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Competition control in juvenile hybrid poplar plantations across a range of site productivities in central Saskatchewan, Canada

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Abstract The response of hybrid poplar plantations established on former agricultural land in Saskatchewan to competition from weeds on a range of site productivities was studied. The short-term impact of competition control on the growth of juvenile trees and how tree responses to competition control differed across the productivity gradient was of particular interest, as was the determination of which resource was most highly competed for and was most important in determining tree growth. Eight sets of paired plots in juvenile hybrid poplar plantations were established in central Saskatchewan across a range of site productivities. In each pair, one plot had complete weed control (weed-free) while in the other plot weeds were allowed to grow. The best soil predictor of tree growth was soil texture, represented by a combination of the percentage silt and clay, with finer textures showing better growth. Competition control significantly increased tree growth on all sites with the benefit being greatest on the higher productivity sites. Soil water appeared to be highly competed for between trees and weeds and was a dominant resource controlling growth. For soil nutrients, nitrogen and phosphorous were highly competed for between trees and weeds. However, leaf phosphorous concentration of the weed-free plots had a strong positive relation to tree growth while nitrogen did not, indicating that when trees are free of competition they can access sufficient nitrogen from these soils.

Keywords Agricultural soils · Productivity · Competition control · Foliar nutrition · Soil moisture · Growth rates · Leaf weights

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Introduction

Afforestation projects establishing tree plantations, in particular hybrid poplars, on agricultural land are currently being advanced on the Canadian prairies. The goal of these plantations is to supply timber for the forest products industry and meet a variety of other environmental objectives such as sequestering carbon and increasing landscape biodiversity (McKenney et al. 2004). The transitional zone between forest to the north and prairie to the south has been suggested as a prime candidate area for these projects (Schroeder et al. 2003). The natural soils of the area are generally Chernozems with a topsoil layer rich in organic matter and nutrients (Soil Classification Working Group 1998). However, a wide range of site productivities is observed within this zone due to differences in soil factors such as texture and organic matter content (Schroeder et al. 2003).

Hybrid poplar (HP) clones bred specifically for the growing environment of the northern prairies, i.e. dry climate and short growing season, have shown the most promise for meeting these afforestation goals. However, these clones are intolerant of competition and have relatively high resource demands (Wittwer and Immel 1980; Hansen et al. 1988; Shock et al. 2002). These HP plantations are expected to grow on a 20-year rotation with yields averaging about 12 m^3 ha^{-1} $year^{-1}$ (van Oosten 2006). The major restriction to successfully establishing these plantations is the severe interspecific competition the trees experience from agricultural weeds which can lead to greatly reduced tree growth or even plantation failure if the weeds are not controlled (van Oosten 2006).

There have been many studies examining the effects of interspecific competition in young tree plantations but almost all of these studies have focused on coniferous trees in forested landscapes (see review by Wagner et al. (2006)). Moreover, most experiments have been designed using only one or two sites so that the differences in tree responses to competition across a range of site productivities cannot be examined. Studies that have included a range of productivity have most often used differences in climatic factors rather than soil properties as the basis for the differences in productivity and response to competition (e.g. Little et al. 2007). Similarly, there have been significant challenges in ecological research in determining how interaction intensity between plant species varies as a function of site productivity. The most recognized theories are that competition intensity augments with increasing site productivity (Grime 1973) or it can be about the same across a range of site productivities (Newman 1973; Tilman 1988), but other models now suggest that competition intensity decreases with site productivity (e.g. Goldberg et al. 1999). Clearly, more work is needed to elucidate this important question.

This study is unique in that it deals with the response of HP plantations to competition from weeds on a range of site productivities due to soil factors within a single climatic region. In particular, the goals of this study are to examine: (1) the impact of competition control on the growth of juvenile trees, (2) how tree responses to competition control differ across a gradient of site productivities and (3) which resource is most highly competed for and is most important in determining tree growth.

