

1 **Early recruitment of boreal forest trees in hybrid poplar plantations of different densities**  
2 **on mine waste rock slopes**

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13 **Declaration of interest**

14 None for Hugo Bouchard, Marie Guittonny or Suzanne Brais.

15

16 **Role of the funding bodies**

17 This study was funded by the Natural Sciences and Engineering Research Council of Canada  
18 (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT) and the  
19 Canadian Malartic Partnership. The industrial partner (Canadian Malartic Partnership) was  
20 consulted during the preliminary study design phase in order to improve the applicability of the  
21 results. Nonetheless, funding bodies had no involvement in the collection, analysis and  
22 interpretation of data, in the writing of the manuscript, or in the decision to submit the  
23 manuscript for publication.

24

26 **Abstract**

27 Mine wastes create harsh recruitment conditions for forest tree seedlings, especially waste rock  
28 piles where erodible slopes are prone to drought. Plantations using fast-growing tree species can  
29 potentially accelerate the conversion of degraded mine sites into forests through facilitation of  
30 tree recruitment, while contributing to the stability of slopes. In this study, hybrid poplars were  
31 tested as a means of achieving reclamation objectives by providing shelter for forest tree  
32 seedlings on waste rock slopes (3H:1V ratio) in the Canadian southern boreal region. Density  
33 effects of young hybrid poplars were assessed on the emergence and survival of early, mid and  
34 late successional species, naturally occurring or hand-seeded, and on the understory micro-  
35 environmental parameters in plantations of different spacings (1x1, 2x2, 4x4 m and control  
36 without planted trees). Results were also compared in 2x2-m plantations with and without a  
37 hydroseeded herbaceous cover, traditionally used to control erosion in slopes. During the 2<sup>nd</sup>  
38 growing season of the plantations, seedling emergence of naturally established *Salicaceae*  
39 (*Populus* and *Salix*) species followed a quadratic pattern along the density gradient, as  
40 emergence values were higher under an intermediary density. Nonetheless, decrease in light  
41 transmission emerged as a limiting factor of seedling survival for these early-successional,  
42 shade-intolerant species by the next summer. Following a spring sowing experiment in the 3<sup>rd</sup>  
43 growing season of the plantations, emergence rates for later-successional *Picea glauca* and *Abies*  
44 *balsamea* seedlings increased with hybrid poplar density. During their peak emergence period, in  
45 early season, higher soil moisture content was found under denser cover. However, at the end of  
46 the third year of the plantations, only *A. balsamea* showed moderate increase in early recruitment  
47 success rates under denser tree cover. In hydroseeded plots, a competitive effect of the  
48 herbaceous cover was observed on *Salicaceae* emergence and *A. balsamea* survival. These

49 results suggest that planting of young plantations without a hydroseeded cover may offer a more  
50 suitable solution in order to quickly provide early recruitment opportunities for later-successional  
51 seedlings in waste rock slopes. Despite this, a significant decrease in moisture content recorded  
52 during the second half of the 3<sup>rd</sup> growing season under the 1x1-m cover, compared to the 2x2-m,  
53 likely signalled an increasing competitive effect from hybrid poplars, which may compromise  
54 their nursing potential in the longer term. Therefore, further monitoring is imperative for a better  
55 understanding of longer-term facilitation and competition interactions between nurse trees and  
56 understory seedlings in waste rock slopes, where competition for limited resources, such as  
57 water, may be severe.

58

59 Keywords: mine revegetation, afforestation, nurse plantation, hydroseeded cover, understory  
60 micro-environment, forest succession

## 62 1 Introduction

63 Understanding the processes involved in ecosystem recovery provides useful insights for re-  
64 establishing successional trajectories towards productive and self-sustaining ecosystems (Del  
65 Moral & Walker 2007; Walker & del Moral 2009; Polster 2011). There is growing scientific  
66 evidence that tree plantations can have a *catalytic effect* (Parrotta *et al.* 1997) on forest  
67 succession on severely degraded sites, where ecological barriers would otherwise impede  
68 recolonization by native species (Guariguata *et al.* 1995; Parrotta 1995; Carnevale & Montagnini  
69 2002; Boothroyd-Roberts *et al.* 2013). In the boreal region, vast areas of land supporting forest  
70 ecosystems are rendered unproductive because of mining activities. Recruitment is often the  
71 stage that hinders the natural regeneration of native forest trees (Young *et al.* 2005). The  
72 facilitation successional theory (Connell & Slatyer 1977), as applied in restoration practice,  
73 suggests that planting of pioneer tree species able to grow on the newly exposed mine landform  
74 will assist the colonization of other species into the restored community (Nichols *et al.* 2010),  
75 and especially of later-successional species. The stress-gradient hypothesis predicts that positive  
76 interactions among plants increase with abiotic stress exposure (Bertness & Callaway 1994),  
77 hence hinting at the potential of facilitation in reclamation efforts because of the inhospitable  
78 nature of mining substrates.

79 When surface-mined, all the biotic components are removed from the forested area –including  
80 tree canopy, shrub layer, soil, rootstock and seed bank (Burger & Zipper 2002)– and replaced by  
81 accumulations of waste material. Waste rocks form one of the two main solid mine wastes along  
82 with mill tailings, and originate from rock material surrounding the ore, extracted by explosion  
83 and dumped in piles with steep slopes and flat tops (Brooks 1990). The main forest reclamation

84 strategy on the flat areas consists in tree planting on a respread topsoil (Drake 1986; Kost &  
85 Vimmerstedt 1994; Ashby 1997; Emerson *et al.* 2009; Pietrzykowski 2010; Landhäusser *et al.*  
86 2012; Sloan & Jacobs 2013). On the other hand, fast-growing herbaceous plants seeding with  
87 agronomic species is generally used on the slopes (Torbert & Burger 1994; Aubuchon 2010;  
88 Fields-Johnson *et al.* 2012), where soil erosion proves to be a significant barrier to plant  
89 establishment (Espigares *et al.* 2011). A ground cover of fast-growing herbaceous species allows  
90 the rapid stabilization of the soil surface and limits soil erosion on slopes (Helm 1995). However,  
91 species commonly used (mainly grasses and legumes) often compete with tree seedlings for  
92 water, nutrients and light resources (Rizza *et al.* 2007; Polster 2010; Franklin *et al.* 2012). Tree  
93 seedling establishment, survival and growth are thus often found to be very low on sites  
94 revegetated with herbaceous species (Andersen *et al.* 1989). Traditional reclamation treatments  
95 used in waste rock slopes to minimize short-term erosion may consequently hinder long-term  
96 recovery goals (Holl 2002).

97 As an alternative reclamation strategy, fast-growing tree plantations could benefit the  
98 regeneration of native species that can hardly grow in open environments or in competition with  
99 a herbaceous ground cover (Carnevale & Montagnini 2002). This nursing effect is first mediated  
100 by a *tree cover effect*. A number of mechanisms have been proposed to account for the better  
101 recruitment of native tree species under a plantation canopy, especially changes in understory  
102 microclimatic conditions (Lugo 1997; Otsamo 2000), reduction in competitive herbaceous  
103 species (Powers *et al.* 1997; Otsamo 2000) and improvement of soil fertility through readily  
104 decomposable litter (Filcheva *et al.* 2000). Secondly, fast-growing trees develop an extensive  
105 root system which rapidly colonizes the available soil volume (Wilkinson 1999; Douglas *et al.*  
106 2010). Tree roots thus provide soil reinforcement that improves the stability of slopes (Abe &

107 Ziemer 1991), where soil erosion could adversely affect tree colonization by reducing the  
108 availability of seeds, nutrients, and water in soil (Espigares *et al.* 2011).

