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Complex impacts of logging residues on planted hybrid poplar seedlings in boreal ecosystems

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Abstract We studied three hybrid poplar plantations in Quebec (Canada) established on sites with varying soil and environmental characteristics to investigate the effects of logging residues on the water potential, carbon isotope ratio and foliar nutrients of planted trees. On each site, four treatments representing different residue loads, as well as treatments aimed at manipulating specific factors of the environment (Herbicide, Geotextile) were applied to test their effects on seedling water potential, carbon isotope ratio and foliar nutrients. Along with analyses of variance, we used structural equation modelling to infer causal relationships of logging residues on height, basal diameter and foliar nutrition of trees through their effects on soil temperature, soil water content and competing vegetation cover. Logging residues decreased soil temperature at all sites and woody plants cover at one site out of three. Height, basal diameter and unit leaf mass were strongly related to each other. Foliar $\delta^{13}C$, N concentration and unit leaf mass increased with decreasing cover of woody plants suggesting an important role of competition for resources. Overall,

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logging residues had no direct influence on hybrid poplar dimensions after two growing seasons: their effects on the microenvironment of this resource demanding tree species were either cancelling out each other, or were not significant enough to have a significant impact on the growth drivers measured. For example, presence of logging residues might reduce soil temperature, impeding overall seedling performance. Our study highlights the fact that any given silvicultural method aimed at manipulating logging residues has a complex influence involving the interaction of multiple environmental drivers and that the net effect on tree productivity will depend on species and site specific conditions.

Keywords Structural equation modelling (SEM) · Hybrid poplar · Forest logging residues · Water potential · Foliar nutrients · Carbon isotope

Introduction

The demand for forest biomass as a feedstock source for bioenergy production has generated a renewed interest in the environmental effects of removing logging residues (branches and tops of trees) on tree nutrition and productivity. Reviews by Thiffault et al. (2011) and Achat et al. (2015) concluded that the effects of logging residue extraction on stand productivity are inconsistent and the exact mechanisms still poorly understood.

We know that logging residues can modify the soil nutritional environment, competing vegetation abundance, soil temperature and water content (Harrington et al. 2013; Proe et al. 2001; Stevens and Hornung 1990). However, we don't know how the effects of logging residues on the above-mentioned factors influence the performance of regenerating trees, including planted ones. Also, these effects are time-dependent. Proe and Dutch (1994) suggested that microclimate and competition effects are the main drivers of tree growth shortly after planting, whereas Egnell (2011) suggested that effects of removal of logging residues on tree nutrition became apparent 8–12 years after planting, i.e. close to or after crown closure. However, Smolander et al. (2015) found little correlation between the effect of harvest residues on soil properties (chemical and biological) and tree growth. These authors suggested that some non-nutrient factor brought about by the residues, such as changes in soil physical conditions, was still driving the response of trees to residue retention, even 10 years after stand establishment.

At a very early stage of stand development, logging residues modify planting microsites mostly through light and water availability and soil temperature (Harrington et al. 2013; Proe et al. 2001; Stevens and Hornung 1990). Light and water availability can increase for seedlings with the presence of logging residues due to its controlling effect on competing vegetation cover (Roberts et al. 2005; Stevens and Hornung 1990). Increased light availability promotes higher photosynthetic rates, thereafter favouring growth (Raven et al. 2005). Logging residues can also affect soil water through a sheltering effect that limits evaporation but intercepts precipitation (Raven et al. 2005; Trottier-Picard et al. 2014). Increased water availability should decrease drought stress of planted trees, prevent stomatal closure and increase leaf conductance, thereby increasing photosynthetic rates and growth over the long run (Farquhar et al. 1989). Apart from competing vegetation and soil water, logging residues can affect planting microsites by decreasing soil temperature (Proe et al. 2001; Roberts et al. 2005; Zabowski et al. 2000), which can in turn reduce nutrient and water uptake of seedlings (Chapin et al. 1986; Landhäusser et al. 2001). However, the net effects of residues on tree growth will depend on the limiting factors of productivity, which vary both in space (e.g. among sites) and time (e.g. among seasons and years and among stages of forest development).

In a recent study (Trottier-Picard et al. 2014), we quantitatively evaluated if logging residues had a linear, quadratic or non-linear effect on environmental conditions (soil temperature and water content, competing vegetation and soil nutrients) and growth of four planted tree species. In the present study, we aim to explore causal relationships by assessing the performance and second-year seedling dimensions of hybrid poplars (*Populus* spp.) planted on a gradient of temperate and boreal sites in Quebec (Canada) to changes in environmental conditions due to on-site maintenance of logging residues, by using structural equation modelling. Hybrid poplar was selected as a study case because of its high sensitivity to changes in its environment (Stettler et al. 1996): even small variations in competing vegetation control, water and nutrient availability and soil temperature were expected to induce noticeable tree responses. We expected logging residues to have a net positive effect on hybrid poplar performance by increasing resource availability (light, water and nutrients) for seedlings.

Materials and methods

Site description

Three hybrid poplar plantations representing different bioclimatic conditions and soil properties across Quebec were selected: Bouchette in Saguenay–Lac-Saint-Jean, Kamouraska in Bas-Saint-Laurent and Weedon in Estrie. Detailed temperature and precipitation profiles for these sites were published in Trottier-Picard et al. (2014). All sites are characterized by a continental humid climate without specific dry or wet period. Precipitations occur all year long; they are typically in solid form (snow) from December to March. Bouchette (48°7′N, 72°12′W) is located in the balsam fir (*Abies balsamea* L.)–paper birch (*Betula papyrifera* Marsh.) bioclimatic domain described by Saucier et al. (2009), has an average annual precipitation of 1030 mm (rainfall 700 mm, snowfall 330 mm) with an average daily temperature of 1.5 °C, imperfect drainage and a sandy loam soil texture. Kamouraska (47°24′N, 69°36′W) is in the balsam fir–yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain, has an average annual precipitation of 960 mm (rainfall 670 mm, snowfall 290 mm) with an average daily temperature of 4.1 °C, imperfect drainage and a sandy clay loam soil texture. Weedon (45°37′N, 71°31′W), in the sugar maple (*Acer saccharum* Marsh.)–basswood (*Tilia americana* L.) bioclimatic domain, has an average annual precipitation of 1140 mm (rainfall 870 mm, snowfall 270 mm) with an average daily temperature of 4.1 °C, poor drainage and a loam soil texture (Environment Canada 2012; Saucier et al. 2009; Soil Classification Working Group 1998).