Methods

Study area

Four HP plantations located on old agricultural crop land in central Saskatchewan, Canada, near the cities of Saskatoon (52°08′ N 106°39′ W) and Prince Albert (53°12′ N

105°42′ W) were selected for study in areas that have been identified as having potential for hybrid poplar plantation establishment (Schroeder et al. 2003). This is a relatively dry area receiving on average 380 mm of precipitation per year and having a significant summer moisture deficit. However, the summer of 2006 when this study took place had higher than normal precipitation (400 mm of rain during the growing season) which was approximately the same between all of the sites. A summary of soil properties for each of the plots is given in Table 1.

The sites were planted in the spring of 2005 at a spacing of 3 m × 3 m which is the recommended spacing in Saskatchewan for pulpwood crops (van Oosten 2006). Operational weed control was performed by the individual land owner at each site prior to and after planting during the first growing season and consisted of cultivation with a small tractor, mowing of the weeds or herbicide application. At each plantation, two sets of paired plots were established with 10 trees in each plot. Plots were generally arranged in a 4 tree × 3 tree pattern since there were almost always two trees in this area that were missing or dead resulting in 10 trees per plot. Both plots for each pair were placed in similar topographic positions within the plantation and were separated by less than 15 m. However, the two pairs within each plantation were in different topographic positions; one of the pairs of plots was located in an upper slope position and the other pair was located in a lower lying area. This enabled the selection of plots to cover the widest range of site productivities. A single HP clone was used in each of the plantations but the specific clone used varied by site resulting in three different, but genetically related clones: Assiniboine, Hill and Walker. Although these clones may not react in the same way to different site conditions, a much stronger impact on poplar growth is expected from site and weeding treatments than clonal effects.

For each pair of plots, one of the plots was randomly chosen to have complete weed control and the other was allowed to have weeds grow. Weed control was done manually by hoeing the plots every 2 weeks to a radius of at least 1.5 m around each tree and resulted in almost complete weed control. This weeding treatment has likely reduced most, but not all, of the impacts of weeds on competition with the trees for resources because the roots of hybrid poplars grown at the sites had probably expanded slightly more than 1.5 m laterally over 2 years (Guillemette 2006) and would thus have experienced competition with the weeds outside of the cleared area. At all of the plantations there was a high abundance of common agricultural weeds such as lambsquarters (*Chenopodium album*), kochia (*Kochia scoparia*) and Canada thistle *(Cirsium arvense).*

Table 1 General soil properties of the study plots

Plot	Plantation	Silt + clay (%)	pH	Total C (mg/g)	Total N (mg/g)
1	A	34.9	7.8	21	2.5
2	A	38.6	7.0	25	2.9
3	B	52.7	8.1	19	2.2
4	B	38.7	7.7	16	1.9
5	C	25.6	6.3	29	3.2
6	C	23.8	6.4	30	3.1
7	D	18.4	6.0	14	1.6
8	D	9.2	6.2	10	1.2

Field sampling

Throughout the growing season from mid-May until early September, the plots were sampled every two weeks (i.e. total of eight sampling dates in 2006). Within each sampling period, the plots were weeded, the heights and basal diameter of each tree were measured, soil moisture around each tree at a depth of 15 cm using a Field Scout time domain reflectometry 300 probe (Spectrum Technologies, Plainfield, Illinois) was measured, and soil temperature at a depth of 10 cm was measured using an electronic thermometer at four locations in each plot. During August, before significant retranslocation of nutrients occurs within trees, fifteen leaves were collected from the top of each tree and then oven-dried for nutrient analysis. At the end of the growing season, one sample of topsoil to a depth of 15 cm was collected from one location in each plot for texture and nutrient analysis. Also at this time, all of the above-ground weed biomass within a 0.5 m radius of four of the trees in each weedy plot were collected, dried and weighed for competition biomass estimates and species identification. Light was measured with an integrating ceptometer on a clear day within one hour of solar noon at 50, 100 and 200 cm above ground around each tree. This was then compared to a reading in full sunlight to give a per cent light transmission value.

