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Grass interference limits resource availability and reduces growth of juvenile red pine in the field

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Application. Site preparation methods can influence the intensity of grass interference and early seedling performance on routine reforestation sites in temperate and boreal regions. Removal of grass interference increases solar radiation reaching the canopy, reduces seedling water stress, improves mineral nutrition, and stimulates juvenile growth of red pine in the field.

Abstract. The effects of competing grasses on resource availability, growth and ecophysiological characteristics of 3-0 red pine (*Pinus resinosa* Ait.) seedlings were examined the first two years following outplanting in Anoka County, Minnesota, USA. Equal numbers of seedlings were planted into suppressed and undisturbed grass communities in a sandy soil. Grass suppression was maintained throughout the first growing season, but partially discontinued thereafter on the site. During the first field season interference from grass reduced pine seedling root collar diameter, needle length, number of new root tips, and lateral root length by over 40%. Mean pre-dawn needle water potential was 0.55 MPa lower in undisturbed grass plots during a brief drought in year one, but otherwise water stress was not significantly ($p = 0.05$) influenced by grass interference. The presence of grass also reduced, up to 50%, the photosynthetically active radiation reaching the seedling canopy. At the end of year one, total biomass N, P, K, and Ca content were significantly ($p = 0.05$) less in seedlings growing in the undisturbed grass community. Nitrogen was deficient in seedlings growing in grass. After two growing seasons, seedling shoot length ($p = 0.03$), root collar diameter ($p = 0.001$), and needle length ($p = 0.001$) were significantly less (40, 54 and 20%, respectively) for seedlings growing in undisturbed grass. Seedling growth reductions induced by grass competition were associated with multiple environmental stressors in the field and not restricted to water stress as was observed in earlier studies with pine species at low and mid-latitude sites.

Introduction

Interspecific interference from herbaceous plants, especially grasses, significantly reduces field survival and juvenile growth of temperate and tropical pine (*Pinus*) species (Coates et al. 1993; Lowery et al. 1993; Morris et al. 1993; Nambiar and Zed 1980). Limiting soil moisture is cited as the principal detrimental effect of competing grasses in establishment of some pine species

(Grossnickle and Heikurinen 1989; Gjerstad et al. 1984). However, interference with seedling light reception (Strothman 1967) and nutrient uptake (Squire 1977) have not been fully considered in field assessments. Moreover, in boreal and sub-boreal regions the impact of prolonged cool soil temperature may also contribute to reductions in juvenile growth of conifers (Lopushinsky and Kaufmann 1984; Lavender 1980). Chemical and physical site-preparation treatments have been designed to provide suitable microsite conditions for establishment of pine seedlings, but not all treatments are equally effective (Sutton 1993; Graham et al. 1989).

Controlled environment studies suggest that limiting light, nutrition or temperature may suppress juvenile shoot and root growth of red pine (*Pinus resinosa* Ait.) seedlings. Needle elongation, terminal bud formation, and root growth were depressed in seedlings subjected to low soil moisture levels (Becker et al. 1987; Clements 1970). Reductions in shoot and root biomass were observed in seedlings grown under less than half of full light (Smith 1982; Logan 1966). Shifts in mineral nutrition also influence early development of container-grown red pine seedlings (Timmer and Armstrong 1989). Furthermore, root length and number of root tips of red pine seedlings are limited at soil temperatures below 16 °C (Andersen et al. 1986).

Preliminary field surveys suggest grass competition in juvenile red pine plantations may influence a number of environmental factors including: soil water and temperature, ambient light and temperature, and mineral nutrition (Cannell and Grace 1993; Nambiar and Sands 1993). Relatively few assessments have quantitatively considered the impact of resource availability conditions on the early growth red pine or associated high-latitude forest species (Grossnickle and Heikurinen 1989). Lambert et al. (1972) attributed the field growth response of 7-year-old red pine released from grass competition to increased soil water availability. Two years after planting red pine seedlings in a shrub cover, Strothman (1967) observed positive root and shoot growth responses attributable to release from light and soil moisture competition. Thus, the relative or concomitant importance of environmental stressors associated with neighboring plants to the juvenile growth of red pine has not been fully established.

