0	67.2	4 979	6.2	44.2
2345	69.2	297.3	66.9	5 068	5.3	45.3
345	69.2	241.1	58.8	3 255	3.7	42.4
45	74.2	248.0	59.4	3 443	3.9	42.6
5	70.0	248.9	54.1	3 057	3.1	47.5

Note: Values are mean of four blocks. Treatment codes indicate year in which vegetation control was applied after planting (e.g., 0 = no treatment; 1 = year 1 only; 12 = years 1 and 2; 123 = years 1, 2, and 3, etc.).

curve would be model inadequacy, because there is no possible biological explanation. We do not consider this limitation to be a significant shortcoming of segmented regression for modeling the CP.

Vegetation community dynamics

The sequence of total vegetation cover produced by the weed-free and weed-infested treatments over the 10 years is presented in Fig. 3. The pattern for the first 5 years was reported by Wagner et al. (1999). The question explored here was how the treatment sequences, which end in year 5, influenced future vegetation development. It is clear from Fig. 3 that repeated herbicide treatments had a suppressing effect on vegetation development through the 10th year. An ANOVA of the treatment effects on total cover in year 10 indicated that this suppression was statistically significant (*p*

Table 2. Probability values for experimental factors and interactions in sequential ANOVA of response surfaces for variables in Table 1.

Factor	Survival	Height	Root-collar diameter	Mean tree volume	Stand volume	HDR
Intercept	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Species	0.003	<0.001	<0.001	<0.001	<0.001	<0.001
Years	0.282	<0.001	<0.001	<0.001	<0.001	<0.001
Years^2	0.345	0.061	<0.001	0.033	0.344	<0.001
Timing	0.370	0.012	0.925	0.808	0.993	<0.001
Species × years	0.948	0.001	0.132	<0.001	<0.001	0.081
Species × years^2	0.186	0.507	0.256	0.119	0.483	0.042
Species × timing	0.276	0.220	0.012	0.020	0.036	0.057
Years × timing	0.557	0.950	0.196	0.638	0.390	0.001
Years^2 × timing	0.844	0.006	0.031	0.023	0.084	0.078
Species × years × timing	0.871	0.864	0.646	0.592	0.402	0.717
Species × years^2 × timing	0.164	0.774	0.679	0.441	0.406	0.303

Note: Factors are the following: intercept, regression model intercept; species, tree species; years, number of years of vegetation control; years^2, quadratic effect of years; timing, whether treatment was applied immediately after planting or delayed.

< 0.001). Interestingly, subplots containing jack pine had slightly higher cover among the treatments than the other conifers ($p < 0.001$).

Results from the PCA revealed interesting differences in vegetation development through year 10, depending on the specific treatments that were applied (Fig. 4). The first two components accounted for 92% of the variation, and were dominated by fern, moss, and shrub cover variables. Therefore, we focused on the response of these three life forms. The mean cover for the shrub, fern, and moss species relative to one another is shown in Fig. 4. The trajectories of the four blocks, which are assumed to be independent, were remarkably consistent, indicating that the effect of the herbicide treatments on the plant community were quite consistent over the 10 years.

It is clear from these trajectories that untreated plots had high shrub and fern cover, and low moss cover (Fig. 4). A single herbicide application, whether early or late, substantially reduced shrub cover, increased fern dominance, and produced low moss cover. Two herbicide applications reduced both shrub and fern cover, and increased cover of mosses. Increasing the number of herbicide applications systematically reduced shrub and fern cover, and progressively increased moss cover. In the 10th year of the study, plots that were treated 5 continuous years had very low shrub and fern cover, and high moss cover.

Despite substantial differences in the total cover of vegetation among treatments, species richness of higher plants in year 10 declined only somewhat as number of years of herbicide application increased. Fifty-one species were identified on untreated plots, while 43 species were found on plots that had been treated for 5 continuous years.

Tree growth versus vegetation abundance and composition

Results from the difference models quantified how annual stand volume growth ($m^3 \cdot ha^{-1} \cdot year^{-1}$) during the first 10 years varied with age, conifer species, total vegetation cover each year, whether the vegetation cover was woody (hardwoods, tall shrubs, and shrubs) or herbaceous (grasses, ferns, forbs, and sedges), development period (years 1–5 versus 6–10), and the interactions of these factors (Table 4).