Laboratory analysis

Soil samples were air-dried and then sieved through a 2 mm mesh to remove any coarse fragments before analysis. To determine the particle size distribution, samples were first treated with NaOCl due to the high carbon levels. Sodium hexametaphosphate and sonication were then used to disperse the samples before measurement on the Horiba Partica LA-950 Laser Particle Size Analyzer. Soil sub-samples were also ground for determination of total C and N using the Leco CNS-2000 Analyzer. Exchangeable cations were determined using atomic absorption after extraction with an unbuffered 0.1 M $BaCl_2$ solution (Hendershot et al. 1993).

Weed and leaf samples were oven-dried at 40°C immediately after collection to a constant weight and then ground prior to leaf C and N determination using the Leco CNS-2000 Analyzer. Leaf samples were digested in a concentrated HNO_3 solution at a ratio of 0.5 g leaf sample and 5 ml HNO_3 for four hours at 100°C in Teflon beakers covered with a Teflon watch glass. Calcium, Mg and K levels were then analyzed using atomic absorption/emission. Phosphorous was analyzed colourimetrically (molybdenum blue) from the same digests with a Technicon Auto-Analyzer.

Leaf samples from the four largest trees from each plot were also finely ground (<60 µm) and then analyzed for $\delta^{13}C$ by mass spectrometry using a RoboPrep Sample Converter interfaced with a TracerMass Stable Isotope Detector (Europa Scientific, Crewe, UK). The working standard was lentil (*Lens culinaris*) straw with a $\delta^{13}C$ of $-27.6‰$ relative to the PeeDee belemnite (PDB) standard. The average difference of duplicate samples was less than 0.1‰. $\delta^{13}C$ values from tree leaves can be used as an integrative measure of soil moisture availability throughout the entire growing season with more negative values indicating more water available to the plant. This method has been used in forestry to examine the effects of harvesting and silviculture operations on seedling water status (Gomez et al. 2002) and differences in plant community moisture availability (Stewart et al. 1995).

Statistical analysis

A mixed-model ANOVA was used to compare the effects of competition control on tree growth (Little et al. 1996). Data transformations were not needed to meet the ANOVA prerequisites so raw data are presented here. This model incorporated plantation, plot level variability nested within plantation, competition control treatment and the interaction between competition treatment and plantation. This model was chosen since the plots were specifically chosen to have the widest range of productivity possible and were not randomly selected. Paired t-tests were used to compare nutrient levels, soil moisture availability and soil temperature variables between treatments based on the results of the mixed-model ANOVA. Simple linear regression and Pearson correlation analyses were used to examine the relationships between soil properties, foliar nutrient status and tree growth for both competition treatments. Both absolute and relative growth differences were used to evaluate the impact of competition across a gradient of site productivities. Relative growth parameters account for differences in site productivity and eliminate the effects of the environment on the response (Goldberg et al. 1999). The relative interaction intensity (RII) index as proposed by Armas et al. (2004) was used with tree diameter growth as the response variable. Using this variable, potential values range from -1 to $+1$ with more negative values indicating more intense competition and positive values indicating facilitation. The equation for RII as adapted for this study is:

$$\mathrm{RII} = \frac{\mathrm{DGrowth_w} - \mathrm{DGrowth_{wf}}}{\mathrm{DGrowth_w} + \mathrm{DGrowth_{wf}}}$$

where ‘DGrowth’ is diameter growth, ‘wf’ is the weed-free treatment and ‘w’ is the treatment with weeds. All statistics were completed using SPSS version 15.0 (SPSS Inc., Chicago, Illinois).