The objectives of this study were: (i) determine the effect of grass interference on the juvenile shoot and root growth of 3-0 red pine seedlings following outplanting; and (ii) characterize how factors associated with grass interference influences seedling water balance, nutrient status, light interception, and soil temperature.

Materials and methods

Seedling history

Red pine (*Pinus resinosa* Ait.) seedlings (3-0) were lifted from the General Andrews Nursery, Willow River, Minnesota USA, in late April before bud flush and stored at (7 ± 1 °C) in Kraft/polyethylene bags until outplanting (approximately one week) to maintain dormancy. The lifting, packing and storage regimes followed operational procedures of the Minnesota Department of Natural Resources (Caldwell et al. 1986). A sub-sample of the seedling population prior to outplanting revealed mean total dry weight was approximately 30 ± 2 g and shoot length was 17 ± 1.5 cm.

Site description

The study was conducted in Anoka County, Minnesota, USA. All woody vegetation had been removed from the site several years before the study was implemented. Composition of indigenous plants was determined from biomass clipped in year one (June) at the soil surface of 40 randomly selected field plots at the study site. Each circular plot was 40 cm in diameter. The vegetation present, as a percent of total oven dry weight, was: 66% quackgrass (*Agropyron repens* (L.) Beauv.); 30% redtop (*Agrostis alba* L.); and 4% other grasses and forbs, chiefly fowl meadowgrass (*Poa palustris* L.). Historically, species composition shifts less than 5% annually on sites with this soil and vegetation complement (Tilman 1983).

Historical mean ambient temperature and precipitation from May to September on this site are 19.1°C and 43 cm, respectively (Baker et al. 1985; Baker and Kuehnast 1978). The soil is a Soderville fine sand with mottling at 50 cm (Grigal et al. 1974). Soil texture in the top 30 cm is 90% sand, 1% silt, and 9% clay. Bulk density of the soil was 1.3 g/cm^3. Soil nutrient concentrations in the upper 15 cm did not differ significantly between blocks and mean values were 1300, 192, 35, 673 and 57 mg kg^{-1} for N, P, K, Ca and Mg, respectively. Soil sampling and analysis procedures are described by Grigal et al. (1974).

Site preparation, seedling establishment and experimental design

Grass was suppressed (by hand weeding) around one-half of the seedlings by removing all vegetation in a 1.5 m diameter planting plot centered on the shoot to create a interference-free planting area (Sutton 1993). At least 1 m of native vegetation remained between planting areas. Seven days later, all planting areas were sprayed with simazine at 2.8 kg a.i. /ha to discourage revegetation

(Eckert 1979). Glyphosate in a water carrier was later applied, with a pressurized back-pack sprayer equipped with a flat fan nozzle, at approximately 1.0 kg/ha a.i. to kill green vegetation in circular plots unaffected by the previous treatments. The planting areas were continuously weeded throughout the first growing season (April–September) to prevent revegetation.

In May of year one, two weeks after grass was removed from circular plots, the red pine seedlings were hand planted in areas with and without grass interference. The experimental design was a randomized complete block design. The planting area treatments (with undisturbed grass and grass suppressed) were randomly assigned to rows within four blocks (replicates). Each block contained 85 seedlings per treatment. The total number of seedlings established was 680 (4 blocks × 2 treatments × 85 seedlings per treatment).

Grass was not suppressed in planting area plots during the second growing season to evaluate seedling performance in partial grass interference. When not controlled, quackgrass and various annuals, primarily groundsel (*Senecio* spp.), reinvaded in 14–21 days. The vegetation density, based on percentage of plot covered, was approximately half that of the undisturbed grass plots (Wilson and Tilman 1991).

Environmental measurements

Soil temperature was recorded at 1 cm and 15 cm depths at one location in each treatment. Ambient precipitation and mean temperature data were taken from a US Weather Bureau station approximately 400 m from the site (Baker et al. 1985). Soil water content of the upper 30 cm was measured gravimetrically during the first growing season (Dixon and Hiol Hiol 1992). Photosynthetically active radiation (PAR) was measured bi-weekly immediately adjacent to 12 seedlings in each treatment (Grossnickle and Heikurinen 1989). Radiation levels (W) were measured vertically at 5 cm, 20 cm, and 30 cm above the soil surface using a portable sensor (LI-COR, LI-185, Lincoln, Nebraska, USA).