109 While most trees can arguably exert a facilitating role, fast-growing broadleaf species are  
110 generally regarded as better catalysts (Parrotta *et al.* 1997). Hybrid poplar plantations were  
111 recently observed to accelerate the colonization of native species and the restoration of forest  
112 attributes on abandoned farmlands (Boothroyd-Roberts *et al.* 2013). Hybrid poplar cultivars have  
113 some of the most vigorous growth among trees available for reclamation (Guy & Bateman 1989;  
114 Casselman *et al.* 2006) and generally show good survival rates on mine sites (Czapowskyj 1978;  
115 Clark Ashby 1995; McGill *et al.* 2004). Some clones allocate a large proportion of their  
116 resources to roots (Larchevêque *et al.* 2011), which could foster the development of an extensive  
117 root system as well as a fast canopy closure to stabilize the soil and improve the understory  
118 micro-environment.

119 Tree spacing or density is regarded as an important factor of plantation design, potentially  
120 mediating facilitation performances in the restored community through its structuring effect on  
121 the understory micro-environment (Geldenhuys 1997; Paquette *et al.* 2008; Trindade & Coelho  
122 2012). Denser tree covers generally offer less extreme temperatures and moisture deficiencies,  
123 but provide a more limiting light environment (Man & Lieffers 1999). If soil moisture is known  
124 to be the main limiting factor for the germination of boreal tree species (Greene *et al.* 1999),  
125 light quickly becomes limiting for the survival of shade-intolerant pioneer tree species  
126 (Karrenberg *et al.* 2002). Shading also hinders the development of light-demanding, weedy  
127 herbaceous species (De Keersmaeker *et al.* 2004). Dense weed layers not only compete for  
128 resources, but create a barrier to tree seedling establishment through leaf litter accumulation  
129 (Coates *et al.* 1994). The increased tree cover effect may thus maintain availability of favourable

130 recruitment microsites and create opportunities for later-successional tree species (Boothroyd-  
131 Roberts *et al.* 2013), more vulnerable to desiccation than to constraints in light (Lieffers & Stadt  
132 1994; Landhäusser & Lieffers 2001).

133 The restoration objective associated to this project was defined within a conceptual framework of  
134 community ecology (Naeem 2006) and aimed at reestablishing native boreal tree species to  
135 restore the structure of a forest community. The facilitating role of plantations in mining  
136 conditions was examined by few studies in relation to soil redevelopment process (Dutta &  
137 Agrawal 2002; Singh *et al.* 2004; Singh & Singh 2006; Singh & Zeng 2008) but remains largely  
138 unexplored regarding tree recruitment (Densmore 2005; Frouz *et al.* 2015), especially on waste  
139 rock slopes. This study aimed to test the facilitation hypothesis using young hybrid poplar  
140 plantations and to understand how nurse tree spacing influences the limiting factors for the  
141 recruitment of boreal tree species in a waste rock slope (3H:1V ratio). Three hybrid poplar  
142 spacings were compared to two control treatments: bare soil without planting or seeding, and soil  
143 with planted trees and a traditional hydroseeded cover treatment. Field experiments were carried  
144 out to evaluate the effects of these plantation designs on the understory micro-environmental  
145 parameters, and on the emergence and early survival of early, mid and late successional tree  
146 species. First, we monitored soil humidity and temperature conditions, available light at ground  
147 level, leaf litter accumulation and herbaceous biomass in the plantation understories. Second, we  
148 surveyed the naturally established pioneer seedlings in each plantation designs. Third, we  
149 surveyed later-successional *Picea glauca* and *Abies balsamea* seedlings following a seed-sowing  
150 experiment. We first hypothesized that planting of hybrid poplars as nurse trees would quickly  
151 exert a structuring effect on the understory micro-environmental parameters. Secondly, it was  
152 postulated that the nurse tree cover would benefit forest tree seedling performances compared to



153 bare soil. More specifically, we predicted better seedling emergence under denser tree cover in  
154 the young plantations because of higher soil moisture content. However, seedling mortality rates  
155 are expected to increase during canopy closure for shade-intolerant pioneer species. Thirdly, we  
156 hypothesized that the presence of a hydroseeded cover would adversely affect the emergence and  
157 survival of forest tree seedlings.

## 158 **2 Materials and methods**

### 159 2.1 Mine site and waste rocks

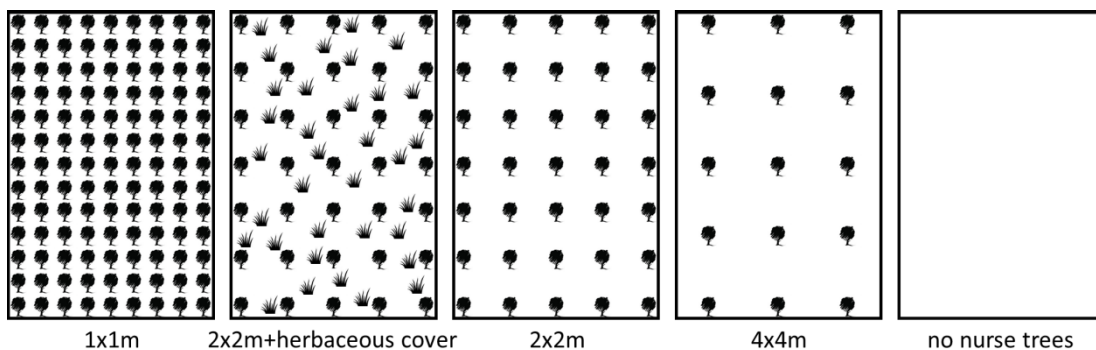
160 The field experiments were conducted at the Canadian Malartic mine site, located in  
161 Northwestern Quebec, Canada (48°13'N, 78°12'W). Climate is cold-temperate continental with  
162 an average annual temperature of 1.5°C and a mean annual total precipitation of 929 mm  
163 (Government of Canada 2015). Average length of growing season ranges between 120 and 130  
164 days with a mean frost-free period of 97 days (Agriculture and Agri-Food Canada 2014). The  
165 region belongs to the balsam fir-white birch bioclimatic domain in the southern portion of the  
166 boreal zone (MERN 2003). Forest stands surrounding the mine site includes balsam fir (*Abies*  
167 *balsamea* (Linnaeus) Miller), black spruce (*Picea mariana* (Miller) BSP), trembling aspen  
168 (*Populus tremuloides* Michaux), white birch (*Betula papyrifera* Marshall), balsam poplar  
169 (*Populus balsamifera* Linnaeus), jack pine (*Pinus banksiana* Lambert), white spruce (*Picea*  
170 *glauca* (Moench) Voss) and tamarack (*Larix laricina* (Du Roi) K. Koch).

171 The site is an active open-pit gold mine since 2011, where 55,000 tons of ore are being processed  
172 each day. Canadian Malartic ore is a mineralized greywacke. Waste rocks have low-sulphide  
173 content (around 1% S) and contain calcite. Mean trace metal concentrations in waste rocks are  
174 below Quebec regulatory thresholds for residential land use (Government of Quebec 2017).

