Relationships between understory vegetation and hybrid poplar growth and size in an operational plantation

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ABSTRACT

The effect of varying composition and abundance of neighbouring herbaceous vegetation on tree growth in commercial hybrid poplar plantations remains unclear. We evaluated relationships between tree stem volume, volume increment, and the abundance of various growth forms (perennial grasses, legumes, and perennial forbs excluding legumes) adjacent to the tree base in four-year-old plantation trees under conditions protected from ungulate herbivory. Associations between tree metrics and the understory revealed that perennial grasses consistently reduced tree size and current annual volume growth, and the negative effects of grasses were made worse by increasing legume cover. Under little to no perennial grass cover however, the presence of legumes had a positive impact on tree size and growth, suggesting net facilitative versus competitive effects. The presence of forbs other than legumes led to no apparent competitive effects after four years, and may instead signify the absence of more competitive understory vegetation, particularly grasses. While final modelled relationships showed that the understory accounted for a limited amount of variance in tree volume ($R^2=0.10$) and volume increment ($R^2=0.09$) in four-year-old trees, these results nevertheless have implications for the development of silvicultural prescriptions targeting understory vegetation in order to maximize commercial hybrid poplar plantation yields.

Keywords: competition, facilitation, farmed plantations, legumes, volume increment, yield loss

RÉSUMÉ

L'effet qu'ont la composition et l'abondance de la végétation herbacée avoisinante sur la croissance des arbres des plantations commerciales de peuplier hybride demeure mal compris. Nous avons évalué les relations entre le volume de la tige des arbres, l'accroissement en volume et l'abondance de différentes formes de végétation herbacée (graminées vivaces, légumineuses et dicotylédones herbacées vivaces autres que légumineuses) avoisinant la souche des arbres dans des plantations de quatre ans protégées des ongulés herbivores. Une comparaison entre les mesures des arbres et la végétation en sous-étage a permis de constater que les graminées vivaces ont réduit systématiquement la taille des arbres et l'accroissement annuel en volume et que l'impact négatif des graminées a augmentait avec le couvert de légumineuses. Cependant, dans le cas d'un couvert réduit ou d'une absence de graminées vivaces, la présence de légumineuses a eu un effet positif sur la taille et la croissance des arbres, laissant entrevoir un effet net positif plutôt qu'une compétition. La présence de dicotylédones autres que légumineuses ne semble pas avoir occasionné de compétition visible après quatre ans et pourrait au contraire traduire l'absence d'une végétation compétitive en sous-étage, notamment par les graminées. Même si les relations finales modélisées indiquent que la végétation en sous-étage comptait pour une faible part de la variance du volume des arbres ($R^2 = 0,10$) et de l'accroissement en volume ($R^2 = 0,09$) chez les arbres de quatre ans, les résultats ont néanmoins des implications au niveau des prescriptions sylvicoles visant la végétation en sous-étage pour maximiser le rendement des plantations commerciales de peuplier hybride.

Mots clés : compétition, facilitation, entretien des plantations, légumineuses, accroissement en volume, perte de rendement

Introduction

The relatively high yields and short rotation cycles possible with hybrid poplar (*Populus* spp.) provides a viable option to help meet the increasing global market demand for fibre (Balatinecz *et al.* 2001, Perry *et al.* 2001, Weih 2004, Park and Wilson 2007). This is particularly true in the southern boreal region where the short but intense growing season is efficiently utilized by the rapid growth of hybrid poplar (Weih 2004). The use of hybrid poplars allows for fibre yields com-

parable to other areas with longer growing seasons and greater rainfall (Balatinecz *et al.* 2001, Weih 2004, Park and Wilson 2007, Christersson 2010).