Stands were clear-cut in 2009 at each site by whole-tree harvesting before leaf fall; logging residues were piled along the roadside and mechanical site preparation for planting was performed in autumn. Mechanical site preparation differed at each site (harrowing at Bouchette, shearing using a V-blade at Kamouraska and mounding at Weedon) so that site characteristics are confounded with effects of mechanical site preparation. Hybrid poplars were planted in May 2010 at a density of 1111 trees per hectare. Planted hybrid poplar clones were chosen according to recommendations from provincial guidelines that are based on clone hardiness and resistance to specific pests (Périnet et al. 2010). Planted stock were as follows: at Bouchette, dormant bare root stock of *Populus maximowiczii* A. Henry × *P. balsamifera* L. (clone 915319; average initial height 99 ± 28 cm); at Kamouraska, dormant non-rooted cuttings of *P. maximowiczii* × *P. balsamifera* (clone 915308; average initial height 73 ± 4 cm); and at Weedon, bare root stock of *P. canadensis* Moench (*deltoides* Bartram ex H. Marshall × *nigra* L.) × *P. maximowiczii* (clone 915508; average initial height 181 ± 27 cm). Therefore, clone and stock type effects were confounded with site characteristics. The combination of site, management history, microsite and stock type conditions were further considered as a random sampling of typical management practices for hybrid poplar plantations in eastern Canada. Stock quality at planting followed governmental guidelines for hybrid poplars, which comprise an extensive list of standards including nutritional status, height, diameter, h/d ratio, root system architecture, stem inclination and sinuosity (Périnet et al. 2010).

Experimental design

Seven treatments representing contrasting conditions of soil temperature and competing vegetation cover were replicated at the tree level within 2 months after planting in 2010 at each site; treatments were applied on 9 m^2 plots, each plot centred on a single seedling, with a minimum buffer of 3 m between plots.

The seven treatments included: Control, i.e. no residues added, where the plot was left untouched after whole-tree harvesting; addition of a 20 kg (half) residue load; addition of a 40 kg (single) residue load; addition of a 80 kg (double) residue load; Geotextile mulch; Herbicide; and Herbicide + addition of 40 kg of residues. Half, single and double residue loads were based on an estimation of stand basal area prior to harvest considering the species that had been harvested, site index and stand density (Pothier and Savard 1998) and a consequent calculation of the average branch biomass per hectare that was expected from clearcutting of these forest stands, using above-ground biomass equations (Lambert et al. 2005). The corresponding load of logging residues for 9 m^2 was then estimated and designated as the single load. Residues were selected from roadside piles and comprised branches and tree tops of various sizes (ranging up to 9 cm in diameter) and species that were representative of the material in the piles. Loads were weighed in the field using an adapted butcher scale and manually distributed on plots.

The “Geotextile mulch”, consisting of a square of 1.75 m × 1.75 m of grey textile (Texel 7609, Texel Géosol inc., Sainte-Marie, QC, Canada) centred on the tree, was used to mimic the physical effect of logging residues on soil temperature and competition cover compared to Control (i.e. whole-tree harvesting treatment). We used the “Herbicide” treatment to decrease competition cover compared to Control and Herbicide + 40 kg residue load to isolate the residue effect compared to Control while completely controlling competing vegetation. For both treatments requiring herbicide, we applied glyphosate (1.3 % v:v in water, VisionMAX^{MC}, Monsanto Canada Inc., Winnipeg, MB, Canada) on the entire 9 m^2 plot in July of 2010 and 2011, at a rate varying from 2484 to 4590 g of active ingredient per hectare, depending on site. Poplar trees were protected with a cone covering during spraying to avoid contact with the herbicide; no damage to seedlings was observed after spraying.

Each treatment was replicated 8 times at each site (Bouchette, Kamouraska and Weedon), following a completely randomised design. All measurements (see below) were conducted in 2011, during the second growing season following planting.

Environmental measurements

Competing vegetation cover was defined as the proportion of the plot area that was covered by the vertical projection of aerial competing vegetation parts. In July 2011, the same observer visually estimated the competing vegetation cover (in 5 % classes), using a 1 m^2 square plot centred on each hybrid poplar. Competing vegetation was recorded by species and aggregated in two groups: (1) woody plants and (2) herbaceous plants, the latter including ferns and gramineae. Measurements were conducted on all plots ($n = 168$). Competing vegetation measurements on herbicided plots reflected the July 2010 application only.

Soil nutrient availability was assessed with mixed bed ion exchange resins (Ionac NM-60, Lenntech, Delft, The Netherlands; H^+/OH^- Form, Type I, Bead) installed at a depth of 10 cm during the first 2 weeks of June 2011 and recovered in October 2011. Resin-NH_4^+, resin-NO_3^-, resin-P and sum of exchangeable cations were extracted following the method described in Trottier-Picard et al. (2014). Resin bags were installed in close proximity (i.e. <50 cm) from the planted seedlings within all plots; 8 resin bags per treatment were installed within each site (56 resin bags per site).

Finally, soil volumetric water content and soil temperature were measured episodically following Buitrago et al. (2015), in the uppermost 12 cm at the base of planted trees by time-domain reflectometry (FieldScout TDR 300, Spectrum Technologies Inc., Plainfield, IL, USA) and a hand-held digital thermometer (DURAC 3818, H-B Instrument Company, Collegeville, PA, USA), respectively. A depth of 12 cm was preferred to get close to the root system while coping with rocky soils, which made deep measurements difficult. We conducted measurements in 2011, which were taken at least 24 h after the last rain event and between 13:00 and 15:00 h EDT. Soil water content was measured and averaged three times within each plot for each measuring event. We measured soil water content and temperature three times at Bouchette (4 July, 26 July and 24 August) and Kamouraska (6 June, 27 June, 20 July) and twice at Weedon (8 June and 14 July) and averaged measurements by plot over all measuring events.

Seedling measurements

We measured pre-dawn and midday leaf water potentials within a 24 h period once at each site with a pressure chamber (PMS Model 600, PMS Instrument Company, Albany, OR, USA), following the methods described by Ritchie and Hinckley (1975). Pre-dawn measurements were made between 2:00 and 5:00 EDT and midday measurements were made between 13:00 and 16:00, at least 3 days after the previous precipitation. Three replicates per treatment were randomly selected. All treatments were sampled, with the exception of the 20 kg and 40 kg residue loads.