175 2.2 Experimental setting, soil and plant material

176 The hybrid poplar plantations were established in May 2013 on a 50-cm overburden topsoil layer  
177 over a 3H:1V (33%) waste rock slope facing southwest and adjacent to a mature forest patch.  
178 Distance between the slope toe and the nearby forested area was slightly over 30 m. The  
179 overburden soil taken prior to ore excavation from the uppermost 30 cm (O- and A-horizons) of  
180 the partially wooded swamp above the pit was a luvic gleysol  
181 (Soil Classification Working Group 1998). The soil contained 20% organic matter and its  
182 mineral fraction was composed of 42% clay, 27% silt and 31% sand. The overburden soil was  
183 stockpiled in 7-m-high piles (2.5:1 slope) for 36 months before being respread.

184 Fifteen experimental plots of 8x12 m located along the lower half of the slope and separated by  
185 4-m-wide buffer zones were treated according to a randomized complete block design. Five  
186 treatments within three replicate blocks were applied: 1) 1x1-m (10 000 stems/ha), 2) 2x2-m  
187 (2 500 stems/ha) and 3) 4x4-m (625 stems/ha) hybrid poplar spacing treatments, 4) a control  
188 treatment with an intermediary (2x2 m) poplar spacing and a traditional hydroseeded herbaceous  
189 cover, and 5) a control treatment without planting or hydroseeding (Figure 1).



190 Figure 1. Hybrid poplar plantation designs grouped in each block of the experimental  
191 layout (not drawn to scale nor randomized).  
192

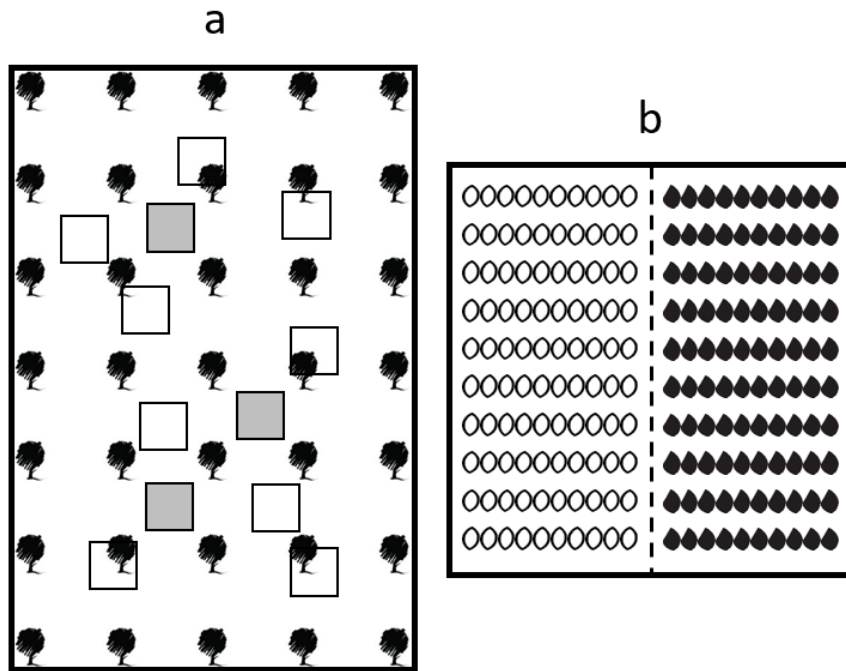
193 The hybrid poplar stock consisted of clonally propagated one-year-old whips (1-m long cuttings)  
194 from *Populus maximowiczii* Henry × *P. balsamifera* L. (M×B, clone number 915319), locally  
195 produced by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) and well  
196 adapted to the local conditions. Grass and legume species in the hydroseeded plots included the  
197 following commonly used reclamation species: *Festuca rubra* Linnaeus (15%), *Poa pratensis*  
198 Linnaeus (15%), *Pennisetum glaucum* (Linnaeus) R. Brown (12%), *Lolium perenne*  
199 Linnaeus (12%), *Avena sativa* Linnaeus (11%), *Lotus corniculatus* Linnaeus (15%), *Trifolium*  
200 *pratense* Linnaeus (10%), *Trifolium repens* Linnaeus (7%) and *Trifolium hybridum* Linnaeus  
201 (3%). Seeding rate was 100 kg ha<sup>-1</sup> while a fertilizer (8% N, 32% P, and 16% K, di- and  
202 mono-ammonium phosphates and potassium chloride) was applied once at seeding in May 2013  
203 at 750 kg ha<sup>-1</sup>.

204 *A. balsamea* and *P. glauca* seeds were also provided by the MFFP. The seed lots received a 48-  
205 hour-priming treatment followed by a 21-day cold moist stratification treatment to promote  
206 higher germination rates (Colas & Bettez 2014). A viability test was performed by placing 3x100  
207 seeds of both species on wet paper in Petri dishes placed under controlled conditions at ~20°C  
208 for 20 days to assess the germination capacity of the seed lots before experimentation (Charron  
209 & Greene 2002; Johnstone & Chapin III 2006). The germination rates obtained were close to  
210 those reported by the MFFP: 72 and 92% respectively for *A. balsamea* and *P. glauca*.

### 211 2.3 Understory micro-environment measurements (2014-2015)

212 Three 1-m<sup>2</sup> microsites were placed systematically within each experimental plot for micro-  
213 environment measurements during the 2014 and 2015 growing seasons. Microsites were  
214 positioned at the intersection of the diagonals of the square formed by four adjacent planted

215 hybrid poplars in each third of the plot along the slope (Figure 2). Continuous measures of soil  
216 water volumetric content were taken at 3-cm depth (ECH2O 5-cm probe, Decagon, calibrated for



218  
219 Figure 2. Sample units in individual experimental plot.  
220 a) Microsites for the micro-environmental measurements and the  
221 sowing experiment are symbolized by coloured squares; quadrats  
222 for the natural colonization survey, by blank squares. b) Magnified  
223 representation of microsites, sown with *Abies balsamea* and *Picea*  
224 *glauca* seeds (numbers shown are different to those in the  
225 experiment).

226 the soil type used) in the microsite located in the centre of each plot. From June to August 2014  
227 and May to August 2015, hourly measurements were recorded to calculate weekly averages. Soil  
228 temperature at 3-cm depth (Acorn probe, Oakton Instruments) and photosynthetic photon flux  
229 density (PPFD) at ground level (Sunfleck Ceptometer, Decagon) were measured every two  
230 weeks in the three microsites of each plot during the same period. Measurements for these two  
231 parameters were taken around noon, under clear sky conditions. Aboveground herbaceous  
232 biomass was assessed during the period of maximal biomass (mid-July) in 2014 and 2015. A  
233 non-destructive point intercept method (Jonasson 1983; Jonasson 1988) was used to estimate the

234 herbaceous biomass in the microsite located in the centre of each plot. A narrow rod placed  
235 perpendicularly to the soil surface was shifted along a 100 (10x10cm) intersection point grid  
236 which covered the microsite area. The number of contacts between the rod and each plant species  
237 was registered. In order to calibrate the method for biomass estimation, 12 1-m<sup>2</sup> quadrats  
238 (selected to include a wide range of biomass of the different species) were previously sampled in  
239 July 2014 using the same grid pattern. The vegetation within each of these quadrats was then  
240 clipped at ground level and dried in order to compute regression equations between contact  
241 points and dry biomass for the main herbaceous species. The summed number of contacts by  
242 species sampled in each experimental plot could then be used to estimate total herbaceous  
243 biomass per m<sup>2</sup>. Finally, total leaf litter percentage cover (from hybrid poplars and herbaceous  
244 species) was measured in early and late summer 2014 and 2015. A 25 (20x20cm) point grid was  
245 used for this measurement in the three microsites for each plot. Each intersection point where the  
246 rod touched at least one leaf on the ground was noted as a litter occurrence to estimate the  
247 percentage cover as follows: number of occurrences/total number of measurement points x 100.