In addition to increasing economic returns (Anderson and Luckert 2007), the conversion of marginal farmland into forestry has the potential to enhance ecological quality (Campbell *et al.* 1997), thereby increasing regional biodiversity (Rojo and Orois 2005, Boothroyd-Roberts *et al.* 2013). Farmland converted to hybrid poplar production however, is

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often subject to a high diversity and abundance of agricultural weeds; this is particularly important given the low competitive ability of poplar during the early establishment phase (Welham *et al.* 2007, Goehing 2015). Effects of tree-understory interactions on hybrid poplar growth can therefore be an important determinant of plantation success, necessitating a comprehensive understanding of where and when targeted weed control is warranted to maximize tree performance (Powell and Bork 2004, Van Oosten 2006, Goehing 2015).

Previous studies have found that hybrid poplar shows considerable sensitivity to competition from herbaceous species, with disproportionately large effects on trees less than four years of age (Buhler *et al.* 1998, Shock *et al.* 2002, Pinno and Belanger 2009, Otto *et al.* 2010). Competition effects also vary depending on the identity and abundance of competitors, and generally results in a loss of tree biomass and altered crown morphology (Marino and Gross 1998, Kabba *et al.* 2007). Of particular interest is the highly damaging effects that neighbouring grasses, especially aggressive perennials, have on poplar growth due to competition for root space, nutrients, light, and soil moisture (Powell and Bork 2004, Kabba *et al.* 2007, Messier *et al.* 2009, Henkel-Johnson *et al.* 2016). On the other hand there are the uncertain but potentially facilitative effects of understory legumes that contribute to soil nitrogen availability (Jose *et al.* 2004, Powell and Bork 2004).

Recent studies suggest that examining the impact of neighbouring vegetation by functional categories such as plant growth form and longevity may be an effective approach for isolating weed effects on hybrid poplar (Henkel-Johnson *et al.* 2016). This approach provides information needed to prioritize silvicultural management efforts in operational plantations (Henkel-Johnson 2014). Henkel-Johnson *et al.* (2016) conducted an examination of the effect of *in-situ* understory vegetation, including neighbour species identity, abundance and spatial proximity on hybrid poplar diameter growth in plantations in an equivalent ecoregion. Their conclusions were limited however, due to a lack of quality tree height and volume increment data which was the result of unexpected recurrent winter moose browsing, as well as low variability in the underlying vegetation. Since volume increment may be assumed to reflect competitive effects and offer an understanding of net tree-neighbour relationships when compared to total standing tree volume, this was a key constraint for Henkel-Johnson *et al.* (2016).

Our objective in this study was to understand how the size and growth of recently established hybrid poplar trees varied as a function of the specific identity, abundance and composition of neighbouring understory vegetation within a hybrid poplar plantation free of ungulate herbivory. This information is needed to facilitate informed understory control management decisions within existing operational-scale poplar plantations. To address this we related variation in hybrid poplar tree size and annual growth increment within a four-year-old plantation that was fenced to exclude large herbivores, and which had substantial natural variation in the adjacent herbaceous understory.

Materials and Methods

Field work for this study was undertaken during the summer of 2012 on a four-year-old commercial forestry plantation on leased private land managed by Alberta-Pacific Forest Industries Inc. (Al-Pac). The plantation was located near the ham-

let of Sangudo, Alberta (53°46' N, 114°55' W) in the Central Dry Mixedwood Natural Subregion (Strong and Leggat 1992). The area's climate is temperate and cold-continental, with brief warm summers and long cold winters. Thirty year (1982–2012) average annual and mean January and July temperatures were 1.9 °C, -14.4 °C and 15.2 °C, respectively, for the Evansburg weather station situated 47 km south-west of the study site. Annual average precipitation for this same location was 526 mm, 374 mm of which falls during the May to September growing season. Growing season conditions from the year of planting (2009) to the year of assessment (2012) averaged 397.8 mm of precipitation and 12.6 °C (data not shown). The study site was situated on predominantly well-drained, upland areas. Plantation soils were primarily medium textured loam to clay-loam Orthic Grey Luvisols of the Cooking Lake series intermixed with Dark Grey Luvisols of the Uncas series in lowland areas (CAESA Soil Inventory Working Group 2001).

Plantation history and silvicultural treatments

An operational hybrid poplar plantation with spacing of 3 x 3 m was sampled. The area was formerly in pasture and used for raising elk. As a result, the plantation was fenced in such a way that it excluded all large herbivores, including moose, elk and deer, and therefore provided the benefit of allowing trees to grow in height without being impacted by wildlife browsing.