In August 2011, we sampled ten leaves from all hybrid poplars from top and bottom of the tree crown and from the four cardinal directions. Foliar samples were oven-dried at 60 °C for 72 h and weighed; unit leaf mass was calculated as the average of the 10 leaves. Leaves were then combined into one composite sample per tree and ground. Composite samples from three trees per treatment per site were finely ground using a Mixer Mill MM301 ball grinder (Retsch Inc., Newtown, PA, USA) and carbon isotope ratio ($\delta^{13}C$), as influenced by stomatal behaviour and drought stress (Moreno-Gutiérrez et al. 2012), was determined (Stable Isotope Facility, University of California, Davis, CA, USA) using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK). The carbon isotope ratio was calculated as:

$$\delta^{13}C = \frac{R_i - R_s}{R_s} \times 1000$$

where R_i and R_s refer respectively to $^{13}C/^{12}C$ ratio in the leaf sample and in the standard, in this case international standards V-PDB (Vienna PeeDee Belemnite).

All samples were then used to determine total N and total P concentrations in the foliage. Total N was determined on an elemental analyser (CNS-2000, LECO Corporation, St. Joseph, MI, USA). Total P was determined after overnight combustion at 500 °C and dilution in 0.1 M HCl, and analysed by inductively coupled plasma optical emission spectrometry (Optima 7300 DV, PerkinElmer, Waltham, MA, USA). Finally, basal diameter and height of trees were measured in October 2011, i.e. representing final dimensions after 2 years of growth.

Statistical analyses

All statistical analyses were conducted in R version 3.0.1 (R Core Team 2013) using a significance level of $\alpha = 0.05$. We used analyses of variance (ANOVA) to test for differences among treatments on physiological (leaf water potential, foliar mass, $\delta^{13}C$, N and P concentrations in the foliage), mensurational (basal diameter and height) and environmental variables (competition cover, soil resin-NH_4^+ and NO_3^- exchangeable base cation concentrations, soil temperature and volumetric water content). Treatment was considered as fixed effect, and Site as a random effect. The latter was meant to encompass all characteristics that distinguished study sites, i.e. climate, soil, poplar clone and stock type. Prior to ANOVA, data were verified for homogeneity and homoscedasticity of variances using standard graphical approaches; variables were transformed accordingly.

When a significant Treatment effect was found, we applied a priori contrasts using the *fit.contrast* function of the *gmodels* package (Warnes et al. 2013). Contrasts were designed to answer the following questions: (1) Do logging residues affect measured variables? (Control vs. 20, 40 and 80 kg); (2) Does the quantity of logging residues affect measured variables? (two contrasts: 20 vs. 40 and 80 kg and 40 vs. 80 kg); (3) Regardless of logging residues, does the control of competing vegetation affect measured variables? (Control and 40 kg vs. Herbicide and Herbicide + 40 kg); (4) Regardless of vegetation control, do logging residues affect measured variables? (Control and Herbicide vs. 40 kg and Herbicide + 40 kg); and (5) When controlling competing vegetation, does soil temperature affect measured variables? (Herbicide vs. Geotextile). This last contrast relies on the Herbicide and Geotextile treatments known to have a similar effect on competing vegetation cover, but with the Geotextile decreasing soil temperature compared to Herbicide (Trottier-Picard et al. 2014).

Structural equation modelling is a statistical method used in ecology and other fields to interpret information about the observed correlations among variables in order to evaluate complex causal relationships (Lei and Wu 2007; Pugesek et al. 2003; Shipley 2016). We used the *sem* function of the *lavaan* package (Rosseel 2012) to understand the indirect effects of logging residues, relative to Control (no residues) on height and basal diameter through environmental and physiological variables. Only treatments representing the gradient of residue load were used for this analysis. Residue load treatments were converted to numerical values so that Control became 0, 20 kg (half) load became 0.5, 40 kg (single) load became 1, and 80 kg (double) load became 2. Multigroup modelling, which makes it possible to assess similarities and differences among groups in particular parameters of the equation models (Vandenberg and Lance 2000), was used to compare sites.

Full information maximum likelihood was used to include all available data in the analysis, including those missing at random (Rosseel 2012) and to fit the structural equation model. The fit between the predicted and observed covariance matrix was assessed with a χ^2 test (Shipley 2016). When the χ^2 test was associated with a *P* value >0.05, we had no good evidence to reject the model and it was assumed to be consistent with the data (Hershberger et al. 2003; Shipley 2016). The Bentler's comparative fit index (CFI) and the root mean square error of approximation (RMSEA) were also used to measure model fit, with CFI >0.95 and RMSEA <0.05 being considered as an acceptable fit (Rosseel 2012; Shipley 2016; Tomer and Pugesek 2003).

We used paired observations between tree physiological and mensurational variables and the environmental measurements of their vicinity that were available for all sites. Tree variables included $\delta^{13}C$, unit leaf mass, foliar [N], foliar [P], basal diameter and height. Environmental variables included residue load, cover of woody plants, cover of herbaceous plants, soil temperature, soil volumetric water content, resin-NH_4^+, resin-NO_3^-, resin-P and sum of exchangeable cations. Cover of competing vegetation was log-transformed to meet normality assumptions.

A model representing theoretical relationships among tree variables and their environment was tested as the starting point (Electronic Supplementary Material 1). Soil available nutrients (resin-NH_4^+, resin-NO_3^-, resin-P, sum of exchangeable cations) were grouped into a latent variable. In structural equation modelling, covariances are correlations (non-causal relationships) between variables. A covariance was established between basal diameter and height to capture their strong correlation without establishing a causal relationship. When a causal relationship was possible in both directions, we tested a covariance to represent the bidirectional relationship between them, accepting that we would not obtain the detail of this effect in each direction. If this saturated model was rejected, an exploratory method was used to propose a model that was not rejected by our data: a relationship that was not significant ($\alpha = 0.05$) at a majority of sites was removed; an environmental variable (cover of woody or herbaceous plants, soil temperature, soil water content and latent variable soil) that was not related to any tree variable ($\delta^{13}C$, unit leaf mass, foliar [N] or [P], basal diameter and height) was excluded from the analysis; or a tree variable that was not related to any other tree variable was excluded from the analysis. For every change, we checked that it did not induce any anomalies (negative s^2, negative r^2) and that it decreased the AICc of at least two units, based on the *AICcmodavg* package (Mazerolle 2013) and the *aictab.lavaan* function (Byrnes 2012). In the opposite case, the concerned relationship or variable was reintroduced into the model. We removed relationships or variables until a model had an acceptable fit (*P*-value of χ^2 >0.05, CFI >0.95 and RMSEA <0.05). The resulting model was then compared to the same model, with path coefficients restricted to be the same across groups. These two models were compared using ANOVA, and the model without restrictions on path coefficients was accepted only if it was better at $\alpha = 0.05$. The resulting model could only be hypothesised not to contradict data as the same data had been used to create the model.