Environmental conditions

The first growing season following outplanting was relatively cool with precipitation above historical means (Baker et al. 1985; Baker and Kuehnast 1978). The ambient mean temperature from May through September was 17.5 °C. A short drought occurred July 3–16, but otherwise, rainfall was well distributed over the growing season (Fig. 1), and totalled 46 cm, slightly above normal for this region. During the second growing season, May through September, mean ambient temperature was approximately 18.6 °C. Over 10

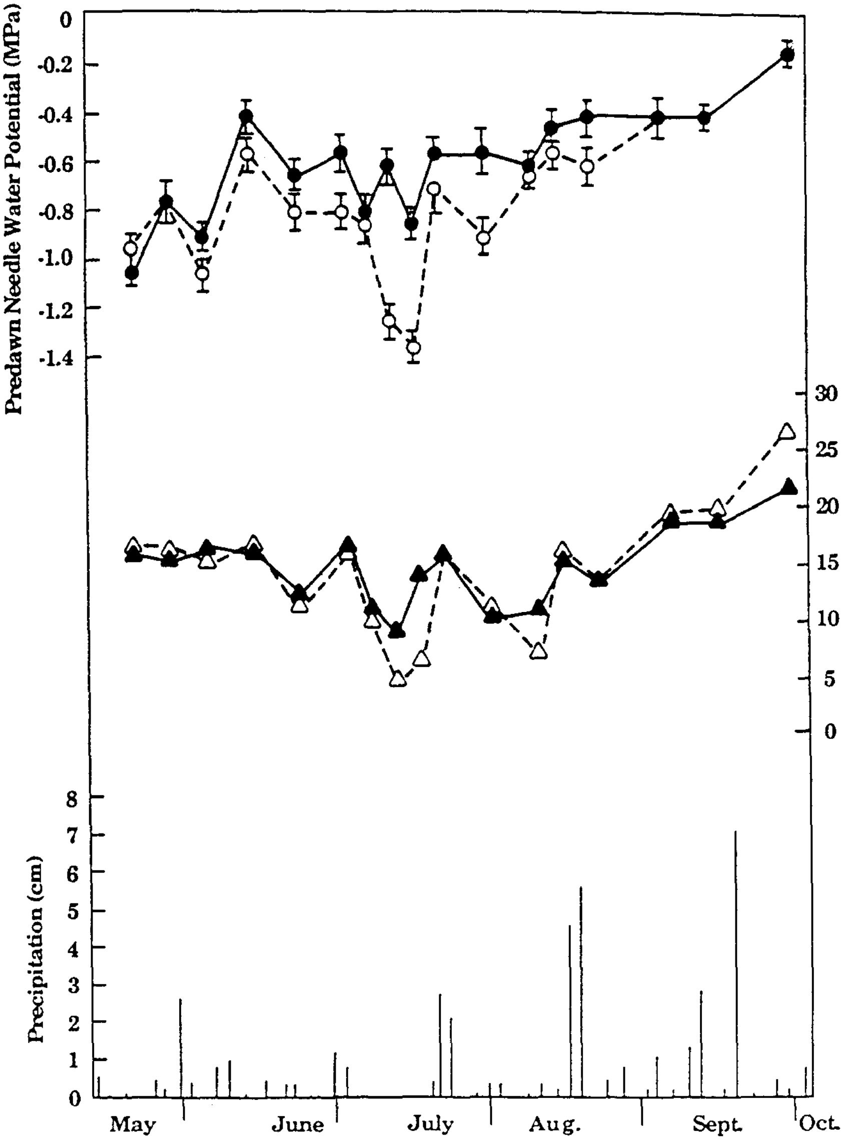

Fig. 1. Pre-dawn needle water potential of 3-0 red pine seedlings, soil water content in the top 15 cm, and precipitation during the first growing season after outplanting in Anoka County, Minnesota, USA. Closed symbols (•) indicate grass suppression treatment; open symbols (o indicate undisturbed grass treatment. Bars indicate one standard error.

cm of precipitation fell each month from June through August, contributing to a May through September total of approximately 60 cm.