Trees were sourced from commercial stool-beds at the Smoky Lake Forest Nursery near Smoky Lake Alberta from one year-old whips which were then harvested, cut to size, and grown in styroblocks the summer prior to planting. Over-winter dormant rooted plugs were planted into the plantation field on June 28, 2009 following cold storage.

Herbicide applications occurred using a boom-spraying before and after planting (Table 1), consistent with business-as-usual silvicultural practices for plantation establishment of all Al-Pac operational fields (Henkel-Johnson *et al.* 2016). Similarly, disking of soil was done prior to planting and occurred again between tree rows at approximately monthly intervals from May through August of all years from 2009 to 2012. Regular cultivation of the plantation resulted in the area being relatively weed free with the exception of areas near the base of individual trees (e.g., out to about 0.5 m radius).

Field sampling

Two separate sites were sampled, each about 57 and 61 ha in size within the larger plantation. Site 1 consisted of 500

Table 1. Pesticide application schedule for the study plantations. Initial planting occurred on June 28, 2009.

Pesticide	Active Ingredient	Date Applied	Pre/Post Planting	Rate (kg ai* ha ⁻¹)
Vantage	Glyphosate	17-Aug-08	Pre	0.9
Lorox	Linuron	27-May-09	Post	2.2
Poast Ultra	Sethoxydim	07-Jun-10	Post	0.2
Merge	NA (Surfactant)	07-Jun-10	Post	0.2
Matador	lambda-cyhalothrin	25-Jul-09	Post	0.01
Lorox	Linuron	29-Jun-10	Post	2.2

*ai indicates active ingredient

Walker (female parent *P. deltoides* and male parent *P. x petrowskyana*: cross name *P. "Walker"*) and Okanese (female parent *P. x "Walker"* and male parent *P. x petrowskyana*: cross name *P. "Okanese"*) hybrid poplar trees planted in unknown proportions (Lindquist *et al.* 1977, Schroeder *et al.* 2013). Site 2 consisted of 150 randomly selected hybrid poplar trees of the clonal variety P38P38 (female parent *P. balsamifera* and male parent *P. simonii*: cross variety *P. x "P38P38"*), which has demonstrated favorable growth rates but whose competitive ability is unknown (Tupker *et al.* 2003, Schreiber *et al.* 2013). In June and September 2010, additional hybrid poplar stock of unknown parentage was used to replace dead trees. All 650 trees were randomly selected for measurement in the spring of 2012 and labelled with unique identifying tags to facilitate relocation and re-measurement in the fall of 2012. Due to the interspersed mix of clones planted throughout these plantations, clone identity was not considered in the analysis.

Maximum bole height and DBH (diameter at 1.3 m breast height) were measured for all tagged trees at Sites 1 and 2 at the beginning and end of their fourth growing season (early May and September of 2012). While initial measurements were taken prior to any tree growth that year, the final assessment was taken after growth was completed. To provide consistency between May and September measurements, a non-toxic paint was used to mark the exact location of spring DBH measurements on all tagged trees.

Percent cover of each understory plant species was recorded (to the nearest 1%) in September 2012 using a 1 x 1 m quadrat centered at the base of each tree. Sampling was limited to this zone because areas further away were kept relatively free of competing vegetation (<10% plant cover) by periodic cultivation. Vegetation was categorized following the USDA Plants Database for longevity (annual, biennial and perennial) and growth habit categories (forb, grass, subshrub; USDA 2010). No herbivory was detected from ungulates.

Data analysis

Statistical analyses were conducted with R software version 3.2.2 using the RStudio interface (RStudio Team 2015). Preliminary analyses (using the R package *nlme*) determined that the inclusion of site failed to improve model effectiveness as determined using Akaike Information Criterion (AIC), and therefore the two sites were combined during subsequent analyses. Scatterplots of residuals were assessed for equal variance and normality and to look for evidence of nonlinear effects; no transformations were necessary.