#### 248 2.4 Natural colonization survey (2014-2015) and field sowing experiment (2015)

249 Naturally established pioneer woody (tree and arborescent shrub) seedlings were monitored in  
250 nine randomly positioned 1-m<sup>2</sup> quadrats in each plot (Figure 2). Seedling numbers were surveyed  
251 by species during early, mid and late summer 2014 and 2015. Data were used to quantify  
252 summer emergence (total number of new seedlings recorded during mid and late summer counts  
253 per m<sup>2</sup>), summer mortality rates (total number of dead seedlings recorded during mid and late  
254 summer counts/total number of seedlings recorded during early, mid or late summer counts) and  
255 late-season abundance (total number of seedlings recorded during the late summer count per m<sup>2</sup>)  
256 in each quadrat, for 2014 and 2015.

257 The sowing experiment was conducted in the three microsites already used for the micro-  
258 environment measurements in each of the 15 experimental plots. Each microsite was divided into  
259 two equal parts sown respectively with *A. balsamea* and *P. glauca* just after snowmelt in  
260 mid-May 2015. Seeds were sown by hand in tiny furrows (40 seeds x 10 rows for both species)  
261 at an interrow spacing of 10 cm and then partially covered to minimize the risk of loss by erosion  
262 on the slope. A total of 1200 seeds (400 seeds x 3 microsites) per species were sown this way in  
263 each plot. Seedling numbers were surveyed for each species every four weeks from June to  
264 August 2015. Data were used to quantify summer emergence rates (total number of emergences  
265 during the growing season/number of seeds), summer mortality rates (total number of dead  
266 seedlings/total number of emerged seedlings during the season) and first-year recruitment  
267 success rates (number of surviving seedlings at the end of the growing season/number of seeds)  
268 in each microsite.

## 269 2.5 Statistical analyses

270 Data from the natural colonization survey and the sowing experiment were analyzed according to  
271 a randomized complete block design using generalized linear mixed models. Models were fitted  
272 with the `glmer` function of the `lme4` package of R (Bates *et al.* 2015; R Core Team –  
273 version 3.2.3– 2015). Maximum likelihood estimation was based on the Laplace approximation  
274 (Laplace 1986). A multiple regression analysis was used to test whether seedling emergence,  
275 mortality and abundance: 1) increased or decreased with planted hybrid poplar density (linear  
276 relation), 2) reached a minimum/maximum value under intermediate density (quadratic relation),  
277 and 3) differed between the 2x2-m-spacing treatments with and without a hydroseeded cover.  
278 Blocks and experimental units were treated as random effects with the latter nested in the former.

279 That is, predictive models could be summarized as follows: seedling response variable ~ linear  
280 density + quadratic density + hydroseeding + random effects (block/experimental units).

281 Only the *Salicaceae* family was considered for the statistical analysis of the natural colonization  
282 survey, and tests were performed for all the species combined (pooled *Populus* and *Salix*  
283 species). Seedling emergence, mortality rates and late-season abundance were analyzed on a  
284 growing-season basis. For the sowing experiment, seedling emergence, mortality and recruitment  
285 success were analyzed separately for each species.

286 Data from the micro-environment measurements were analyzed with linear mixed effect models  
287 using the nlme package of R (Pinheiro *et al.* 2015). Model parameter estimates were based on the  
288 restricted maximum likelihood method. A multiple regression analysis was used to test the  
289 effects of hybrid poplar density, as linear and quadratic terms, and hydroseeding, as a binary  
290 variable, on: soil moisture, soil temperature, available light at ground level, herbaceous biomass  
291 and total leaf litter cover. The quadratic term was removed when not significant for a better  
292 estimate of the simple term of density. The analysis was conducted for key periods of seedling  
293 responses to experimental treatments, namely: 1) the highest emergence period of *Salicaceae*  
294 species (late June to late July 2014), 2) the highest emergence period of both *P. glauca* and *A.*  
295 *balsamea* (mid-May to mid-June 2015) and 3) the highest mortality period for any species (mid-  
296 July to mid-August 2015). Average value of micro-environmental variables registered in  
297 microsites within each time period was used for the analysis. A prior first order autoregressive  
298 analysis was conducted for repeated measures to confirm that the effect of treatments was  
299 constant within each period studied. Data were log-transformed when necessary to meet  
300 assumptions of normality and homogeneity of variance. The logarithmic value of hybrid poplar

301 density was also used for all regression analyses, in order to get more regular intervals between  
302 treatment levels along the density gradient.

303 For all analyses, we considered a significance level equal to 0.10 to allow a broader effects-based  
304 analysis. For all models illustrated graphically, we used a Monte Carlo approach (Gelman *et al.*  
305 2014) to estimate predicted values and the 90% confidence interval along the density gradient,  
306 from the median, the 5<sup>th</sup> and 95<sup>th</sup> percentiles of the posterior predictive distribution of model  
307 parameters.

308 Linear relationships between the micro-environmental variables and seedling emergence and  
309 mortality rates were explored using Pearson correlations for the determining periods mentioned  
310 above. A complementary analysis was conducted using the Hoeffding's D measure (Harrell Jr &  
311 Dupont 2006) to test for dependence structures beyond linear and monotonic associations but  
312 was not retained since no additional relationships between variables were detected. For both the  
313 natural colonization survey and the sowing experiment, we used the average value of each  
314 variable during the highest emergence and mortality periods recorded. The Bonferroni correction  
315 was applied to adjust for the significance level of multiple correlation tests, dividing the alpha  
316 level by the number of tests performed for each seedling response. Since five micro-  
317 environmental parameters were considered,  $p\text{-value} = 0.10/5 = 0.02$ .

### 318 3 Results

#### 319 3.1 Tree cover effect on the understory micro-environment (2014-2015)

320 Variations in the understory conditions were observed along the hybrid poplar density gradient  
321 during key periods of seedling responses in the 2<sup>nd</sup> (2014) and 3<sup>rd</sup> (2015) growing seasons of the



322 plantations (Table 1). The effect of the hybrid poplar density on herbaceous biomass was already  
323 noticeable in July 2014, while values measured during the period of maximal biomass decreased  
324 linearly with tree density (Figure 3). Mean dry herbaceous biomass was >3 times lower under the  
325 1x1-m spacing treatment ( $45\text{g}\cdot\text{m}^{-2}$ ; CI limits: 25–70) compared to the control plots without nurse  
326 trees ( $150\text{g}\cdot\text{m}^{-2}$ ; CI limits: 100–225). Herbaceous biomass remained similarly related to poplar  
327 density in 2015, but was overall almost 2 times less important than that of the previous year  
328 under the developing canopies in the plantations (see appendix A for the list of inventoried  
329 herbaceous species).