Annual volume growth increased with age, with both linear ($p < 0.001$) and quadratic ($p < 0.001$) terms being significant. Volume growth varied among conifer species ($p < 0.001$), and the linear and quadratic trajectories also varied among conifers ($p < 0.001$). Growth differed between earlier (1–5 year) and later (6–10 year) development stages ($p = 0.001$), and beyond that was accounted for by the linear and quadratic age terms.

Total vegetation cover strongly reduced volume growth ($p < 0.001$) each year, but the effect did not differ whether the cover was woody or herbaceous ($p = 0.683$). The effect of total cover on volume growth varied with developmental stage ($p = 0.004$), but the effect of woody and herbaceous cover on volume growth did not differ with developmental stage ($p = 0.054$).

Discussion

Results from this study indicated that the influence of vegetation control during the first few years after planting had a substantial influence on the productivity of young conifer stands for the first decade. Volume production increased more than two-fold for all four conifer species, if herbaceous vegetation was controlled for only the first 2 years after planting (Table 1; Fig. 2). Although there were substantial differences in the absolute productivity and shade tolerance among the four conifer species studied, the relative volume growth losses due to interspecific competition were similar among species. The volume gains from vegetation control in this study were consistent with those found in 60 of the longest-term studies in northern forests and other forest types around the world (Wagner et al. 2006). Increases in per hectare volume growth provided by vegetation management and other silvicultural practices will be important to increase wood production on a shrinking global forest and help conserve land for biodiversity (Borlaug 2000; Wagner et al. 2004).

Fig. 2. Predicted weed-free (solid line, solid circles) and weed-infested (dotted line, open circles) curves of 10-year stand volume ($m^3 \cdot ha^{-1}$) for jack pine, red pine, white pine, and black spruce based on change-point regression model. Change points for some curves were estimated outside the plotting area for some graphs and appear as orphaned line segments at those graph edges. These orphaned line segments suggest that the asymptote for the weed-free or weed-infested curve has not yet been reached. Values for CP and TEI for each tree species are shown in Table 3.