Results

Treatment comparisons

Herbicide application (Control, 40 kg vs. Herbicide, Herbicide + 40 kg) had a significant positive effect on most tree variables (basal diameter, height, foliar $\delta^{13}C$, mass, [N] and [P]; Tables 1, 2). Addition of logging residues regardless of vegetation control (Control, Herbicide vs. 40 kg, Herbicide + 40 kg) increased height, foliar $\delta^{13}C$, [N] and [P]. Addition of logging residues (Control vs. 20, 40, 80 kg) also increased foliar $\delta^{13}C$, [N] and [P]. Herbicide increased foliar [N] and [P] compared with Geotextile (Tables 1, 2). The amount of logging residues had no significant effect on any measured tree variable (Table 2).

The increasing amount of logging residues significantly decreased soil temperature (Control vs. 20, 40, 80 kg; 20 vs. 40, 80 kg; 40 vs. 80 kg; Control, Herbicide vs. 40 kg, Herbicide + 40 kg; Tables 3, 4), while herbicide application increased soil temperature (Control, 40 kg vs. Herbicide, Herbicide + 40 kg; Herbicide vs. Geotextile; Tables 3, 4). Regardless of vegetation control, logging residues also decreased herbaceous plants cover (Control, Herbicide vs. 40 kg, Herbicide + 40 kg; Tables 3, 4). Geotextile was more efficient at controlling herbaceous plants cover than Herbicide (Herbicide vs. Geotextile; Tables 3, 4). Regardless of presence of logging residues, herbicide application significantly decreased woody plant cover and increased resin-NO_3^- (Control, 40 kg vs. Herbicide, Herbicide + 40 kg; Tables 3, 4). Treatments had no effect on leaf water potential (Table 2), resin-NH_4^+, exchangeable base cations, resin-P and soil volumetric water content (Table 4).

Structural equation modelling

We first tested the full model saturated with theoretical relationships based on existing knowledge regarding hybrid poplar physiology and nutrition (e.g. (Mamashita et al. 2015; Hansen et al. 1988) (Electronic Supplementary Material 1), which was strongly rejected ($\chi^2 = 628$, degrees of freedom (df) = 189, $P < 0.001$). We then hypothesised that the model resulting from our exploratory method (Fig. 1; Table 5; $\chi^2 = 27.55$, df = 30, $P = 0.594$) best described our data. Starting from the causal structure presented in Fig. 1, we compared a model with path coefficients differing among sites and one with path coefficients constrained to be equal across sites; the latter was strongly rejected ($P < 0.001$) so we allowed path coefficients to differ across sites. This model excluded cover of herbaceous plants, the latent soil nutrient variable (which included resin-NH_4^+, resin-NO_3^-, resin-P and sum of exchangeable cations), soil volumetric water content and foliar [P], because all tested models containing these variables were strongly rejected ($P < 0.001$). Unit leaf mass (i.e. the average mass of single leaves) was the main predictor of height and basal diameter.

Effects of logging residues on height and basal diameter of trees were somewhat minor. Total indirect effects can be computed by multiplying the estimates along the indirect path (Table 5); if several indirect paths are possible, e.g., soil temperature can have an effect on height either through foliar $\delta^{13}C$ or through unit leaf mass, the total effect is given by the addition of all indirect paths. According to the model proposed in Fig. 1, when adding up all indirect paths, an increase of one unit of logging residues (one load, 40 kg/9 m^2) would have a positive effect on height and basal diameter at Kamouraska and Weedon. At

Table 1 Mean (SE) of tree variables for 2-year-old hybrid poplars planted in Quebec, Canada