Seedling morphology

Shoot length and root collar diameter were measured on every seedling at planting and at the end of each growing season. In September of each year, needle length was measured on at least 20 seedlings in each block (80 per treatment), and terminal bud length was measured on 13 seedlings in each block (52 per treatment). New root tips (white, >2 mm in length) and total root biomass were determined monthly (June thru September) in year one for three randomly chosen seedlings excavated from each block using techniques described by Dixon et al. (1981). Total lateral root length was determined by applying a root biomass/root length relationship, using techniques described by Voorhees et al. (1980). Seedling survival was quantified after both growing seasons (September).

Seedling ecophysiological measurements

Pre-dawn needle water potential was measured weekly throughout the first growing season using a pressure chamber and techniques described by Ritchie and Hinckley (1975). One fascicle from the previous year's foliage of three randomly chosen seedlings in each block (12 per treatment) was measured. Needles were kept in humid vials up to 10 min before measurement (Kaufmann and Thor 1982).

Leaf and stem samples of seedlings sampled monthly (June through September; sample procedures same as root system analysis above) were digested (Mitchell et al. 1984), and mineral content of tissue was determined. Total tissue N was determined using the Kjeldahl method (Morris et al. 1993). Concentrations of extractable P, K, Ca, and Mg were determined by inductively coupled plasma spectroscopy (Mitchell et al. 1984). The mineral deficiency of the seedling needle tissue was ranked using procedures of Swan (1972).

Statistical methods

Significant differences (p = 0.001 to 0.10) between treatment means for seedling survival, morphology and water status were detected by t-tests (Snedecor and Cochran 1967). Seedling survival data were subjected to arcsine transformation before analysis. Tissue nutrition data were subjected to an analysis of variance (ANOVA), in which the June and September samples were considered split-plots in time. Duncan's multiple range test was used to separate means when the ANOVA produced a significant F-value (p = 0.05).

Table 1. Vertical profile of incident photosynthetically active radiation (PAR) on a clear day in July, between 1100 and 1230 hours in year one. Values are mean ± one standard error.

Height above soil surface (cm)	Undist. grass		Grass suppression	
	% full $W \cdot m^2$	PAR ($\mu E \cdot m^2 \cdot s$)	% full $W \cdot m^2$	PAR ($\mu E \cdot m^2 \cdot s$)
100	187 ± 6	100.0	189 ± 5	100.0[a]
30	135 ± 18	72.4	176 ± 11	92.9
20	100 ± 25	53.4	171 ± 10	90.5
5	57 ± 19	30.6	152 ± 17	80.6

[a] Values are percentage of maximum.

Results

Light

Seedlings growing in grass received less PAR than those growing in grass suppressed plots (Table 1). At 20 cm, which approximated the top of the seedling during the first growing season, and the mid-crown during the second growing season, incident PAR was approximately 40% lower in the undisturbed grass treatment.

Soil temperature and moisture

Soil temperature and moisture conditions in year one differed by depth and treatment (undisturbed grass vs. suppressed grass). Mean soil temperatures at 15 cm depth were more constant and ranged 5–20 °C lower than at 1 cm. In the undisturbed grass treatments, mean daily temperatures at 15 cm depth were 2–3 °C lower until August than in the suppressed grass treatment. At 1 cm, mean daily soil temperatures were 4–5 °C lower in the undisturbed grass until mid-July. Thereafter, the two treatments had similar soil temperatures. Soil water content in the upper 15 cm was 6% (approximately −0.45 MPa) in both treatments during most of the first growing season (Fig. 1). Soil moisture was less in the undisturbed grass plots during brief droughts in July and August.

Seedling survival and morphology

Seedling survival after two growing seasons was 82% with and without grass suppression (no significant difference). However, several measures of

Table 2. Shoot and root system morphology of 3-0 red pine seedings in grass suppression and undisturbed grass plots following outplanting in Anoka County, Minnesota, USA.