Standing tree volume was calculated in the spring and fall of 2012 using the Ontario region hybrid poplar volume equation developed by Boysen (1991) and the Canada-Ontario Forest Resource Development Agreement, as follows:

$$V = e^{-1.064079 + 1.562891 \cdot \ln(\text{DBH} + 0.101423 \cdot (\text{Height}) * 1.013689 / 1000}$$

Where *V* is total tree volume (m³), DBH is the diameter in centimetres at breast height (1.3 m) and Height is the total tree height (m). Separate volumes for the beginning of the growing season (May

2012) and end of the growing season (October 2012) were then combined (final volume – initial volume) to derive the volume increment for each tree during 2012.

Growth parameters, including total standing volume and volume increment, were regressed against various measures of cover of the surrounding understory vegetation. Preliminary analyses were conducted in which each of the two dependent variables was regressed against vegetative cover by functional grouping [Perennial Grass (PG), Perennial Forbs (PF), Perennial Forbs excluding Legumes (PF-L), Annual Forbs (AF), and Legumes (L)] as well as cover values for individual species previously considered to be influential in regulating hybrid poplar growth: *Agropyron repens* L. (Shultz *et al.* 1994, Singh 2008) and *Taraxacum officinale* F.H. Wigg. (Kabba *et al.* 2007, Otto *et al.* 2010).

The three most influential independent variables were total perennial grass cover (PG), total perennial forb cover excluding legumes (PF-L), and the total cover of legumes (L). Next, multiple regressions were performed using various combinations of these three simple predictor variables and their interactions with stepwise elimination used to determine the best possible model to explain variation in standing stem volume and stem volume increment per tree. AIC was used to select the best model. For both response variables, the stepwise drop test suggested removal of two interaction terms. Re-running the model with the three simple predictor variables and one interaction term resulted in the lowest AIC. An additional re-running of the model using the stepwise drop test confirmed that eliminating individual predictor variables would not improve the model.

Results

Mean stem volumes after four years of growth exceeded 5000 cm³, with average volume increments of more than 645 cm³ in the last year (Table 2). By the end of the fourth year, trees had reached an average of nearly 5 m in height (Table 2). Relative volume (i.e., volume increment divided by May volume), height and DBH increments during the fourth year of growth were 0.14, 0.42 and 0.53, suggesting rapid growth in height and diameter of the trees within this commercial plantation at the time of assessment in the absence of ungulate herbivory.

Understory vegetation

A total of 41 different herbaceous plant species were found adjacent to the plantation trees, including two shrubs, 31 forbs and eight graminoids (including dryland sedges). Of the

Table 2. Mean values for different tree parameters measured in the plantations.

Size/Growth Metric	Mean	Standard Dev.
Final Stem Volume - SV (cm ³)	5003.3	0.0035
Volume Increment - VI (cm ³ /2012 growing season)	645.5	0.00045
Relative Volume Increment in 2012 (VI/ initial SV)	0.14	0.057
Final Tree Height - TH (cm)	490.4	1.16
Height Increment - HI (cm/2012 growing season)	211.1	0.72
Relative Height Increment in 2012 (HI/ initial TH)	0.42	0.085
Final Diameter at Breast Height - DBH (cm)	4.44	1.5
DBH Increment - DBHI (cm/2012 growing season)	2.32	0.76
Relative DBH Increment in 2012 (DBHI/ initial DBH)	0.53	0.097

forbs, 16 were perennials, including six legumes, with the balance being annuals, one of which was also a legume. Correlations were evident among the cover values for most of the different vegetation functional groups. Total PG and total PF-L cover were negatively correlated with one another ($r = -0.51$, $p < 0.001$), as were total PG and L cover ($r = -0.26$, $p < 0.001$). In contrast, total L and PF-L cover were positively correlated ($r = 0.18$, $p < 0.001$).

Table 3. Comparison of regression models for volume and volume increment as a function of the three strongest understory predictor variables and their interactions. The best overall model (with lowest AIC value) is in bold. Individual species were summed for each group (PG = perennial grass; L = legumes; PF-L = perennial forb excluding legumes).