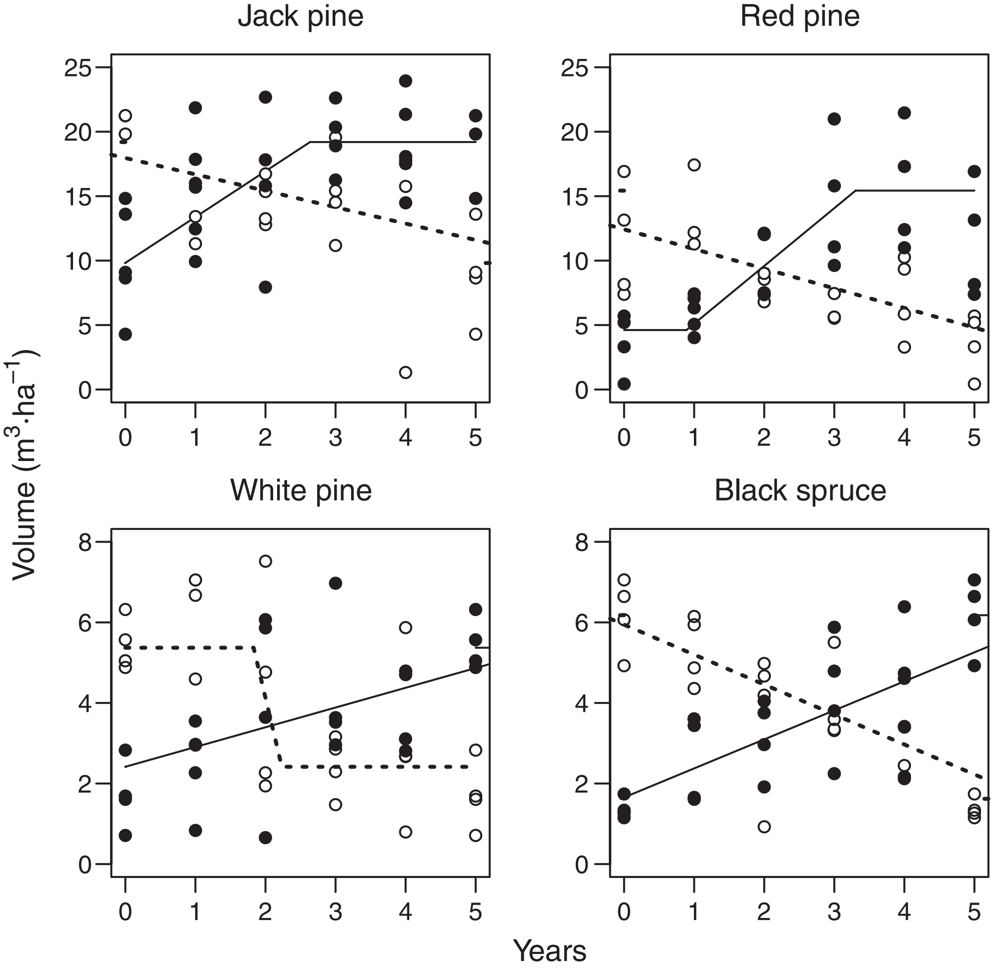


Table 3. Summary statistics for critical-period prediction using segmented regression and maximum likelihood model.

Species	x_i	SE(x_i)	CP	SE(CP)	TEI	SE(TEI)	s_v	RMSE
Jack pine	–0.972	1.83	3.61	2.11	1.69	0.301	5.02	4.06
Red pine	–1.970	1.68	5.28	1.96	1.96	0.198	4.80	3.13
White pine	1.830	7.34	4.20	7.68	2.09	3.840	1.91	1.55
Black spruce	–0.316	640	6.6	1.3×10^3	2.93	0.297	1.69	1.14

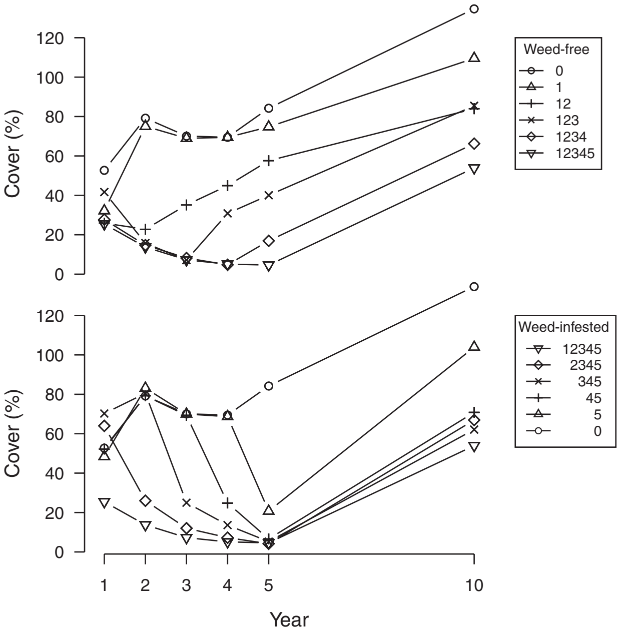
Note: x_i, start of the critical period (years); CP, length of critical period (years); TEI, time of equal interference (years). Estimated standard errors (SE) for each parameter are in the same units. s_v, standard deviation of the stand volume; RMSE, conditional standard deviation of residuals. When x_i is negative, the critical period starts at planting and concludes at CP + x_i.

Critical-period interpretations in 5th and 10th years

A primary objective of this study was to determine whether the CP and related components assessed in the 5th year of this study (Wagner et al. 1999) changed as the stands develop over time. While interpreting the CP based on early tree growth responses clearly has value for understanding the temporal interactions of interspecific competition in young stands, the CP only has silvicultural value if it is correlated with substantial changes in long-term stand development and productivity. The weed-free and weed-infested curves in the 10th year were similar to those derived in the 5th year (Fig. 2; Wagner et al. 1999). Thus, general patterns of stand development established immediately after the vegetation treatments ended in year 5 were largely maintained through the 10th year after planting for all four conifer species.

Although we used a different analytical approach to derive the weed-free and weed-infested curves in the 10th year, the general shapes for most of the curves were maintained. The weed-free curves for jack and red pine did not change, indi-

Fig. 3. Total vegetation cover resulting from treatments used to produce the weed-free and weed-infested curves over 10 years. Cover was calculated as the sum of cover for individual species and thus could exceed 100%. Treatment labels indicate years when herbicide application was applied.