Site Prep. Treatment	Annual shoot growth (cm)		Annual diameter growth (mm)		Needle length (mm)		Bud length (mm)	Shoot weight (g)	Root weight (g)
	year								
	1	2	1	2	1	2	1	1	1
Suppression	6.2	6.9	0.6	2.6	67	133	11	8.85	2.82
Grass	7.4	4.1	0.2	1.2	39	105	9	4.26	1.43
P value	0.10	0.03	0.001	0.001	0.001	0.001	0.05	0.04	0.001

seedling growth were lower in the undisturbed grass treatments during both growing seasons (Table 2). After one growing season, annual seedling root collar diameter growth (p = 0.001), needle length (p = 0.001), and biomass (p = 0.04) were all reduced by 40% or more. Shoot biomass changed little in the undisturbed grass plots between June and September. After the second growing season, reductions in the same plots for seedling shoot length (p = 0.03) and root collar diameter (p = 0.001) were 40% and 54%, respectively. Also a 20% significant (p = 0.001) reduction in needle length was observed in year two.

During the first year in the field, the occurrence of new seedling root tips were significantly (p = 0.05) more numerous from late June through mid-October in the controlled grass plots (Fig. 2). The greatest differences in root growth were observed from August through September. Significant (p = 0.05) reductions in total lateral root length occurred in undisturbed grass plots from July to September of year one.

Seedling water potential

Although soil moisture was near field capacity, June pre-dawn needle potentials in both treatments were approximately −0.75 MPa (Fig. 1). From mid-June to late August, pre-dawn needle water potential of seedlings growing in grass were significantly (p = 0.05) lower than water potentials of seedlings in the controlled grass plots. The greatest difference between treatments (about 0.55 MPa) was measured during a brief drought in July of year one. Needle water potential and soil water content were correlated only in the undisturbed grass treatment plots (r^2 = 0.69; p = 0.05).

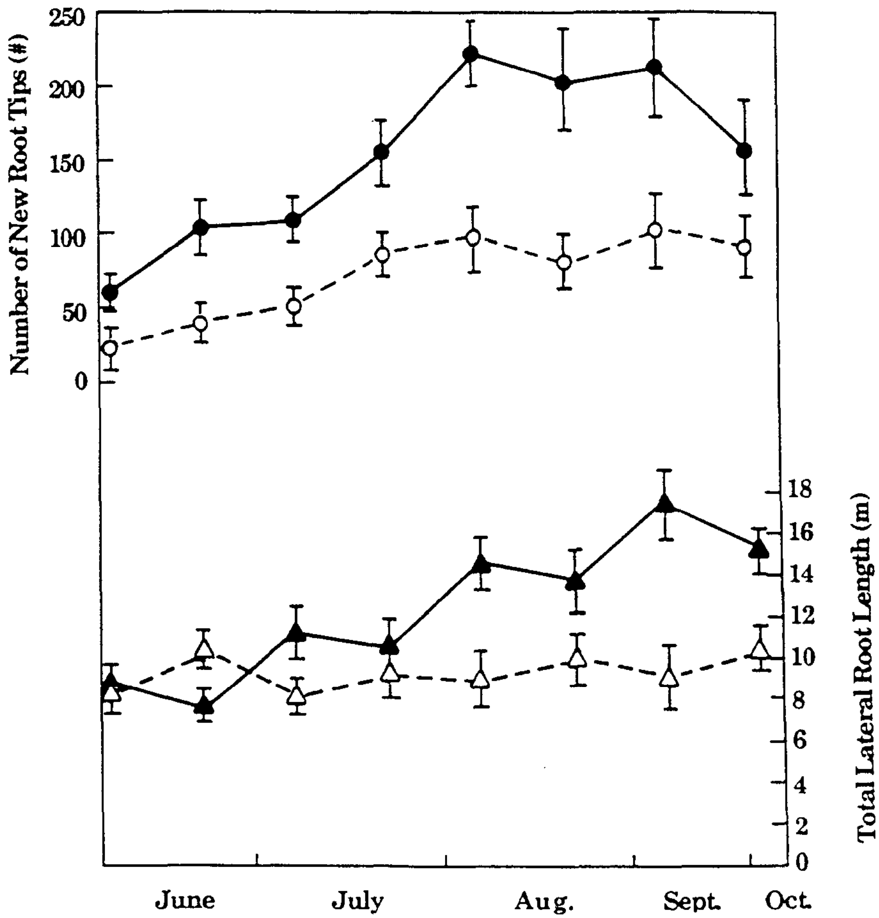

Fig. 2. Number of new root tips and lateral root length of 3-0 red pine seedlings during the first growing season after outplanting at Anoka County, Minnesota, USA. Closed symbols (•) indicate grass suppression treatment; open symbols (o) indicate undisturbed grass treatment. Bars indicate one standard error.