Results

Tree growth

Site productivity was based on the height growth of weed-free plots, similar to the determination of site index in forestry (Carmean 1975). Average height growth of the weed-free plots ranged from 46 to 234 cm year^{-1}, indicating a large range in potential site productivities (Table 2). The best soil characteristic for predicting height growth was soil texture expressed as the percentage of silt + clay (ΣSilt + Clay) for both weed-free ($r^2 = 0.562$, $P = 0.020$) and weedy plots ($r^2 = 0.691$, $P = 0.006$) (Fig. 1). The best sites had a loamy texture with more silt and clay particles than the poorer sites which were either of loamy sand or sand texture. Other soil factors such as total C concentration ($P = 0.217$), total N concentration ($P = 0.124$) or C/N ($P = 0.796$) were not well correlated with height growth. The only other soil characteristic significantly related to average height growth was pH which was positively related ($r^2 = 0.507$, $P = 0.048$), indicating that the more productive sites also had more favorable soil nutrient availability. The soil textures in this study did not include heavier textured soils such as silty clay loams and heavy clays. As these heavier textured soils are considered to provide more productive agricultural land, the range of soil textures covered in this study represents the soils on which HP plantations will be established.

Table 2 Summary information (average of the 10 trees) for all plots for weed-free (WF) and weedy (W) treatments

Plot	Plantation	Weed-free plots		Weedy plots		
		Height growth (cm)	Diam. growth (cm)	Height growth (cm)	Diam. growth (cm)	Weed biomass (g)
1	A	234 (18)	4.0 (0.47)	81 (42)	1.1 (0.67)	126
2	A	224 (32)	2.6 (0.46)	86 (22)	0.9 (0.52)	130
3	B	195 (29)	3.2 (0.37)	112 (17)	1.3 (0.30)	261
4	B	165 (27)	2.8 (0.59)	105 (23)	1.0 (0.27)	361
5	C	150 (24)	2.4 (0.41)	46 (14)	0.8 (0.53)	151
6	C	145 (29)	2.4 (0.66)	31 (24)	0.5 (0.35)	317
7	D	114 (29)	2.1 (0.53)	81 (14)	1.3 (0.53)	238
8	D	46 (14)	0.9 (0.44)	48 (15)	0.8 (0.22)	59

Weed weight is the average weed dry weight from 0.5 m radius plots around 4 trees per plot in the weedy treatments (g/0.8 m^2). The values in parentheses are standard deviations

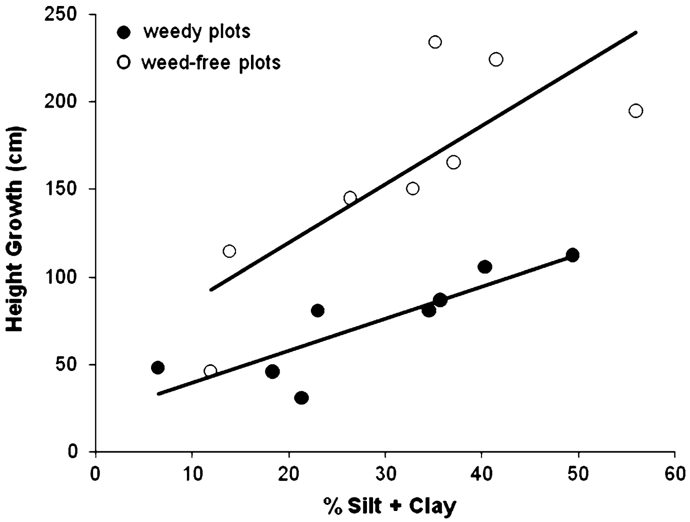

Fig. 1 Average height growth of weed-free ($r^2 = 0.562$, $P = 0.020$) and weedy ($r^2 = 0.691$, $P = 0.006$) plots in relation to the sum of % silt and clay in the soil

Competition control had a significant positive impact on diameter and height growth ($P < 0.001$). The plantation and plot effects nested within the plantation were also both significant ($P < 0.001$), indicating that there are differences in responses between plantations and between the individual pairs of plots in each plantation. Therefore, each pair of plots was subsequently treated as a distinct data point.