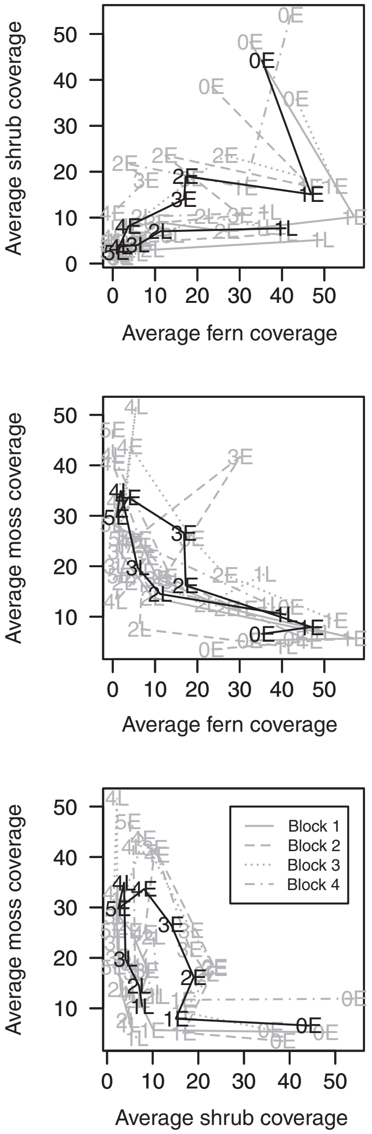


cating that no additional volume gains were achieved by extending vegetation control beyond 2 and 3 years after planting for jack and red pine, respectively. The nearly linear weed-free curves for white pine and black spruce observed in the 5th year were maintained through the 10th year, indicating that additional volume gains were achieved by repeated herbicide applications for all 5 years after planting for both species. Therefore, the shade-tolerant conifers (white pine and black spruce) appeared to continue benefiting from a longer period of vegetation control than the intolerant species (jack pine and red pine).

Negative exponential models provided the best description of the weed-infested curves in the 5th year, and the slope of the curves was equal for all four conifer species (Wagner et al. 1999). In the 10th year, similar negative linear relationships were found for jack pine, red pine, and black spruce. Therefore, significant volume reductions for these species, when vegetation control was not initiated immediately after planting, were still true in year 10. The weed-infested curve for white pine was the only one of the eight weed-free and weed-infested curves that departed substantially from that derived in year 5. Results in the 10th year indicated that no volume loss occurred by delaying the start of vegetation control until the 2nd year after planting. Interpretations of growth responses for white pine in this study, however, should be interpreted with caution. Substantial increases in variation among blocks between years 5 and 10 were evident, and were likely the result of weevil and blister rust infections that now appear to be confounding interpretation of interspecific competition effects.

Jack and red pine at year 10 were consistent with model C (early period) of the archetypal CP patterns described by Wagner et al. (1996). Black spruce appears to be following

Fig. 4. Shrub, moss, and fern cover in the 10th year resulting from 10 vegetation control treatments. Shrub, fern, and moss cover accounted for 92% of the variation in a principal components analysis comparing vegetation communities among treatments. The three graphs show changes in shrub, moss, and fern cover relative to one another. The mean response among the four blocks is shown in black. The first digit of the treatment label is the number of years of repeated vegetation control, and the second letter refers to whether the vegetation control was initiated earlier (E) or later (L) during the 5-year period. The gray lines show the patterns exhibited by each of the four blocks.



model A, where growth losses are proportional to the number of years that trees are associated with vegetation. White pine followed model A or E (later period) depending on the influence of the weevil and blister rust.

The TEI in year 10 was 1.7, 2.0, 2.1, 2.9 years for jack pine, red pine, white pine, and black spruce, respectively (Table 3). The TEI calculated in year 5 using a different method was 1.4, 1.7, 1.9, and 1.8 for jack pine, red pine, white pine, and black spruce, respectively. The only substan-

Table 4. ANOVA table describing effects on mean annual stand volume growth ($m^3 \cdot ha^{-1} \cdot year^{-1}$) during the first decade from woody (hardwoods, tall shrubs, and shrubs) and herbaceous (grasses, ferns, forbs, and sedges) vegetation cover, conifer species (conifer), and whether the growth occurred during years 1–5 or 6–10 (development) over time (age).