Treatment	Pre-dawn leaf water potential (Mpa)	Midday leaf water potential (Mpa)	$\delta^{13}C$ (‰)	Foliar unit mass (g)	Foliar [N] (%)	Foliar [P] (g/kg)	Basal diameter (cm)	Height (m)
Bouchette								
Control	−0.25 (0.03)	−1.63 (0.20)	−30.24 (0.19)	1.74 (0.22)	1.24 (0.07)	1.75 (0.16)	1.5 (0.2)	1.22 (0.14)
20 kg of residues	NA	NA	−30.02 (0.49)	2.40 (0.39)	1.36 (0.10)	1.99 (0.14)	1.8 (0.2)	1.40 (0.14)
40 kg of residues	NA	NA	−29.51 (0.43)	2.06 (0.38)	1.52 (0.13)	1.99 (0.19)	2.0 (0.3)	1.40 (0.30)
80 kg of residues	−0.25 (0.05)	−1.75 (0.19)	−29.20 (0.62)	1.98 (0.39)	1.52 (0.10)	1.97 (0.16)	1.7 (0.2)	1.25 (0.12)
Geotextile	−0.18 (0.06)	−1.73 (0.25)	−29.72 (0.10)	2.47 (0.24)	1.47 (0.09)	1.84 (0.17)	2.0 (0.1)	1.53 (0.10)
Herbicide	−0.37 (0.10)	−1.88 (0.56)	−29.29 (0.33)	3.11 (0.36)	1.66 (0.08)	1.73 (0.16)	2.6 (0.4)	1.66 (0.22)
Herbicide + 40 kg	−0.15 (0.03)	−2.50 (0.42)	−28.81 (0.38)	2.83 (0.42)	1.69 (0.07)	2.24 (0.17)	1.8 (0.1)	1.53 (0.13)
Kamouraska								
Control	−1.22 (0.30)	−1.68 (0.04)	−30.34 (0.13)	1.94 (0.42)	1.90 (0.09)	1.69 (0.06)	1.7 (0.2)	1.66 (0.19)
20 kg of residues	NA	NA	−29.31 (0.06)	2.36 (0.27)	1.85 (0.07)	2.01 (0.13)	1.9 (0.1)	1.76 (0.23)
40 kg of residues	NA	NA	−29.28 (0.34)	2.75 (0.29)	1.88 (0.05)	2.01 (0.08)	1.9 (0.1)	1.85 (0.13)
80 kg of residues	−0.86 (0.24)	−1.62 (0.46)	−29.24 (0.05)	3.28 (0.64)	1.99 (0.06)	2.26 (0.09)	2.1 (0.2)	2.07 (0.28)
Geotextile	−1.05 (0.37)	−1.80 (0.30)	−28.99 (0.11)	2.66 (0.26)	2.19 (0.06)	1.90 (0.15)	1.9 (0.1)	1.68 (0.19)
Herbicide	−1.09 (0.29)	−1.93 (0.15)	−28.91 (0.14)	3.31 (0.27)	2.40 (0.14)	1.98 (0.11)	2.1 (0.2)	1.76 (0.23)
Herbicide + 40 kg	−0.83 (0.13)	−1.97 (0.31)	−28.46 (0.61)	2.92 (0.29)	2.36 (0.11)	2.01 (0.13)	2.3 (0.3)	1.92 (0.22)
Weedon								
Control	NA	NA	−30.26 (0.19)	2.28 (0.13)	1.19 (0.04)	1.15 (0.05)	2.5 (0.1)	1.90 (0.11)
20 kg of residues	NA	NA	−29.95 (0.33)	2.33 (0.17)	1.38 (0.08)	1.30 (0.08)	2.5 (0.2)	1.86 (0.16)
40 kg of residues	NA	NA	−30.39 (0.15)	2.12 (0.14)	1.43 (0.08)	1.31 (0.08)	2.4 (0.2)	1.95 (0.14)
80 kg of residues	NA	NA	−30.22 (0.26)	2.44 (0.17)	1.32 (0.05)	1.17 (0.07)	2.5 (0.1)	2.01 (0.09)
Geotextile	NA	NA	−29.75 (0.16)	2.68 (0.23)	1.42 (0.07)	1.29 (0.07)	2.9 (0.2)	1.98 (0.12)
Herbicide	NA	NA	−29.41 (0.28)	3.04 (0.48)	2.01 (0.08)	1.66 (0.09)	3.0 (0.2)	1.86 (0.15)
Herbicide + 40 kg	NA	NA	−29.73 (0.26)	4.03 (0.27)	2.05 (0.08)	1.58 (0.08)	3.8 (0.2)	2.61 (0.11)

Table 2 Analyses of variance and planned contrasts for physiological and mensurational variables of 2-year-old hybrid poplars planted in Quebec, Canada

Fixed effect	Pre-dawn leaf water potential (Mpa)			Midday leaf water potential (Mpa)			$\delta^{13}C$ (‰)			Foliar unit mass (g)		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Treatment	4	1.44	0.250	4	0.80	0.535	6	5.78	**<0.001**	6	6.88	**<0.001**
Contrasts							df	*t*	*P*	df	*t*	*P*
Control versus 20, 40, 80 kg							53	−3.11	**0.003**	210	−1.47	0.143
20 versus 40, 80 kg							53	−0.50	0.621	210	−0.20	0.840
40 versus 80 kg							53	−0.55	0.584	210	−1.05	0.296
Control, 40 kg versus Herb, Herb + 40 kg							53	−5.55	**<0.001**	210	−6.07	**<0.001**
Control, Herb versus 40 kg, Herb + 40 kg							53	−2.33	**0.024**	210	−1.39	0.167
Herbicide versus Geotextile							53	1.24	0.221	210	1.97	0.051

Fixed effect	Foliar [N] (%)			Foliar [P] (g/kg)			Basal diameter (cm)			Height (m)		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Treatment	6	26.75	**<0.001**	6	4.26	**0.002**	6	6.06	**<0.001**	6	2.73	**0.014**
Contrasts	df	*t*	*P*	df	*t*	*P*	df	*t*	*P*	df	*t*	*P*
Control versus 20, 40, 80 kg	211	−2.64	**0.009**	210	−2.98	**0.003**	214	−0.73	0.464	214	−1.01	0.312
20 versus 40, 80 kg	211	−1.04	0.300	210	0.01	0.989	214	−0.34	0.738	214	−0.78	0.436
40 versus 80 kg	211	0.44	0.662	210	0.19	0.846	214	−0.29	0.772	214	−0.33	0.741
Control, 40 kg versus Herb, Herb + 40 kg	211	−11.22	**<0.001**	210	−4.13	**<0.001**	214	−5.38	**<0.001**	214	−2.58	**0.011**
Control, Herb versus 40 kg, Herb + 40 kg	211	−2.01	**0.046**	210	−2.51	**0.013**	214	−1.33	0.186	214	−2.63	**0.009**
Herbicide versus Geotextile	211	5.72	**<0.001**	210	2.03	**0.043**	214	1.42	0.156	214	−0.05	0.957

Values in bold are significant at $\alpha < 0.05$

Table 3 Mean (SE) of environmental variables measured in summer 2011 at each site as influenced by treatments