330 Relationships between poplar density and soil moisture content followed a quadratic pattern from  
331 late June to late July 2014 (Table 1). The mean volumetric water content under an intermediary  
332 spacing treatment (26%; CI limits: 24–28) was higher than under the 1x1-m spacing level (22%;  
333 CI limits: 20–25) or the control without nurse trees (21%; CI limits: 19–23, Figure 3). For early  
334 season 2015, linear regression coefficients indicated a significant positive effect of poplar  
335 density on soil moisture conditions, while the highest mean volumetric water content was found  
336 under the 1x1-m spacing treatment (36%; CI limits: 34–38) and the lowest, under the control  
337 without nurse trees (31%; CI limits: 29–33). Similarly to 2014, the moisture content under denser  
338 cover dropped compared to intermediary spacing levels in the second half of the summer. The  
339 relation between poplar density and moisture content thus switched from a linear to a quadratic  
340 pattern, with lower mean values found at both ends of the density gradient (29%; CI limits: 27–  
341 30, and 27%; CI limits: 25–28, respectively for the control and 1x1-m treatments) from mid-July  
342 to mid-August 2015. Notwithstanding, soil volumetric water content remained higher than the  
343 wilting point measured (results not shown) for the soil material considered –with values over  
344 18.5% for all types of cover treatment– during the whole growing season.

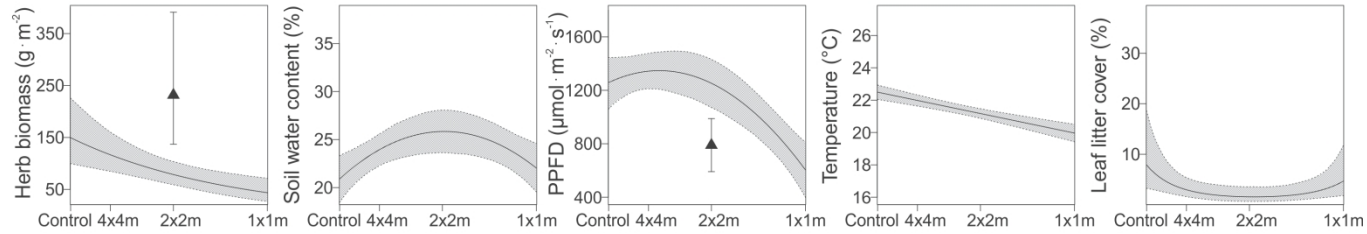
345 Table 1. Effect of hybrid poplar density and hydroseeded herbaceous cover treatments on herbaceous biomass, soil  
 346 moisture, soil temperature, available light (PPFD) at ground level and leaf litter cover. Results are presented for the highest  
 347 emergence period of *Salicaceae* (*Populus* and *Salix*) species (late June to late July 2014), the highest emergence period of  
 348 *Picea glauca* and *Abies balsamea* (mid-May to mid-June 2015) and the highest mortality period for any species (mid-July  
 349 to mid-August 2015) in the plantations. P-values are shown in bold when under the 10% significance threshold. N=15 for  
 350 herbaceous biomass and soil moisture; N=45 for soil temperature, available light and leaf litter cover.

| Effect                             | Herbaceous biomass <sup>a</sup> |               |                  | Soil moisture |               |              | Available light <sup>b</sup> |               |              | Soil temperature |               |              | Leaf litter cover <sup>a</sup> |               |              |
|------------------------------------|---------------------------------|---------------|------------------|---------------|---------------|--------------|------------------------------|---------------|--------------|------------------|---------------|--------------|--------------------------------|---------------|--------------|
|                                    | Esti-<br>mate                   | Std.<br>Error | P-<br>value      | Esti-<br>mate | Std.<br>Error | P-<br>value  | Esti-<br>mate                | Std.<br>Error | P-<br>value  | Esti-<br>mate    | Std.<br>Error | P-<br>value  | Esti-<br>mate                  | Std.<br>Error | P-<br>value  |
| <b>late June to late July 2014</b> |                                 |               |                  |               |               |              |                              |               |              |                  |               |              |                                |               |              |
| Intercept                          | 4.451                           | 0.272         | <0.001           | 25.728        | 1.539         | <0.001       | 1299.228                     | 151.868       | <0.001       | 21.357           | 0.624         | <0.001       | 0.493                          | 0.746         | 0.525        |
| Linear density                     | -0.512                          | 0.178         | <b>0.018</b>     | 1.220         | 0.943         | 0.228        | -215.925                     | 76.068        | <b>0.019</b> | -1.051           | 0.414         | <b>0.029</b> | -0.447                         | 0.354         | 0.239        |
| Quadratic density                  | –                               | –             | –                | -3.047        | 1.269         | <b>0.040</b> | -234.338                     | 102.331       | <b>0.048</b> | –                | –             | –            | 0.928                          | 0.477         | <b>0.084</b> |
| Hydroseeding                       | 0.991                           | 0.437         | <b>0.049</b>     | -3.105        | 2.065         | 0.167        | -515.549                     | 166.483       | <b>0.013</b> | 0.294            | 0.843         | 0.735        | 0.249                          | 0.776         | 0.755        |
| <b>mid-May to mid-June 2015</b>    |                                 |               |                  |               |               |              |                              |               |              |                  |               |              |                                |               |              |
| Intercept                          | NA                              | NA            | NA               | 33.143        | 0.733         | <0.001       | 7.395                        | 0.083         | <0.001       | 21.075           | 0.494         | <0.001       | 25.555                         | 1.394         | <0.001       |
| Linear density                     | NA                              | NA            | NA               | 2.202         | 0.800         | <b>0.020</b> | -0.166                       | 0.049         | <b>0.008</b> | -0.917           | 0.354         | <b>0.029</b> | 3.167                          | 1.012         | <b>0.011</b> |
| Quadratic density                  | NA                              | NA            | NA               | –             | –             | –            | -0.236                       | 0.065         | <b>0.006</b> | -1.696           | 0.476         | <b>0.006</b> | –                              | –             | –            |
| Hydroseeding                       | NA                              | NA            | NA               | -0.110        | 1.629         | 0.948        | -0.044                       | 0.106         | 0.690        | -1.096           | 0.775         | 0.191        | 9.891                          | 2.060         | <b>0.001</b> |
| <b>mid-July to mid-August 2015</b> |                                 |               |                  |               |               |              |                              |               |              |                  |               |              |                                |               |              |
| Intercept                          | 62.660                          | 5.024         | <0.001           | 32.333        | 0.989         | <0.001       | 1395.965                     | 116.349       | <0.001       | 26.438           | 1.055         | 0.000        | 47.662                         | 5.841         | <0.001       |
| Linear density                     | -12.753                         | 5.543         | <b>0.044</b>     | -0.132        | 0.640         | 0.841        | -165.920                     | 79.613        | <b>0.067</b> | -1.205           | 0.275         | <b>0.002</b> | 3.707                          | 4.080         | 0.385        |
| Quadratic density                  | –                               | –             | –                | -3.253        | 0.861         | <b>0.004</b> | -324.514                     | 107.102       | <b>0.014</b> | -0.841           | 0.370         | <b>0.049</b> | –                              | –             | –            |
| Hydroseeding                       | 65.541                          | 11.287        | <b>&lt;0.001</b> | -1.104        | 1.400         | 0.451        | -548.331                     | 174.244       | <b>0.012</b> | -1.305           | 0.602         | <b>0.058</b> | 9.689                          | 8.307         | 0.271        |