The absolute and relative benefits of competition control on diameter growth was greater on better quality sites (Fig. 2). By the end of the growing season, diameter was significantly ($P < 0.05$) greater in all weed-free plots compared to weedy plots and height was significantly ($P < 0.05$) greater in all but the lowest productivity site (Table 2). Leaf biomass was also significantly greater in all weed-free plots ($P = 0.001$).

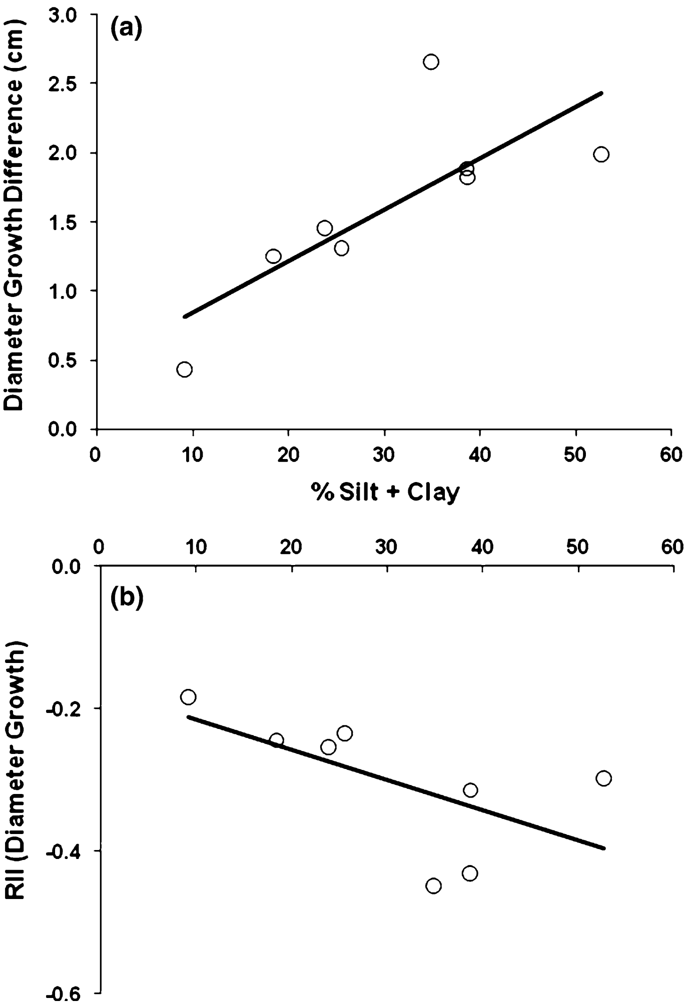

Fig. 2 Diameter growth benefit of competition control in relation to % silt + clay for both **a** absolute difference ($r^2 = 0.516$, $P = 0.027$) and **b** relative difference—RII ($r^2 = 0.275$, $P = 0.10$)

Site resources

Few weeds above 50 cm were present in the weedy plots which was below the level of tree leaves at most sites. Consequently, there was little negative effect on the light status of the trees due to weeds (data not shown). The average soil temperature was slightly higher in weed-free plots (0.5°C, $P = 0.003$) but this difference in soil temperature between treatments was not correlated to any differences in tree growth ($P = 0.654$).

Average summer soil moisture was significantly higher in weed-free compared to weedy plots ($p = 0.003$) and was strongly positively related to the amount of silt and clay in the soil ($p = 0.914$, $p = 0.002$). These general trends are supported by δ^{13}C values which show the weed-free trees had significantly lower ($p = 0.025$) average δ^{13}C values

(−27.1‰) than weedy trees (−26.0‰), indicating that weed-free trees had more water available to them throughout the growing season.

Tree nutrition was assessed by comparing foliar nutrient concentrations between weeding treatments and to optimal foliar N, P, K, Ca and Mg levels developed from HP plantation fertilizer studies in the north-central United States (Hansen 1994; Coleman et al. 2006) with similar growing conditions to those experienced in central Saskatchewan. Foliar N concentrations were significantly higher in the weed-free plots ($P < 0.001$) but foliar N was not strongly related to diameter growth in either weed-free ($P = 0.119$) or weedy plots ($P = 0.232$) (Fig. 3). Most of the weed-free plots were also above the optimal N concentrations.