Treatment	Herbaceous plant cover (%)	Woody plant cover (%)	Resin-NH_4^+ (mg/kg)	Resin-NO_3^- (mg/kg)	Exchangeable base cations (cmol +/kg)	Resin-P (mg/kg)	Soil temperature (°C)	Soil volumetric water content (%)
Bouchette								
Control	5 (1)	28 (7)	9.0 (4.2)	6.3 (5.7)	6.7 (2.2)	7.2 (1.6)	16.3 (0.4)	27.4 (2.0)
20 kg of residues	3 (2)	26 (4)	9.2 (4.7)	0.8 (0.3)	7.5 (3.7)	9.8 (1.8)	15.6 (0.1)	30.2 (3.7)
40 kg of residues	6 (4)	19 (5)	12.7 (3.1)	14.3 (8.0)	10.4 (3.7)	17.7 (8.6)	15.3 (0.2)	25.7 (3.0)
80 kg of residues	1 (0.4)	8 (4)	52.1 (43.1)	2.4 (1.1)	10.4 (4.3)	11.2 (3.8)	15.1 (0.2)	29.8 (1.4)
Geotextile	1 (0.3)	3 (1)	10.5 (4.5)	1.3 (0.4)	10.2 (4.4)	25.4 (14.9)	16.0 (0.2)	32.1 (3.5)
Herbicide	7 (5)	5 (2)	17.9 (8.3)	36.0 (20.1)	7.1 (1.7)	9.5 (3.0)	17.0 (0.2)	30.9 (2.5)
Herbicide + 40 kg	3 (1)	4 (1)	22.4 (14.4)	11.4 (4.9)	13.1 (2.3)	23.4 (6.3)	15.6 (0.2)	33.1 (2.6)
Kamouraska								
Control	3 (2)	41 (12)	4.3 (2.3)	2.4 (1.6)	1.7 (0.7)	2.1 (0.9)	15.8 (0.4)	17.6 (1.0)
20 kg of residues	5 (2)	18 (4)	0.8 (0.5)	0.7 (0.2)	3.1 (1.1)	2.2 (1.0)	14.8 (0.2)	25.6 (1.8)
40 kg of residues	3 (2)	19 (6)	2.0 (1.5)	5.0 (2.9)	2.8 (0.8)	1.9 (0.9)	14.4 (0.2)	25.4 (2.4)
80 kg of residues	4 (1)	16 (5)	1.1 (0.3)	3.5 (1.6)	1.7 (0.5)	1.4 (0.6)	14.3 (0.1)	24.2 (1.5)
Geotextile	3 (1)	21 (8)	2.4 (1.4)	5.9 (2.5)	0.6 (0.1)	0.7 (0.2)	16.2 (0.2)	21.4 (1.1)
Herbicide	11 (9)	3 (1)	2.7 (1.7)	38.2 (15.8)	1.8 (0.5)	1.3 (0.6)	16.3 (0.3)	23.0 (1.8)
Herbicide + 40 kg	3 (1)	2 (1)	8.3 (5.5)	12.1 (9.2)	1.7 (0.4)	1.7 (0.5)	14.8 (0.1)	22.1 (1.1)
Weedon								
Control	11 (5)	21 (5)	0.1 (0.1)	0.4 (0.1)	0.2 (0.04)	0.3 (0.1)	20.4 (0.4)	32.9 (2.8)
20 kg of residues	4 (1)	23 (5)	0.5 (0.3)	2.1 (0.8)	0.3 (0.1)	0.5 (0.2)	19.8 (0.4)	31.5 (2.2)
40 kg of residues	2 (1)	21 (4)	1.7 (1.3)	1.5 (0.6)	0.7 (0.1)	1.0 (0.3)	19.0 (0.3)	33.6 (2.9)
80 kg of residues	7 (3)	19 (4)	1.4 (0.7)	2.9 (1.7)	0.3 (0.1)	0.4 (0.1)	18.1 (0.3)	36.9 (3.5)
Geotextile	1 (0.3)	6 (2)	2.6 (1.5)	85.0 (54.0)	0.5 (0.2)	0.4 (0.1)	19.9 (0.2)	37.1 (2.5)
Herbicide	9 (3)	7 (2)	0.6 (0.3)	15.9 (11.0)	0.3 (0.1)	0.3 (0.1)	21.2 (0.3)	34.3 (3.7)
Herbicide + 40 kg	2 (1)	6 (1)	1.0 (0.9)	9.4 (6.7)	0.4 (0.1)	0.7 (0.3)	19.2 (0.3)	32.9 (3.3)

Table 4 Analyses of variance for environmental variables measured in summer 2011

Fixed effect	df	Herbaceous plant cover (%)			Woody plant cover (%)		Resin-NH_4^+ (mg/kg)			Resin-NO_3^- (mg/kg)	
		F	*P*		*F*	*P*	*F*	*P*		*F*	*P*
Treatment	6	3.60	**0.002**		12.71	**<0.001**	1.26	0.278		5.95	**<0.001**
Contrasts	df	*t*	*P*	df	*t*	*P*			df	*t*	*P*
Control versus 20, 40, 80 kg	209	1.54	0.125	208	1.31	0.191			146	−1.54	0.125
20 versus 40, 80 kg	209	0.35	0.723	208	1.15	0.253			146	−1.47	0.143
40 versus 80 kg	209	−1.02	0.311	208	1.34	0.182			146	0.16	0.870
Control, 40 kg versus Herb, Herb + 40 kg	209	−0.54	0.591	208	7.91	**<0.001**			146	−4.32	**<0.001**
Control, Herb versus 40 kg, Herb + 40 kg	209	2.89	**0.004**	208	0.54	0.589			146	0.05	0.963
Herbicide versus Geotextile	209	4.19	**<0.001**	208	−1.97	0.050			146	0.86	0.390

Fixed effect	Exchangeable base cations (cmol +/kg)		Resin-P (mg/kg)			Soil temperature (°C)		Soil volumetric water content (%)	
	F	*P*	*F*	*P*		*F*	*P*	*F*	*P*
Treatment	1.97	0.073	0.92	0.482		21.94	**<0.001**	1.01	0.422
Contrasts					df	*t*	*P*		
Control versus 20, 40, 80 kg					214	6.25	**<0.001**		
20 versus 40, 80 kg					214	3.68	**0.002**		
40 versus 80 kg					214	2.14	**0.034**		
Control, 40 kg versus Herb, Herb + 40 kg					214	−2.67	**0.008**		
Control, Herb versus 40 kg, Herb + 40 kg					214	8.40	**<0.001**		
Herbicide versus Geotextile					214	3.74	**0.002**		

Planned contrasts are shown in the lower part of the table if treatment effect was significant at $\alpha < 0.05$. Values in bold are significant at $\alpha < 0.05$