Standing Tree Stem Volume After 4 Years (cm ³ /tree)	
Model Structure	AIC ¹
PG + PF-L + L + (PG*L)	-7070.4
PG + PF-L + L + (PG*PF-L) + (PG*L)	-7068.5
PG + PF-L + L + (PF-L*L)	-7067.9
PG + PF-L + L	-7067.9
PG + PF-L + L + (PG*PF-L) + (PG*L) + (PF-L*L)	-7066.9
PG + PF-L + L + (PG*PF-L)	-7066.2
PG + PF-L + L + (PG*PF-L) + (PF-L*L)	-7066.1
Tree Volume Increment – 4 th (2012) growing season (cm ³ /year)	
Model Structure	AIC
PG + PF-L + L + (PF-L*L)	-9579.2
PG + PF-L + L	-9577.4
PG + PF-L + L + (PG*PF-L) + (PF-L*L)	-9577.2
PG + PF-L + L + (PG*L)	-9576.4
PG + PF-L + L + (PG*PF-L)	-9575.5
PG + PF-L + L + (PG*PF-L) + (PG*L) + (PF-L*L)	-9575.4
PG + PF-L + L + (PG*PF-L) + (PG*L)	-9574.5

¹AIC = Akaike information criterion assessing the relative quality of comparative statistical models explaining tree metrics; lower scores indicate a superior fit.

Standing tree volume

While the cover of annual forbs (AF) ($r^2 = 0.007$, $p = 0.03$), *Agropyron repens* ($r^2 = 0.008$, $p = 0.02$), and *Taraxacum officinale* ($r^2 = 0.03$, $p < 0.001$) each had significant associations with observed tree volumes, they explained a relatively small amount of variance in volume. Total cover of perennial grasses (PG) and total cover of perennial forbs excluding legumes (PF-L) demonstrated the strongest relationships with tree volume and were therefore selected for inclusion in the multiple regression analysis. Although legume cover (L) was not in itself significantly ($r^2 = 0.0005$, $p = 0.08$) related to volume, it was included in the multiple regression analysis due to its interaction with the other understory functional groups (Table 3).

Standing tree volume after four years was best explained by a model incorporating all three tested predictor variables (PG, PF-L, L) and the interaction between PG and L ($r^2 = 0.103$; Table 3). Cover of PF-L and of L had a weakly positive

Table 4. The final best regression model fixed effects for standing tree volume (cm³) and stem volume increment (in the fourth growing season, cm³/yr). Given are the estimates (β) and their standard errors for the understory vegetation predictor variables. PG, L and PF-L represent the cover of perennial grasses, legumes and other perennial forbs excluding legumes, respectively.

Fixed Effect	Standing Tree Volume		Tree Volume Increment	
	β	SE	β	SE
Intercept	6572.87	609.02	937.42	73.91
PG	-19.96	7.34	-3.77	1.75
PF-L	17.07	8.88	-0.0082	0.70
L	4.58	18.66	-5.04	1.68
PG*L	-0.62	0.29	ns*	–
PF-L*L	ns	–	0.12	0.06
Model R ²	0.103		0.088	

*Indicates fixed effect was non-significant

Table 5. Slope of the significant interaction terms in the models of hybrid poplar stem volume (PG*L) and stem volume increment (PF-L*L) based on variation in understory cover components. Results show the influence (slope) of one term at different levels of the other term in the interaction. PG, L and PF-L indicate the cover of perennial grass, legume and other perennial forbs excluding legume, respectively.