Source	Numerator df	Denominator df	*F*	*p*
Intercept	1	585	477.1	<0.001
Age	1	585	10 176.6	<0.001
Age^2	1	585	42.8	<0.001
Conifer	3	585	313.0	<0.001
Development	1	159	10.5	0.001
Total cover	1	585	107.1	<0.001
Woody vs. herbaceous	1	585	0.2	0.683
Age × conifer	3	585	81.6	<0.001
Age^2 × conifer	3	585	14.1	<0.001
Total cover × development	1	585	8.2	0.004
Woody vs. herbaceous × development	1	585	3.7	0.054

tial difference in estimated TEI between years 5 and 10 among the species was for black spruce. The increase in TEI of just over 1 year for black spruce likely resulted from an increased separation in volume production among treatments that included 3, 4, and 5 years of continuous vegetation control.

As discussed by Wagner et al. (1999), the TEI has practical value for forest managers because it can be used to determine whether earlier or later control measures are more effective. The TEI values for the 10th year indicate that 1.9, 1.5, and 1.4 years of vegetation control were required after the TEI for jack pine, red pine, and white pine, respectively, to produce the same volume as 1 year of vegetation control before the TEI. Thus, beginning vegetation control immediately after planting was more efficient than delaying treatments until later years. For black spruce, however, the 10th-year TEI indicated that 1 year of vegetation control before the TEI was only 72% as effective as 1 year of control after the TEI.

Analytical approach to determining critical period

We introduced a new statistical approach for modeling the weed-free and weed-infested curves, and simultaneously estimating the beginning and end of the CP, as well as the TEI (Fig. 1). Simultaneous three-segment regression was able to adequately describe the weed-free and weed-infested curves for all four conifer species. This approach provides an additional analytical method for CP determination to those recommended by Knezevic et al. (2002).

In addition to providing precise quantitative estimates for all components of the CP and simultaneously using all experimental data, the standard errors provided for each regression parameter allow calculation of confidence intervals for all estimates, and can therefore include use of the acceptable yield loss (AYL) approach commonly used in CP calculations for agronomic crops. Thus, use of segmented regression models can address both biological and statistical considerations at the same time, satisfying some criticisms of Cousens (1988) regarding CP analyses.

Contrast with other critical-period studies in planted forests

Since 1992, when this study was initiated, two other CP studies have been established in different forest systems around the world. Results from these works are now providing an early indication of whether the results presented here will hold for other forest systems.

In 1996, Adams et al. (2003) established a CP study with *Eucalyptus globulus* (Tasmanian blue gum) and the introduced grass *Holcus lanatus* L. (Yorkshire fog grass) in Tasmania. Because of high growth rates and the relatively continuous growing season, the CP treatments were spaced approximately 6 months apart for the first 24 months after planting. As with results from this study, there was no period after planting when association with grass did not reduce the diameter growth of Eucalyptus. The weed-infested curves had a similar negative exponential shape as those observed in year 5 of this study. The weed-free curve had a similar shape to those in this study, but leveled off 20 months after planting. Grass interference reduced height and diameter growth to 52% and 40%, respectively, of that observed for weed-free trees at 2 years.

In 2000 and 2001, a CP study was installed on three coastal Oregon sites and includes four conifer species: Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) (Vegetation Management Research Cooperative 2005). Annual herbicide treatments for up to 5 years after planting are being examined as with our study. Fourth- and fifth-year results from the Oregon study indicated a rapid decline in stem volume with a 1- or 2-year delay in vegetation control after planting for all four tree species. Therefore, results from the Oregon and Tasmanian studies also suggest that any delay in vegetation control after planting reduces the volume growth of young stands. Results from the oldest Oregon sites also suggest that the CP is at least 3 years long after planting and that increases in Douglas-fir, hemlock, cedar, and grand fir volume growth, as with jack and red pine in our study, levels off after 3 or 4 years of continuous vegetation control.