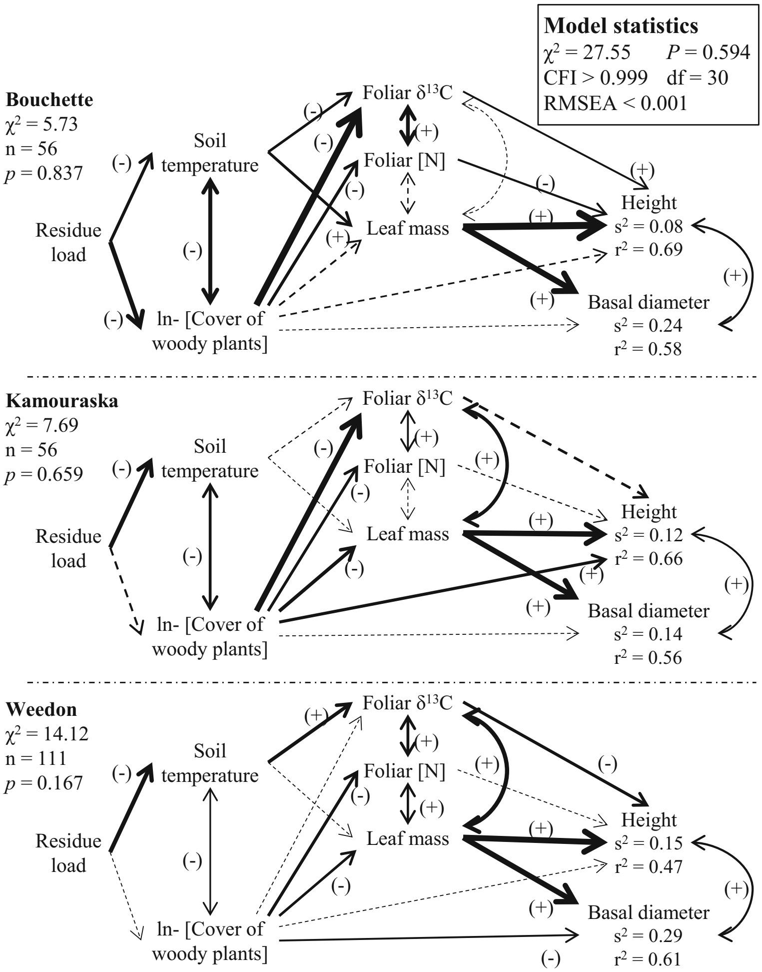

Fig. 1 Selected path diagrams of physiological responses of hybrid poplars to changes in microenvironment due to logging residues for three plantations in Quebec (Canada). Model χ^2, degrees of freedom (df), *P*-value, CFI, and RMSEA are presented, as well as site χ^2, n, and *P*-value, and residual variances (s^2) and explained variations (r^2) of response variables. *Dashed lines* represent relationships whose path coefficients are not significantly different from zero ($\alpha < 0.05$). The sign of path coefficients significantly different from zero are presented. Line widths are proportional to standardised path coefficients and represent their relative importance

Kamouraska, one load of logging residues led to an increase of 5.6 cm in height and 0.097 cm in basal diameter. At Weedon, one load of logging residues led to an increase of 9.2 cm in height and 0.030 cm in basal diameter. However, there was a slightly negative effect of indirect paths at Bouchette (one load of logging residues led to a decrease of 1.1 cm in height and 0.011 cm in basal diameter). When partitioning the effects of logging residues on tree size through soil temperature and cover of woody plants, an increase of one unit (load) of logging residues decreased height and basal diameter through a decrease in soil temperature only at Bouchette (respectively −6.4 and −0.109 cm); conversely, it increased height and basal diameter through, again, a decrease in soil temperature at

Table 5 Estimates (SE) and *P*-values of regressions and covariances from the selected structural equation models at Bouchette, Kamouraska, and Weedon

Explaining variable		Response variable	Bouchette		Kamouraska		Weedon	
			Estimate (SE)	*P*	Estimate (SE)	*P*	Estimate (SE)	*P*
Residue load	→	Soil temperature	−0.44 (0.16)	**0.007**	−0.71 (0.22)	**0.001**	−1.10 (0.21)	**<0.001**
		ln [Cover of woody plant]	−0.84 (0.19)	**<0.001**	−0.51 (0.37)	0.166	0.01 (0.20)	0.963
Soil temperature	→	Foliar $\delta^{13}C$	−0.28 (0.13)	**0.024**	−0.11 (0.09)	0.229	0.14 (0.05)	**0.005**
		Foliar mass	0.45 (0.16)	**0.004**	−0.05 (0.14)	0.693	−0.06 (0.07)	0.395
ln [cover of woody plant]	→	Foliar $\delta^{13}C$	−0.53 (0.13)	**<0.001**	−0.35 (0.06)	**<0.001**	−0.02 (0.06)	0.718
		Foliar [N]	−0.10 (0.03)	**0.002**	−0.08 (0.03)	**0.004**	−0.13 (0.03)	**<0.001**
		Foliar mass	−0.23 (0.12)	0.055	−0.34 (0.10)	**<0.001**	−0.30 (0.09)	**<0.001**
		Height	0.09 (0.05)	0.073	0.17 (0.05)	**0.002**	−0.05 (0.04)	0.174
		Basal diameter	0.01 (0.07)	0.897	−0.04 (0.04)	0.269	−0.15 (0.04)	**0.001**
Foliar $\delta^{13}C$	→	Height	0.19 (0.08)	**0.018**	0.28 (0.17)	0.103	−0.44 (0.14)	**0.002**
Foliar [N]	→	Height	−0.49 (0.16)	**0.003**	−0.26 (0.16)	0.118	−0.04 (0.14)	0.770
Foliar mass	→	Height	0.44 (0.05)	**<0.001**	0.39 (0.08)	**<0.001**	0.36 (0.05)	**<0.001**
		Basal diameter	0.55 (0.07)	**<0.001**	0.37 (0.05)	**<0.001**	0.51 (0.05)	**<0.001**
ln [cover of woody plant]		Soil temperature	−0.43 (0.11)	**<0.001**	−0.50 (0.19)	**0.007**	−0.39 (0.18)	**0.030**
Foliar $\delta^{13}C$	↔	Foliar [N]	0.10 (0.04)	**0.006**	0.05 (0.02)	**0.022**	0.07 (0.03)	**0.017**
Foliar $\delta^{13}C$	↔	Foliar mass	−0.04 (0.14)	0.767	0.34 (0.10)	**0.001**	0.29 (0.11)	**0.009**
Foliar [N]	↔	Foliar mass	0.05 (0.03)	0.134	0.02 (0.04)	0.562	0.15 (0.04)	**<0.001**
Height	↔	Basal diameter	0.10 (0.02)	**<0.001**	0.08 (0.02)	**<0.001**	0.14 (0.03)	**<0.001**

All measurements were made in July–September 2011. Values in bold are significant at $\alpha < 0.05$

Kamouraska (3.6 and 0.013 cm, respectively) and Weedon (9.2 and 0.034 cm, respectively). An increase of one unit of logging residues increased height and basal diameter through a decrease of the cover of woody plants at Bouchette (5.3 and 0.098 cm, respectively) and Kamouraska (2.0 and 0.084 cm, respectively), but had no effect on height and basal diameter through cover of woody plants at Weedon (<0.1 and −0.004 cm, respectively). Therefore, according to our structural equation models (Fig. 1), changes in height and basal diameter of the magnitude likely to be caused by logging residues were far below the variability (as estimated by standard error under Control treatment) of height and basal diameter observed at all sites (respectively, changes <10 cm and 0.10 cm, standard error of 14 and 0.2 cm).