Cover of other vegetation category (%)	Stem Volume		Stem Volume Increment	
	Response to L when PG is given cover	Response to PG when L is given cover	Response to L when PF-L is given cover	Response to PF-L when L is given cover
100	-57.42	-81.96	6.96	11.99
85	-48.12	-72.66	5.16	10.19
65	-35.72	-60.26	2.76	7.79
45	-23.32	-47.86	0.36	5.39
25	-10.92	-35.46	-2.04	2.99
15	-4.72	-29.26	-3.24	1.79
5	1.48	-23.06	-4.44	0.59
0	4.58	-19.96	-5.04	-0.008

effect on standing tree volume (Table 4). In contrast, PG had a large negative effect on volume (Table 4). The interaction between PG and L revealed that at or below 5% PG cover, cover of L had a weak positive effect on volume, but as the cover of PG increased above 5%, the influence of L cover became negative and was progressively more detrimental to volume (Table 5). Cover of PG had a negative effect on tree volume at all levels of L cover, with the most negative effect of PG being evident at the highest levels of neighbouring L cover (Table 5; Fig. 1).

Volume increment

Cover of AF ($r^2 = 0.007$, $p = 0.03$), *Agropyron repens* ($r^2 = 0.008$, $p = 0.02$) and *Taraxacum officinale* ($r^2 = 0.04$, $p < 0.001$) each showed a weak negative association with tree volume increment. Similar to total volume, both PG ($r^2 = 0.06$, $p < 0.001$) and PF-L ($r^2 = 0.05$, $p < 0.001$) demonstrated the strongest relationship with tree volume increment and were therefore selected for inclusion in the multivariate regression analysis. While the cover of L by itself was not significantly associated with volume increment ($r^2 = 0.0009$, $p = 0.45$), we retained this variable in the final model because its inclusion, together with the interaction of L and PF-L, resulted in the model with the lowest AIC value (Table 3).

The final model explaining tree volume increment included all three predictor variables (PG, PF-L, L), together with the interaction of L and PF-L ($r^2 = 0.088$). Total cover of PG once again had a negative effect on volume increment. In contrast to the result for standing volume, there was no significant interaction between PG and the cover of either PF-L or L (Table 4). Interestingly, while the individual effects of L and PF-L cover were weakly negative, there was a positive interaction between the two (Table 4). Closer examination of this response revealed that L cover had a positive effect on tree volume increments only when neighbouring PF-L cover was above 25% (Table 5). Further, cover of PF-L had a positive effect on volume increment at almost all levels of neighbouring L cover, and became progressively more positive as L cover increased (Table 5; Fig. 2).

Discussion

The low importance of site in regulating tree volume was notable given the strong overriding effects of site on poplar growth dynamics found by Henkel-Johnson *et al.* (2016), which in the latter prevented the separation of localized ecosite (i.e., soil and landform) effects from generalized differences in site-specific vegetation composition. Indeed, our best models indicated the near-bole understory accounted for up to 10% of tree growth, suggesting other factors, including potentially soil

conditions together with genotypic variation, were influencing the performance of individual trees. While the variance explained may seem relatively low, this value is nevertheless important, particularly in four-year-old trees that would be expected to have already reached 'free-to-grow' status, as it indicates that the modification of near-bole vegetation may alter tree volume yields by up to 10%. Additionally, we point out that the ongoing mechanical control of in-row vegetation preceding our measurements would also have limited understory impacts.

The absence of ungulate access in the current study was a key factor enabling tree volume to be reliably assessed, as win-

Fig. 1

Fig. 2

ter herbivory (i.e., leader breakage) has previously been found to impede the evaluation of tree height and associated volumes (Henkel-Johnson *et al.* 2016). The current study fills this information gap by isolating neighbouring vegetation effects on hybrid poplar performance in the absence of ungulate herbivory. Moreover, the current investigation was able to quantify these relationships in operational industry plantations which is in contrast to several other studies (Pinno and Belanger 2009, Otto *et al.* 2010) that have tested these relationships under controlled conditions. Past studies utilizing large-scale hybrid poplar plantations have not examined specific tree growth responses to neighbouring vegetation, focussing instead on responses to silvicultural treatments such as aboveground (Hansen 1991) and belowground (Friend *et al.* 1991) tree biomass and distribution, as well as abiotic soil characteristics (McLaughlin *et al.* 1987). The results of this study suggest comprehensive sampling of working plantations may be equally useful for examining complex interspecific vegetation relationships within these agroecosystems.