Foliar P concentrations showed a different response to competition control with no difference between competition treatments ($P = 0.204$) while showing a very strong relationship to growth in the weed-free plots ($r^2 = 0.770$, $P = 0.003$) but not in the weedy

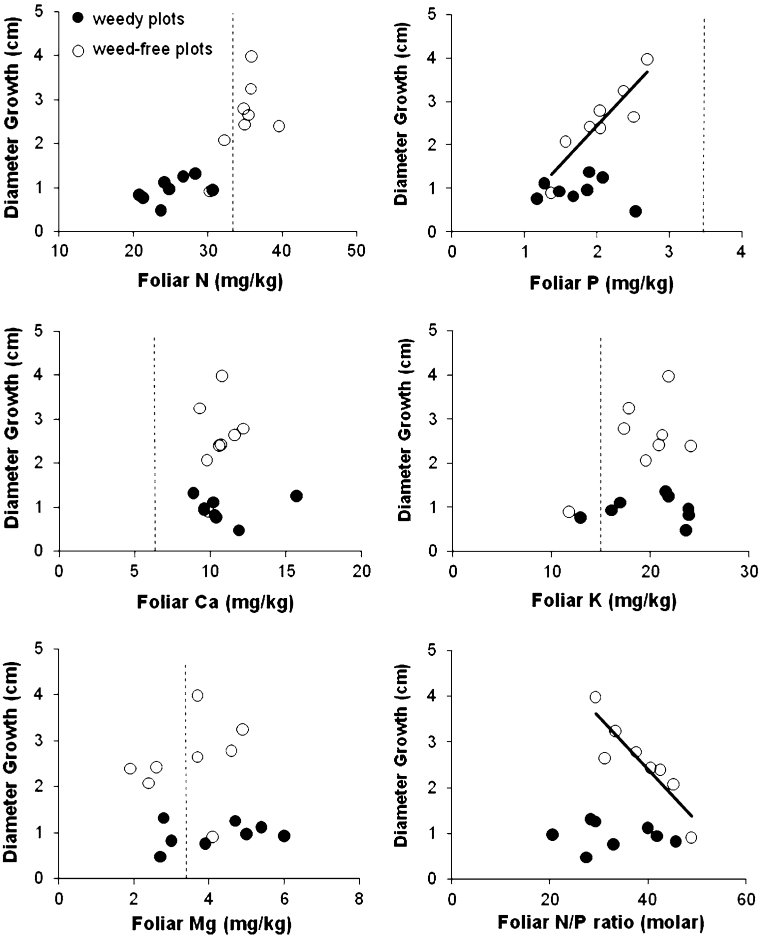

Fig. 3 Diameter growth in relation to foliar nutrient concentrations. The only foliar nutrient concentrations significantly related to tree diameter growth was P and P:N for the weed-free treatment ($r^2 = 0.770$, $P = 0.003$ and $r^2 = 0.798$, $P = 0.003$, respectively). The dotted lines represent the optimal foliar concentrations

Table 3 Foliar nitrogen (N) and phosphorous (P) concentrations for all plots for weed-free (WF) and weedy (W) treatments