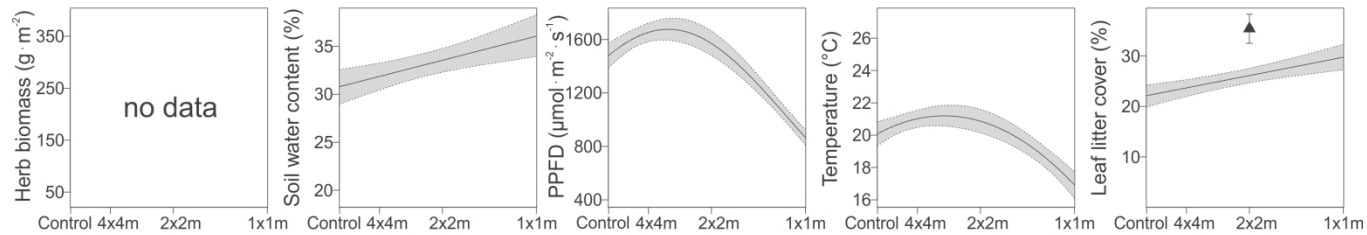
<sup>a</sup> Log transformed for late June to late July 2014

<sup>b</sup> Log transformed for mid-May to mid-June 2015

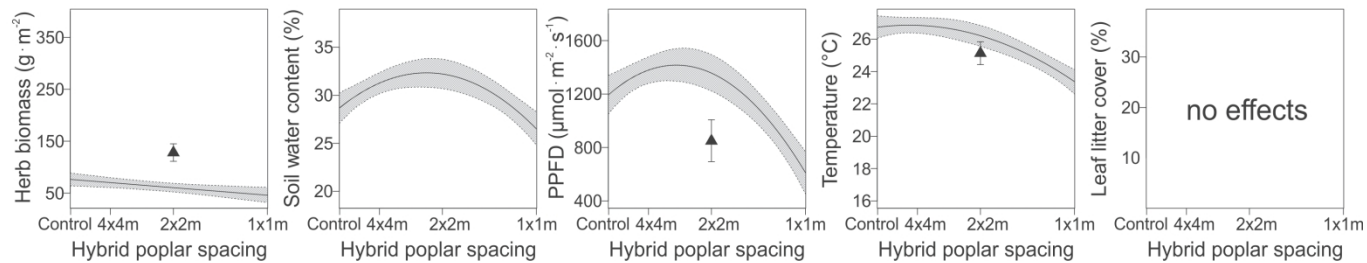
a) late June to late July 2014: highest emergence period of *Salicaceae*



b) mid-May to mid-June 2015: highest emergence period of *P. glauca* and *A. balsamea*



c) mid-July to mid-August 2015: highest mortality period for any species



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Figure 3. Influence of hybrid poplar spacing and hydroseeded herbaceous cover treatments on the understory micro-environmental parameters in key periods of seedling responses, during (a) the 2<sup>nd</sup> (2014) and (b, c) the 3<sup>rd</sup> (2015) growing seasons of the plantations. The solid line bordered by grey margins symbolizes the predicted values and 90% CI along the hybrid poplar gradient; the triangle bordered by arrows symbolizes the predicted values and 90% CI in the 2x2-m spacing treatment with a hydroseeded cover.

360 The influence of hybrid poplar density on available light at ground level and soil temperature  
361 was similar for the late June to late July 2014, mid-May to mid-June 2015 and mid-July to mid-  
362 August 2015 periods, showing significant linear or quadratic effects (Table 1). Mean values for  
363 these parameters were the lowest under the 1x1-m spacing treatment throughout the survey. The  
364 1x1-m poplar cover intercepted on average ~70% of full sunlight ( $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , CI limits:  
365 400–810, compared to  $\sim 2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for full sunlight) during measurements from late June  
366 to late July 2014 (Figure 3). Light interception reached a maximum of ~80% during summer  
367 2015, but was on average ~60% ( $870 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , CI limits: 820–930, compared to  $\sim 2180$   
368  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for full sunlight) and ~70% ( $610 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , CI limits: 460–770, compared to  
369  $\sim 2060 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for full sunlight) respectively for the early and late season periods  
370 considered. Comparatively, light interception for the 2x2m, the 4x4m and the control without  
371 nurse trees was roughly half that of the 1x1-m spacing treatment throughout the survey.  
372 Likewise, soil temperature was the lowest under the 1x1-m spacing treatment for every time  
373 period studied (Table 1, Figure 3). Mean temperature values for the 2x2m, the 4x4m and the  
374 control without nurse trees –as for available light– were generally more alike. Mean differences  
375 between the 1x1m plots and the other spacing levels were  $<2.5^{\circ}\text{C}$  from late June to late July  
376 2014, but increased to  $>4.3^{\circ}\text{C}$  during both periods studied in 2015.

377 The density effect on total leaf litter cover (from hybrid poplars and herbaceous species) changed  
378 over the duration of the study (Table 1, Figure 3). A quadratic pattern was observed from late  
379 June to late July 2014, reflecting a stronger contribution from hybrid poplars and herbaceous  
380 species at opposite ends of the density gradient. However, regression coefficients indicate a  
381 positive linear effect of poplar density on leaf litter cover in early season 2015, but no significant  
382 effect in late season 2015, while mean values reached the 40-50% range.

### 383 3.2 Hydroseeded cover effect on the understory micro-environment (2014-2015)

384 The influence of the hydroseeded cover treatment on the herbaceous biomass was significant  
385 during the period of maximal herbaceous biomass both in 2014 and 2015 (Table 1). Mean  
386 herbaceous dry biomass in hydroseeded plots ( $235\text{g}\cdot\text{m}^{-2}$ ; CI limits: 140–390) was close to 3  
387 times that of unseeded plots ( $80\text{g}\cdot\text{m}^{-2}$ ; CI limits: 60–105) in 2014 and slightly more than twice  
388 that of unseeded plots ( $130\cdot\text{m}^{-2}$ ; CI limits: 110–145 vs  $\sim 60\text{g}\cdot\text{m}^{-2}$ ; CI limits: 50–70) in 2015, with  
389 declining values from 2014 to 2015 (Figure 3). The hydroseeded cover treatment also  
390 significantly affected light availability. From late June to late July 2014,  $\sim 60\%$  ( $790$   
391  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , CI limits: 590–990, compared to  $\sim 2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for full sunlight) of full  
392 sunlight was intercepted on average during measurements in hydroseeded plots compared to  
393  $<35\%$  ( $1250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , CI limits: 1070–1430) in unseeded plots. Treatment effect on light  
394 conditions was not detected from mid-May to mid-June 2015 –before full early season regrowth–  
395 but increased later in the season, with % light transmission for the mid-July to mid-August  
396 period similar to those of 2014. Mean differences in soil temperature were not detected until  
397 mid-July to mid-August 2015) and remained marginal even during this period ( $\sim 25.2^\circ\text{C}$ , CI  
398 limits: 24.4–25.8, for hydroseeded plots;  $26.2^\circ\text{C}$ , CI limits: 25.6–26.8, for unseeded plots). The  
399 influence of the hydroseeded cover on leaf litter cover was not constant. Percentage leaf litter  
400 cover significantly differed only in early season 2015, while mean value was 36% (CI limits: 33–  
401 38) in seeded plots compared to 26% (CI limits: 25–28) for unseeded plots. Finally, soil moisture  
402 content was not impacted by the hydroseeded treatment during any of the period studied.