Though the magnitude of effect from neighbouring herbs on hybrid poplar differed between tree size (volume) and growth (volume increment), total perennial grass (PG) cover consistently had a negative effect on tree growth while the total cover of legumes (L) and perennial forbs excluding legumes (PF-L) had variable effects on tree performance depending on interspecific dynamics among herbaceous groups. The negative influence of PG on hybrid poplar size and annual growth was expected and agrees with findings in other studies; these effects are particularly important given that they occurred despite the intensive understory control measures implemented as part of the ongoing silviculture management of these plantations (Landhäusser and Lieffers 1998, Henkel-Johnson *et al.* 2016). Grasses have been recognized to be a limiting agent for tree growth in potted experiments due to belowground competition for root space (Messier *et al.* 2009) and nutrient uptake (Kabba *et al.* 2007). Field studies examining the effect of the native marsh reed grass (*Calamagrostis canadensis* Michx. P. Beauv.) on *Populus tremuloides* Michx. forests have consistently shown highly competitive effects imposed through its abundant biomass production, which produces an insulating litter mat reducing soil temperatures (Hogg and Lieffers 1991), thereby directly reducing tree growth (Landhäusser and Lieffers 1998). Similarly, mesocosm studies on *Calamagrostis canadensis* show that this species can decrease available light, soil moisture and nutrients for aspen saplings (Powell and Bork 2004). These studies are further supported by Henkel-Johnson *et al.* (2016), where over and above site effects, the primary factor predicting hybrid poplar performance in commercial plantations was the abundance of PG species, largely *Agropyron repens*, *Poa palustris* L. and *Phleum pratense* L.

The generally positive effect of L and PF-L on standing volume and on volume increments when in combination was surprising. Predominant non-leguminous forbs in our study area included *Taraxacum officinale*, which is known to be a competitive species detrimental to poplar growth (Kabba *et al.* 2007). Henkel-Johnson *et al.* (2016) also found that forbs consistently suppressed tree diameter growth during the first three years and speculated that this was due to the tall-statured and broadleaved growth habit of forbs reducing light

availability to young tree saplings. A more recent investigation (Goehing 2015) found that hybrid poplar trees are susceptible to both above and below-ground competition during the first three years of growth, with competition shifting from aboveground for light immediately after planting, to increasingly belowground for water and nutrients over time. However, unlike both Henkel-Johnson *et al.* (2016) and Goehing (2015), the current study examined poplar responses during the fourth year of growth and in the absence of ungulate herbivory, presumably well after free-to-grow status had been reached, and during a period when belowground competition was likely to have increased in importance (Shock *et al.* 2002). We postulate that suppression of PG by both L, and in particular PF-L, may have lowered belowground competition sufficiently to increase relative tree growth, and warrants testing in future studies.

Unlike the consistently negative effects of grasses on tree growth, the positive impacts of L on the size of four-year-old hybrid poplar highlights the key role this group of herbaceous species may play in agro-ecological production systems. While Powell and Bork (2004) found that close proximity to forbs and the legume alfalfa (*Medicago sativa* L.) led to a net reduction in aspen growth, they also found the presence of herbaceous species had a sheltering effect on tree seedlings, reducing wind damage and insect herbivory. Since tree damage vectors appeared to be low or non-existent throughout the current study, and certainly during the year of sampling, sheltering effects were not observable but may have been a factor during early plantation establishment. We also note that instead of *Medicago sativa*, the predominant legumes in plantations of the current study were various species of low statured clover (*Trifolium* spp.), which may impose less competition on trees. Greater L cover may also have aided tree growth through nitrogen (N) fixation, as *Trifolium* spp. can fix up to 545 kg ha⁻¹ of N annually (Carlsson and Huss-Danell 2003). Inter-seeding of legumes within hybrid poplar plantations has been shown elsewhere in Alberta to increase available soil nitrogen (N) levels (Goehing 2015), which in turn may improve the growth of hybrid poplar, provided other resources (light, water) are not limiting.