Plot	Plantation	Weed-free plots		Weedy plots	
		N Conc. (g/kg)	P Conc. (g/kg)	N Conc. (g/kg)	P Conc. (g/kg)
1	A	35.9	2.69	24.2	1.28
2	A	35.5	2.51	30.7	1.48
3	B	35.8	2.37	26.7	2.08
4	B	34.8	2.04	24.8	1.87
5	C	35.0	1.90	20.8	1.67
6	C	39.6	2.05	23.7	2.50
7	D	32.2	1.57	28.3	1.89
8	D	30.3	1.37	21.3	1.18

plots ($P = 0.656$). In all plots, P concentrations were well below the optimal levels (Table 3). The N:P ratio also showed a strong relationship to growth in the weed-free plots ($r^2 = 0.798$, $P = 0.003$). For base cations, foliar K, Ca and Mg concentrations were not different between competition treatments ($P = 0.602$, 0.836, 0.059, respectively). They were also not significantly related to diameter growth in either the weed-free ($P = 0.135$, 0.584, 0.614, respectively) or weedy plots ($P = 0.965$, 0.858, 0.464, respectively). Foliar K and Ca were well above optimal levels for most of the weed-free and weedy plots (Fig. 3).

Discussion

Tree growth

Competition control significantly increased tree growth on all sites which was a response similar to many other studies for a variety of different species and locations (e.g. Mason and Milne (1999) for *Pinus radiata* in New Zealand, Löf and Welander (2004) for *Fagus* and *Quercus* in Sweden and Cain (1999) for pines in the southeast United States). The response to competition control in our study was rapid with significant differences in tree growth appearing during the same growing season as the competition control treatment. This rapid response has also been seen for other fast-growing, intolerant tree species such as loblolly pine (Perry et al. 1993) but slower growing species with determinate growth patterns, such as Engelmann spruce, have taken up to three years after repeated competition control to show any growth response (Biring et al. 2003). The treatment effect in our study, i.e. the growth difference between weed-free and weedy plots, was large with the greatest difference in height of 150 cm for the best sites. The impact of competition control after a single season in our study is comparable to the response shown by Jylhä and Hytönen (2006) for Scots pine in an old agricultural field in Finland 11 years after weed control. This large and rapid response of the HP trees in our study may be due to the growth characteristics of the trees which have been bred specifically for this climatic region but which are highly intolerant of competition or reduction in resource availability (Hansen et al. 1988; Shock et al. 2002). Once obtained, these HP trees were able to utilize these resources more efficiently, resulting in a rapid growth response. However, when they experience reduced resource availability, either through competition or abiotic factors, growth is greatly reduced.

Weed control on more productive growing sites had the largest absolute and relative benefit to tree growth while weed control on the very poorest site, which was of sandy texture, resulted in almost no improvement in tree growth. This is consistent with the theory of Grime (1973) that competition is more intense on more productive sites than on less productive sites since tree growth is controlled more by abiotic factors than by competition on these less productive sites (Goldberg and Novoplansky 1997). Other studies looking at tree growth response to competition on different site qualities have shown contrasting results. For example, Ladd and Facelli (2007) showed a similar response to our study for eucalypt trees in Australia with tree establishment only responding positively to competition control in the more productive environments. On the other hand, ponderosa pine growth in northern California and southern Oregon showed the largest response to competition control on the least productive sites (Powers and Reynolds 1999; Zhang et al. 2006).

The impact of competition control on future stand growth cannot be directly examined in this one year study but it is expected that there will be a Type I response in which the impact of the treatment is carried into the future but does not get larger over time (Snowdon 2002). This is the common response to competition control treatments which advance the stage of stand development but do not change the long-term growth rates and has been seen in other competition control studies (Mason and Milne 1999).

Site resources

This study was designed to demonstrate the effects of competition control in an operational setting and therefore did not include fertilization or irrigation which may have alleviated water and nutrient stress. Determining which resource is actually being competed for between weeds and trees, however, is not usually possible since there is always a combination of water and nutrients being competed for below-ground (Nambiar and Sands 1993). However, some inferences can be made as to the importance of the different resources of light, water and nutrients based on observed soil moisture and foliar nutrient levels along with δ^{13}C indicators of water stress and light measurements.

Competition for light between weeds and trees was not considered to be very important in these plantations since almost all of the leaves were above the level of weeds on the site. We thus observed no reduction in light reaching the tree leaves, meaning that competition is for the below-ground resources of water and nutrients. This has been found in other plantations developed on old agricultural fields such as in Sweden (Löf and Welander 2004). In our plantations, however, there may be intraspecific competition for light between the trees once crown closure is reached which has been seen in short rotation intensive culture of willow (Sage 1999).