In comparing the results of this study with other CP studies, it should be noted that tree seedlings in this study were planted into dense grass to ensure that a high level of interspecific competition was experienced by tree seedlings from the beginning of the study. The establishment of CP studies on forest sites, where postharvest vegetation recovery has been suppressed using site-preparation treatments, may produce results different from those presented here. For example, delaying the onset of interspecific competition from effective site-preparation treatments could reduce the influence of treatments applied immediately after planting and therefore increase the relative importance of later treatments when vegetative competition was higher. This difference could shift the CP and TEI to the right and possibly influence the length of the CP.

Influence of repeated herbicide applications on vegetation dynamics

The influence of vegetation management treatments on the composition and diversity of forest plant communities has been a question of concern (Sullivan et al. 1998; Haeussler et al. 1999; Miller et al. 1999; Schabenberger and Zedaker 1999). Most investigations into the effects of vegetation control on the diversity of plant communities have focused on the effect of one-time site-preparation or competition release treatments intended primarily to reduce the density of shrub and hardwood species. Overall, the diversity of early-successional plant communities, as indicated by species richness and diversity indices, has not been substantially reduced from such treatments (Sullivan et al. 1998; Haeussler et al. 1999; Miller et al. 1999; Boateng et al. 2000). The influence of more intensive vegetation management regimes, however, particularly those involving extended control of herbaceous vegetation using herbicides, has not been documented.

Results from this study demonstrated that repeated herbicide applications had a substantial influence on the plant community not only during the sequence of treatments, but for at least 5 or more years after treatment (Fig. 3). Total cover at year 10 decreased as the number of repeated treatments increased. Despite this reduction in abundance, however, species of all vegetation classes (conifer, hardwood, tall shrub, shrub, grass, forb, fern, sedge, lichens, and moss) were represented in all treatments during the 10th year. Species richness of higher plants was somewhat lower in plots that were treated for 5 continuous years (43 species) relative to untreated plots (51 species). Our PCA of the vegetation community revealed that the primary difference produced by repeated herbicide applications was the proportional shift in the abundance of shrubs, ferns, and mosses. This analysis also revealed that vegetation responses to the treatments were very consistent among the blocks over the 10 years.

An analysis of species diversity resulting from these treatments in year 5 by Wagner and White (2002) indicated that both the Shannon–Weiner and Simpson diversity indices increased over time as herbicide treatments were repeatedly applied. This unexpected result was attributed to the repeated herbicide treatments increasing species evenness more than they reduced species richness, thus leading to increased diversity values when using these indices. As a result, the Shannon–Weiner and Simpson diversity indices were determined to be unsuitable metrics of diversity in plant communities exposed to intensive vegetation treatments.

Interspecific competitive effects on volume growth

Our analysis of how changes in the vegetation community influenced annual volume growth over the decade revealed that total vegetation cover in a given year was among the most important variables accounting for variation in annual volume growth of each conifer species (Table 4). Volume growth increased primarily with the number of years of herbicide treatment, and was less strongly influenced by whether the treatments were applied earlier or later. Separating the influence of treatment timing versus duration was somewhat confounded, however, because large numbers of repeated treatments also had to be applied early in the period.

Although the array of treatments in this study produced different amounts of woody and herbaceous vegetation (Fig. 4), we found no difference in the competitiveness of either class of vegetation on the volume growth of the four conifer species (Table 4). This lack of difference was likely due to the low abundance of tall shrubs (primarily *Prunus pensylvanica*, *Prunus virginiana*, and *Salix* spp.) relative to the abundance of slower-growing shrubs (primarily *Vaccinium angustifolium*, *Diervilla lonicera*, *Lonicera hirsute*, and *Amelanchier sanguinea*) that were apparently no more competitive than associated herbaceous species (primarily grasses and ferns). Several studies have compared the relative competitiveness of woody and herbaceous plants (Perry et al. 1993; Richardson et al. 1993, 1996; Wagner and Radosevich 1998; Bell et al. 2000). In some cases, herbaceous species were found to be more competitive than woody species (Zutter et al. 1986; Morris et al. 1993; Wagner and Radosevich 1998). In cases where vegetation dynamics have been followed over time, herbaceous plants have been shown to be more competitive immediately after establishment and then become relatively less competitive as woody species dominate the stand (Richardson et al. 1993, 1996; Bell et al. 2000; Miller et al. 2003).

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