### 403 3.3 Natural colonization (2014-2015)

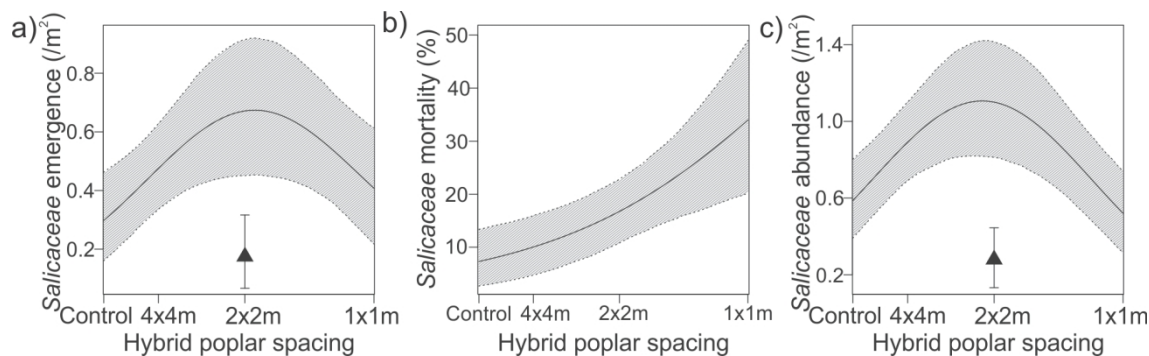
404 Abundance of colonizing woody (tree and arborescent shrub) species after three growing seasons  
405 was largely dominated by *Salicaceae*: *Populus* and *Salix* species accounted for 72 and 10%  
406 of total abundance respectively in the plantations. Other seedlings observed belonged to  
407 the genera (in order of decreasing abundance): *Picea* (10%), *Sorbus* (3%), *Abies* (2%), *Prunus*  
408 (1%), *Betula* (1%) and *Cornus* (1%) (see appendix B for the list of inventoried woody species).  
409 Mean abundance of seedlings in the quadrats for all genera combined was  $1.3 \pm 0.2(\text{CI}) \cdot \text{m}^{-2}$  at the  
410 end of summer 2014, but  $1.0 \pm 0.2(\text{CI})$  seedlings per  $\text{m}^2$  at the end of summer 2015, pointing to an  
411 overall emergence/mortality ratio switching from a  $>1$  (2.7) to a  $<1$  (0.4) value in the plantations.  
412 Variations in seedling emergence, mortality or abundance patterns were observed for the  
413 dominant *Salicaceae* species under both the hybrid poplar density and the hydroseeded cover  
414 treatments (Table 2). In 2014, mean seedling emergence was greater under the intermediary 2x2-  
415 m spacing treatment ( $\sim 0.7 \cdot \text{m}^{-2}$ ; CI limits: 0.5–0.9) and lower under the control treatment without  
416 nurse trees ( $\sim 0.3 \cdot \text{m}^{-2}$ ; CI limits: 0.2–0.4), following a significant quadratic pattern along the  
417 hybrid poplar density gradient (Figure 4). Mean emergences in 2014 were also significantly  
418 influenced by the hydroseeded treatment: nearly 3.5 times less seedlings emerged in hydroseeded  
419 plots ( $< 0.2 \cdot \text{m}^{-2}$ ; CI limits: 0.1–0.3) compared to unseeded plots. In contrast, summer mortality in  
420 2014 was not impacted by either treatment –the same applies for the 2014-2015 winter mortality  
421 (results not shown). In 2015, seedling emergence was too low to test for effects. Summer  
422 mortality rates, on the other hand, increased linearly with hybrid poplar density in 2015: mean  
423 mortality rates were 34% (CI limits: 20–49) under the 1x1-m spacing treatment compared to 7%  
424 (CI limits: 3–13) in control plots without nurse trees. No effect of the hydroseeded cover  
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Table 2. Effect of hybrid poplar density and hydroseeded cover treatments on the emergence, mortality and late-season abundance of naturally established *Salicaceae* (*Populus* and *Salix*) seedlings. Results are presented for the 2<sup>nd</sup> and 3<sup>rd</sup> growing seasons of the plantations. P-values are shown in bold when under the 10% significance threshold. N=135.

|                   | Summer emergence |            |              | Summer mortality |            |              | Late-season abundance |            |              |
|-------------------|------------------|------------|--------------|------------------|------------|--------------|-----------------------|------------|--------------|
|                   | Estimate         | Std. Error | P-value      | Estimate         | Std. Error | P-value      | Estimate              | Std. Error | P-value      |
| <b>2014</b>       |                  |            |              |                  |            |              |                       |            |              |
| Intercept         | -0.435           | 0.275      | 0.114        | -2.047           | 0.258      | <0.001       | 0.338                 | 0.436      | 0.437        |
| Linear density    | 0.244            | 0.193      | 0.207        | 0.295            | 0.303      | 0.329        | 0.165                 | 0.162      | 0.309        |
| Quadratic density | -0.450           | 0.232      | <b>0.052</b> | –                | –          | –            | -0.385                | 0.202      | <b>0.056</b> |
| Hydroseeding      | -1.322           | 0.511      | <b>0.010</b> | 0.529            | 0.688      | 0.442        | -1.310                | 0.398      | <b>0.001</b> |
| <b>2015</b>       |                  |            |              |                  |            |              |                       |            |              |
| Intercept         | NA               | NA         | NA           | -1.713           | 0.294      | <0.001       | 0.064                 | 0.480      | 0.895        |
| Linear density    | NA               | NA         | NA           | 0.789            | 0.328      | <b>0.016</b> | 0.048                 | 0.176      | 0.784        |
| Quadratic density | NA               | NA         | NA           | –                | –          | –            | -0.466                | 0.206      | <b>0.024</b> |
| Hydroseeding      | NA               | NA         | NA           | 0.477            | 0.779      | 0.541        | -1.387                | 0.437      | <b>0.002</b> |

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Figure 4. Influence of hybrid poplar spacing and hydroseeded herbaceous cover treatments on seedling response of naturally established *Salicaceae* (*Populus* and *Salix*) species during the 2<sup>nd</sup> and 3<sup>rd</sup> growing seasons of the plantations. Results summarize (a) summer emergence in 2014, (b) summer mortality in 2015 and (c) late-season abundance in 2015. The solid line bordered by grey margins symbolizes the predicted values and 90% CI along the hybrid poplar gradient; the triangle bordered by arrows symbolizes the predicted values and 90% CI in the 2x2-m spacing treatment with a hydroseeded cover.

443 treatment on the 2015 summer mortality was detected. At the end of the 2015 growing season,  
444 *Salicaceae* seedling abundance was greater under an intermediate level of hybrid poplar density  
445 ( $p=0.024$  for quadratic relation) –with mean values up to  $1.1 \cdot m^{-2}$  (CI limits: 0.8–1.4) in the  
446  $2 \times 2m$ – and in plots without a hydroseeded cover ( $p=0.002$ ) –with mean value as low as  $<0.3 \cdot m^{-2}$   
447 (CI limits: 0.1–0.4) in hydroseeded plots. In other words, differences in the pioneer seedling  
448 abundance observed after the emergence period in 2014 were still noticeable at the end of  
449 summer 2015. However, the lowest abundance values for the spacing treatment were now noted  
450 in the  $1 \times 1m$  level at the end of summer 2015 ( $\sim 0.5 \cdot m^{-2}$ ; CI limits: 0.3–0.7).