Tissue nutrient contents and concentrations

Seedling nutrient concentrations and contents were not significantly different between treatments in June of year one (Table 3). In September needle samples, N concentration was significantly ($p = 0.05$) higher in the grass suppressed plots, as were the total element contents of N, P, K, and Ca. Nutrient contents in stems differed between treatments in the same way as element content in needles, but treatment differences were not statistically significant ($p = 0.05$). Except for the increase in seedling Ca content in the suppressed grass plots in September, the nutrient content of stems did not change between June and September.

Discussion

Grass interference suppressed shoot and root growth of 3-0 red pine seedlings and accelerated loss of lower needles in each of two growing seasons following planting. These results are consistent with the analysis of herbaceous interference and pine species establishment in low- and mid-latitude regions, but the ecophysiological response mechanism(s) appear to be different for red pine (Nambiar and Sands 1993; Cannell and Grace 1993; Morris et al. 1993). Growth of red pine seedlings in the undisturbed grass community was probably reduced by a combination of reduced PAR, lower needle water potentials, less nutrient uptake and accumulation, and low soil temperatures, but the relative contribution of each factor is difficult to quantify because of the research methodology employed (Nambiar and Sands 1993; Morris et al. 1993). A reduction in growth of red pine seedlings in the grass community when water was not continuously limiting suggests light and mineral resources and soil temperature can be significant limiting microsite factors.

Seedlings established in grass received 30–55% of full incident PAR during the first growing season and less than 75% during the second growing season. In shading experiments over 4–5 years, 45% full light reduced red pine shoot biomass by 49%, root collar diameter by 34% and root biomass by 52% (Logan 1966). Further, reduced photosynthesis and translocation of sugars to the roots have been demonstrated for pine seedlings at very low light levels (Gordon and Larson 1970; Shiroya et al. 1966). Half as many new root tips were observed on red pine seedlings grown 28 days at 50% full light compared to full light (van den Driessche 1978). These data suggest that the pine seedlings in the undisturbed grass treatment received less than optimal light in year one (Smith 1982). However, the levels of incident PAR may not have been low enough to account for the total reduction in growth during the second growing season, when seedlings were somewhat taller.

Grass interference increased needle water deficits during the first growing season. Pre-dawn needle water potentials were significantly lower in the undisturbed grass plots (generally 0.2 to 0.4 MPa) from mid-June to late August. This difference increased to 0.55 MPa during a brief drought in July. However, in a complementary study in which seedlings growing in undisturbed grass received regular irrigation, and soil water was not limiting, juvenile growth was also reduced (Caldwell et al. 1986). In the complementary study, except during the brief July drought, seedling needle water potentials were consistently within 0.15 MPa in plots with and without grass

Table 3. Seedling needle element concentrations (%ODW) and total element content (mg) at budbreak and after budset in year one.

	N		P		K		Ca		Mg		Dry Wt
	(%ODW)	(mg)	(%ODW)	(mg)	(%ODW)	(mg)	(%ODW)	(mg)	(%ODW)	(mg)	(g)
June											
Suppression	0.81 a[a]	2.40 a	0.09 a	0.27 a	0.29 a	0.86 a	0.32 a	0.93 a	0.10 a	0.31 a	2.96 a
Grass	0.85 a	2.09 a	0.10 a	0.24 a	0.31 a	0.78 a	0.31 a	0.79 a	0.10 a	0.25 a	2.46 a
September											
Suppression	1.31 c	7.79 b	0.13 b	0.76 b	0.27 a	1.65 b	0.36 a	2.01 b	0.11 a	0.27 a	5.95 b
Grass	1.06 b	2.44 a	0.14 b	0.31 a	0.33 a	0.76 a	0.28 a	0.65 a	0.12 b	0.63 b	2.30 a
Deficiency[b]											
Moderate	1.0–1.3		0.05–0.12		0.20–0.30		0.02–0.03		0.03–0.05		
Marginal	1.3–1.8		0.12–0.15		0.30–0.45		0.03–0.04		0.05–0.07		

[a] Means followed by different letters within a column are significantly different ($p = 0.05$).