Positive effects of L cover on tree size were also contingent on PG abundance, as demonstrated by the interaction term in the final model of standing tree volume. Similar to trees, PG cover may have been aided by the presence of L, presumably due to enhanced access to N; this in turn could lead to greater competition from PG on other neighbouring vegetation, including trees. These findings are supported here by the increasingly negative impact of PG cover on tree size when accompanied by increasing L cover. These results are also consistent with previous studies that have found the N₂ fixation ability of legumes is stimulated by interspecific competition (Carlsson and Hull-Danell 2003, Schipanski and Drinkwater 2011), and decreasing rates of competition are accompanied by an increasing dependency on soil mineralization—rather than fixation—by plant communities (Carlsson and Huss-Danell 2003). Thus, highly competitive PG cover may benefit disproportionately from the nitrogen fixed by legumes, leading to the significant negative interaction between PG and L on total tree stem volume.

Despite the initial positive effect of L on overall tree volume, annual volume increments during the fourth year of

growth were (weakly) negatively related to L and PG cover. While the decline in incremental growth in relation to PG cover was unsurprising, the switch in L effects from positive for tree size to negative for growth increment warrants closer examination. One possible explanation is that while trees were small during the early years of growth the net effects of N addition at that time may have been critical in overcoming a fundamental limiting factor for growth. However, as plantations during the fourth year were beginning to close their canopies, other resources may have played a greater role in constraining growth. Belowground competition tends to prevail in older plantations (Shock *et al.* 2002, Goehing 2015) and competition for not only N but soil moisture as well may have played a greater role in constraining growth. While precipitation remained near normal during 2012, an abundance of fine roots in both clover (the dominant legume) and grasses may have been effective in capturing moisture (Sainju *et al.* 1998), particularly during low to moderate rainfall events.

The most surprising finding regarding the relationship of competing vegetation with tree growth was the positive interaction between L and PF-L on volume increment during 2012. Cover of L had a positive effect on growth but only at cover levels of PF-L exceeding 25%. Similarly, PF-L consistently had a positive effect on growth, although this became weaker when L cover was low. These responses could reflect the fact that the cover of both PF-L and L were negatively correlated with PG abundance, suggesting a greater presence of forbs was associated with reduced abundance of more competitive PG. Increasing displacement of PG by legumes and other forbs could at least partly account for the apparent positive effect of PF-L and L cover on hybrid poplar.

Finally, we note that this study is not without limitations. Variability in the clones planted prevents these results from being applied to any one clone, and may have increased the variability of vegetative effects on tree size and growth. However, the significance of our results, despite genetic variation among trees, suggests competition remained an important factor regulating growth in these operational plantations, a response that may apply more broadly across commercial clones. Moreover, we note that in this study, the interpretation of total tree size (i.e., volume) with respect to variation in the understory was based on the assumption that understory composition and abundance has been relatively consistent (and stable) since planting. Consistent silvicultural treatments, high variability in understory composition among individual trees (i.e., plots), and an abundance of perennial species supports this assumption, at least for the years immediately preceding sampling. This allows for the interpretation of volume increment responses as a reflection of current competition effects, and standing tree volume as a reflection of net historical competition effects within this commercial plantation.

Conclusion

Herbaceous composition and abundance adjacent to the tree base had significant impacts on the growth of plantation grown hybrid poplar prior to and after canopy closure, accounting for up to 10% of stem volume and growth. While no single understory species had a marked influence on growth, tree performance was best explained by a model quantifying the effects of perennial grasses (PG), perennial

forbs excluding legumes (PF-L), and legumes (L). As expected, PG had a consistent negative effect on growth. While the effects of L were positive when alone, L also appeared to increase competition from adjacent PG when they occurred together, thereby heightening net competitive impacts on trees. These results reveal complex competitive and facilitative effects on poplar trees from neighbouring herbaceous vegetation. Ultimately these findings reinforce the importance of controlling PG in poplar plantations, regardless of clone, to maximize growth, but also highlight the variable impacts of broadleaf forbs, including potential benefits to growth from legumes. Future research should investigate competitive understory dynamics as dependent on hybrid poplar variety, the response of annual hybrid poplar volume increment to understory dynamics, and the competitive or facilitative dynamics of understory functional groups, including legumes.

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