Discussion

Our study made use of hybrid poplar, a species with high sensitivity to changes in environmental conditions, with the aim of capturing small variations in physiological processes and drivers of growth that could influence regenerating stands. The study was designed to create a large environmental gradient, so that planted trees would be exposed to a range of conditions and resource availability typical of management practices in eastern Canada, to extend the management implications of our results. The use of site effect as a random factor in our ANOVA reflects this approach. Structural equation modelling made it possible to disentangle specific mechanisms responsible for growth responses.

The effects of logging residues (relative to the control treatment, i.e. whole-tree harvesting) on hybrid poplar dimensions were less than the variability of measurements. Therefore, our results did not support our expectation that modifications of the microenvironment brought about by the residues would have a net positive effect on tree variables and size of hybrid poplars by increasing resource availability. Nevertheless, our results still suggest pathways through which residues influence seedling microenvironment and tree responses.

Unit leaf mass, the main predictor of height and basal diameter in this study according to structural equation modelling, increased as a consequence of the decrease in cover of woody plants. Increased mass average of single leaves could be due to increased availability of resources, for example increased irradiance associated with low cover of woody plants, as leaves exposed to high irradiance are often thicker than leaves under shade (Raven et al. 2005; Reich et al. 1998a). Increased unit leaf mass could also be due to increased access to water and nutrients.

Unit leaf mass was significantly and positively correlated with foliar $\delta^{13}C$ (Fig. 1; Table 5). Foliar $\delta^{13}C$ is both the result of stomatal behaviour, which influences CO_2 entry and water exit from the leaf and of C assimilation rate, which influences CO_2 demand (Duursma and Marshall 2006). Considering that $\delta^{13}C$ integrates information from the whole growing season, higher $\delta^{13}C$ values could reflect periodic drought events due to changes in transpiration rates. Higher $\delta^{13}C$ values could also result from higher C assimilation rate (Farquhar et al. 1989), leading to increased biomass production and larger unit leaf mass.

Foliar $\delta^{13}C$ was in turn influenced by woody plant cover: reduced woody plant competition was associated with higher (less negative) $\delta^{13}C$ (Fig. 1). Moreover, Herbicide and Herbicide + 40 kg residue load had lower woody plant cover than Control and 40 kg load, higher (less negative) $\delta^{13}C$ values but similar soil water content. The compounded effect of stomatal behaviour and foliar C assimilation could also explain the negative effect of woody plant cover on foliar $\delta^{13}C$. Low woody plant cover could have increased above-ground temperature and wind speed, leading to higher transpiration and stomatal closure. On the other hand, less competition from woody vegetation could also have increased fixed ^{13}C by increasing available light, as foliar $\delta^{13}C$ is positively correlated with irradiance (Farquhar et al. 1989; Kranabetter et al. 2010).

However, the negative effect of woody plant cover on $\delta^{13}C$ was not significant at Weedon (Fig. 1). At this site, soil preparation by mounding resulted in planted hybrid poplar having their foliage above most of the competition cover (personal observation), freeing the foliage from above-ground effects. However, access to N could have been a limiting factor for seedlings on this site, as reduction in competition caused an increase in foliar [N], which was in turn positively correlated with unit leaf mass.

According to our SEM analyses, soil temperature had a site-dependent effect on foliar $\delta^{13}C$ (significant positive effect at Weedon and significant negative effect at Bouchette) and unit leaf mass (positive effect but significant only at Bouchette; Fig. 1). Peng and Dang (2003) found that the optimum soil temperature for biomass production of trembling aspen varied from 18.1 to 21.3 °C. When average soil temperatures are cooler than this optimum, an increase of soil temperature could improve water absorption, leading to lower (more negative) $\partial^{13}C$ values and higher unit leaf mass, as was possibly the case at Bouchette (Fig. 1). Indeed, Bouchette has the lowest annual mean air temperatures (1.5 vs. 4.1 °C at Kamouraska and Weedon (Environment Canada 2012); at this site, soil temperatures could possibly be a limiting factor to growth compared with our other study sites.

Hybrid poplar nutrition was influenced by woody plant cover, which decreased foliar [N], but without being linked to differences in availability of soil nutrients (Fig. 1). We found that foliar [N] was positively correlated with $\delta^{13}C$, which could be explained by the reported positive correlation between foliar [N] and photosynthesis (Kazda et al. 2004; Reich et al. 1998b). Kranabetter et al. (2010) and Kaelke et al. (2001) found decreasing foliar [N] with increasing shade, attributed to shifts in root-shoot biomass allocation.

By reducing woody plant cover, logging residues could be beneficial to poplar seedlings on sites with abundant woody competition. However, logging residues might not have a strong enough influence on growth limiting factors (e.g. N availability) for a given site and/or logging residues might have confounding effects on other drivers of tree growth (e.g. by reducing soil temperature), there is yet to be a net positive effect of logging residues on tree growth.

Conclusions

Logging residues decreased competing vegetation and soil temperature, which in turn influenced the response of hybrid poplars during their second growing season after planting, although results varied among sites. However, changes brought about by residues did not significantly influence hybrid poplar dimensions after 2 years: their compound effects on the microenvironment of this otherwise demanding tree species were apparently not significant enough to have an impact on growth drivers, or were cancelling out each other. For example, presence of logging residues might reduce soil temperature, impeding overall seedling performance. Because of these confounding effects, there is yet to be a net positive effect of logging residues on tree growth. Monitoring of treatments over the next years will provide valuable information about their longer-term effects. Although we are confident that the environmental data measured on the three sites provided a good overview of the conditions experienced by the seedlings, a continuous monitoring of soil temperature and moisture from snow melt until the winter season could provide a more complete assessment of growing conditions.

Our study highlights the fact that tree growth is driven by the interaction of multiple factors and that any given silvicultural method, such as site preparation, herbicide application and harvest residue management does not have a singular but rather a complex effect involving several drivers. Silviculture should therefore be based on the understanding of these interactions and the fact that net effects on tree productivity will vary depending on (species and) site conditions.

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