[b] Values associated with "moderate deficiency" and transition from deficiency to sufficiency ("marginal deficiency") in current year's needle of red pine seedlings using ranking system of Swan (1972).

interference. This observation suggests that a water deficit in the undisturbed grass was not the most limiting factor for red pine at all times. This conclusion is supported by a controlled environment study of red pine seedlings subjected to artificial drought cycles (Becker et al. 1987). They observed that all measures of growth except bud size were similar among drought treatments with average seasonal predawn water potentials of -0.8 and -1.1 MPa.

Grass interference with soil nutrient availability may have contributed to reduced seedling growth. In the undisturbed grass plots, total stem or needle content of N, P, K, and Ca did not increase from June to September. Soil and seedling tissue levels of K were marginally deficient in both treatments (Wilde et al. 1964; Swan 1972), yet N appeared to be the chief limiting nutrient in the grass plots. Seedling needle N concentrations in the grass were deficient for red pine (Swan 1972). Further, in contrast to P and K, needle N concentrations were significantly lower in the undisturbed grass treatment than in the suppressed grass treatment, which would be expected of the limiting element (Timmer and Armstrong 1989). Deficiency may have resulted from direct consumption of N by grass roots. Quackgrass and redtop, with thick matted root systems, are N demanding species (Wilson and Tilman 1991). Also significant in this study were the smaller root systems and fewer new root tips present on the red pine seedlings in the undisturbed grass in year one, which decreased access to the available soil nutrients and other resources.

In addition to the limitations of light and nutrients, differences in soil temperature may have affected root growth in the early part of year one. Anderson et al. (1986) observed that the number of new roots in red pine seedlings peaked at 16 °C, and elongation of new roots was greatest at 20 °C. In the current study, mean weekly soil temperature at 15 cm beneath the grass cover during the first growing season reached 16 °C in late June, and 20 °C in early July. Without grass cover, the soil warmed more quickly, reaching optimum temperatures about two weeks earlier (thus, seedling root systems may have access to soil water and nutrients earlier, before occurrence of drought). The greater number of new root tips in the suppressed grass treatment in mid-June may partially be a result of warmer soil temperatures at 15 cm in late spring. Seedling water deficits in the plots with undisturbed grass may have been partially attributable to low soil temperatures (Lopushinsky and Kaufmann 1984).

The causal link between resource limitations and growth impacts on neighboring plants is difficult to detect and quantity (Mitchell et al. 1993; Wagner et al. 1989). However, red pine response to interference induced soil moisture stress is not necessarily similar to that of pines occurring on low- and mid-latitude sites (Coates et al. 1993; Morris et al. 1993). Soil moisture deficits were probably most influential during July of year one, when low rainfall resulted in low pre-dawn needle water potentials in the undisturbed grass treatment. Yet, seasonal water potential trends were not reflected in seedling root growth patterns. Every early and late in the growing season, when soil moisture was adequate, seedlings competing with grasses had less root growth. During this period, reduced light reception and seedling nutrient uptake were most likely the primary factors decreasing root growth in the grass treatment. Nearly half the incident radiation was blocked by competing grasses, and tissue levels of N were deficient.

The benefits of controlling grass in the first growing season carried over to the shoot and root growth patterns of the second growing season (Rehfeldt and Lester 1966). Morris et al. (1993) also observed that second year shoot growth of loblolly pine (*Pinus taeda* L.) was influenced by first year herbaceous plant interference. In this study, vegetation invading the grass suppression plots was less dense than the undisturbed perennial grasses, so interference with light, nutrients, and water availability was probably not as intense. Moreover, seedlings in the controlled grass plots were larger at the beginning of the second growing season, with more developed root systems, enabling them to utilize a greater share of the available resources.

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