Water appears to be highly competed for between trees and weeds as shown by the significantly reduced soil water and the corresponding increase in δ^{13}C values in weedy treatments. There is also a site effect with competition on better quality sites causing the greatest decrease in soil water, paralleling the impact of competition on growth. This is likely because higher levels of silt and clay on more productive sites hold more water than sand particles on the lower productivity sites. Competition for water has also been recorded in trembling aspen trees grown with alfalfa and reedgrass in Alberta (Powell and Bork 2004) and in afforestation plantations in Sweden (Löf and Welander 2004). Interspecific competition for water and the associated water stress is a common feature in young plantations but becomes less significant as trees grow and develop deeper and more extensive root systems which can often tap water reserves that weeds cannot access (Nambiar and Sands 1993).

Although poplar productivity is controlled more through competition for water than for nutrients (Carmean 1996), there was strong evidence in our study of competition for nutrients, particularly N. Nitrogen is the nutrient most often studied in competition trials and is usually the most important nutrient in determining tree growth in northern environments (Carlyle 1986; Reich et al. 1997; Binkley and Högberg 1997). There was a significant increase in foliar N concentration with competition control which was expected given that NO_3^- is mobile in the soil (Havlin et al. 2005) and in high demand by the competing weeds (Kabba et al. 2007). From these data, it can be said that tree growth benefits from greater N availability. Based on foliar concentrations, it appears the trees accessed all the soil N they needed in the weed-free plots for optimal growth [levels being between 3.0 and 3.4 g N kg^{-1} (Hansen et al. 1988)]. Such observations were also made for a HP plantation grown on silt loam in northern Wisconsin (Hansen et al. 1988). No further increase in foliar N is expected to impact growth rates since other nutrients may become limiting and the nutrient ratios within the trees will not be optimal (Knecht and Göransson 2004). These high N levels are probably due to the naturally high organic matter and N contents of the Chernozemic soils and the agricultural history of the sites with repeated annual applications of N fertilizers.

Foliar P concentrations were not statistically different between weeding treatments. There was a strong relationship between foliar P concentrations and growth in the weed-free treatments and all foliar P concentrations were below the optimal levels. Similarly, the decreasing foliar N:P ratio for weed-free trees indicate that weed-free trees responded to the gradient in soil P availability created with the experiment. In these trials, P is an important nutrient controlling productivity and is also highly competed for. This importance of P may help explain the lack of response in N fertilizer trials in HP plantations in Saskatchewan located on medium quality sites (Van Rees et al. 2006) and in plantations developed on agricultural fields in Sweden (Löf and Welander 2004); the trees in weed-free plots could have access to ample N but not P or water.

The foliar base cations K and Ca were present in high levels in all trees and do not appear to be strongly competed for. Also, there was no strong relation to growth. This is different from other studies which have found that base cations, in particular Ca, are very important for growth of trees in HP plantations (Bowersox and Ward 1977; Wittwer and Immel 1980) and trembling aspen seedlings grown in solution (Lu and Sucoff 2001). This lack of response is probably associated with the Chernozemic soils in our study which are characterized by high base cation levels (Soil Classification Working Group 1998).

Conclusion

For the HP plantations studied in Saskatchewan, the results support the theory that plant competition, as expressed through tree growth, is more intense on better quality sites. If large scale tree planting programs do occur on the Canadian prairies in the future, there will be a need to prioritize the limited resources for plantation management activities such as competition control. It is recommended that the best quality sites be given the highest priority for competition control in order to maximize tree growth, further illustrating the need for site specific plantation management rather than trying to incorporate the same management regime on all sites, regardless of potential benefits. Finally, given the short-term nature of this study, further monitoring of the relationships between clone, site productivity and competition effects is required.

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