#### 451 3.4 Field sowing experiment (2015)

452 The hybrid poplar spacing treatment significantly influenced the summer emergence of  
453 *P. glauca* and, more marginally, of *A. balsamea*, while rates increased linearly with poplar  
454 density for both species (Table 3). Mean emergence rates were 15.7% (CI limits: 13.7–17.7) and  
455 6.4% (CI limits: 5.1–7.9) respectively for *P. glauca* and *A. balsamea* under the  $1 \times 1m$  spacing  
456 treatment compared to 11.9% (CI limits: 10.6–13.2) and 4.4% (CI limits: 3.6–5.3) under the  
457 control treatment without nurse trees (Figure 5). On the other hand, emergence rates remained  
458 unaffected by the presence of a hydroseeded cover for both species. After one growing season,  
459 overall mean mortality rates in microsites were  $30.5 \pm 3.8$ (CI) and  $28.6 \pm 3.8$ (CI)% respectively for  
460 *P. glauca* and *A. balsamea*. Mortality rates for *P. glauca* were not significantly impacted by  
461 either treatments. *A. balsamea* mortality also remained unchanged by the hybrid poplar spacing  
462 treatment, but significant differences were observed under the hydroseeded treatment ( $p=0.044$ ),  
463 with higher rates registered in hydroseeded plots (37%; CI limits: 27–48) compared to unseeded  
464 plots (25%; CI limits: 21–28). Overall recruitment success rates in microsites were  $9.8 \pm 1.0$ (CI)

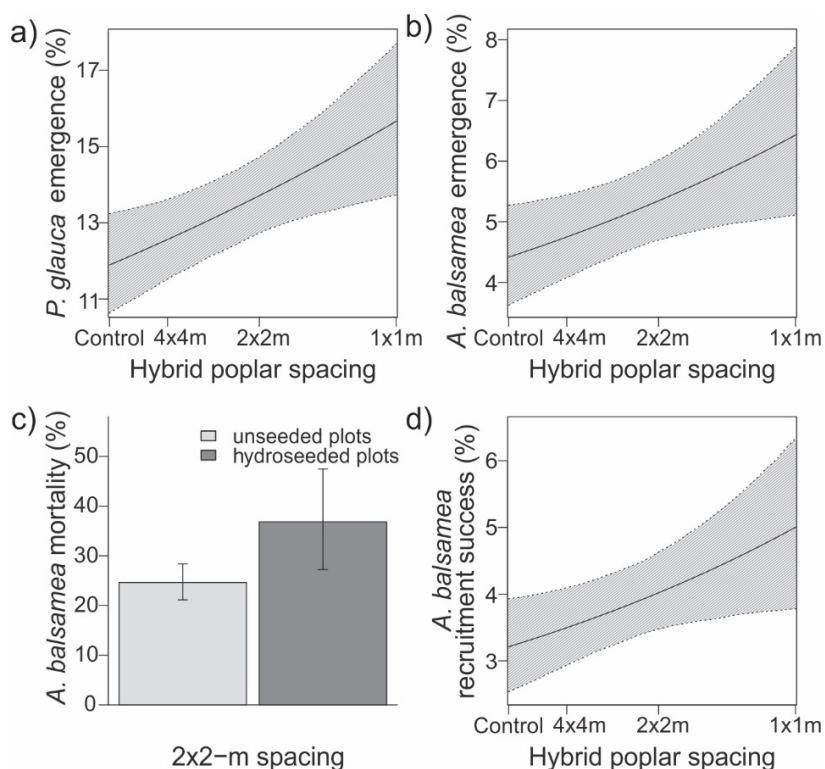


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Table 3. Effect of hybrid poplar density and hydroseeded cover on summer emergence, mortality and late-season recruitment success of *Picea glauca* and *Abies balsamea* seedlings following spring seeding in 3-year-old hybrid poplar plantations. P-values are shown in bold when under the 10% significance threshold. N=45.

|                       | Summer emergence |            |              | Summer mortality |            |              | Late-season recruitment success |            |              |
|-----------------------|------------------|------------|--------------|------------------|------------|--------------|---------------------------------|------------|--------------|
|                       | Estimate         | Std. Error | P-value      | Estimate         | Std. Error | P-value      | Estimate                        | Std. Error | P-value      |
| <i>Picea glauca</i>   |                  |            |              |                  |            |              |                                 |            |              |
| Intercept             | -2.004           | 0.107      | <0.001       | -1.194           | 0.086      | <0.001       | -2.367                          | 0.131      | <0.001       |
| Linear density        | 0.116            | 0.057      | <b>0.041</b> | 0.149            | 0.092      | 0.108        | 0.029                           | 0.067      | 0.660        |
| Quadratic density     | -                | -          | -            | -                | -          | -            | -                               | -          | -            |
| Hydroseeding          | 0.067            | 0.116      | 0.563        | -0.061           | 0.189      | 0.749        | 0.076                           | 0.134      | 0.568        |
| <i>Abies balsamea</i> |                  |            |              |                  |            |              |                                 |            |              |
| Intercept             | -2.953           | 0.218      | <0.001       | -1.374           | 0.090      | <0.001       | -3.235                          | 0.216      | <0.001       |
| Linear density        | 0.161            | 0.093      | <b>0.085</b> | -0.122           | 0.100      | 0.225        | 0.184                           | 0.100      | <b>0.064</b> |
| Quadratic density     | -                | -          | -            | -                | -          | -            | -                               | -          | -            |
| Hydroseeding          | -0.163           | 0.187      | 0.384        | 0.375            | 0.187      | <b>0.044</b> | -0.339                          | 0.211      | 0.108        |

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472 Figure 5. Influence of experimental factors on seedling responses of *Picea glauca* and *Abies*  
473 *balsamea* during the 3<sup>rd</sup> growing season of the plantations. Results summarize (a) *P. glauca* and  
474 (b) *A. balsamea* summer emergence rates in relation to hybrid poplar spacing treatment, (c)  
475 *A. balsamea* summer mortality rates in relation to hydroseeded cover treatment and (d)  
476 recruitment success rates for *A. balsamea* first-year seedlings along the poplar gradient. Fitted  
477 values are presented with 90% CI.

479 and 4.0±0.7(CI)% respectively for *P. glauca* and *A. balsamea* first-year seedlings. The positive  
 480 effect of density on recruitment success after one growing season was significant only for  
 481 *A. balsamea* (p=0.064). Mean recruitment success rates for *A. balsamea* seedlings were ~5.0%  
 482 (CI limits: 3.8–6.3) under the 1x1-m spacing treatment compared to 3.2% (CI limits: 2.5–3.9)  
 483 under the control treatment without nurse trees. On the other hand, the resulting effect of the  
 484 hydroseeded treatment on recruitment success at the end of the growing season was not  
 485 statistically significant for either *P. glauca* or *A. balsamea*, notwithstanding the higher summer  
 486 mortality rates registered for *A. balsamea* in plots with a hydroseeded cover.

### 487 3.5 Relationships between the understory micro-environment and seedling responses

488 The correlation analysis did not reach statistical significance regarding relationships between the  
 489 micro-environmental variables and the *Salicaceae* seedlings emergence during the 2014  
 490 emergence period (Table 4). However, *Salicaceae* seedling mortality was negatively correlated

492 Table 4. Correlations between naturally established *Salicaceae* (*Populus* and *Salix*)  
 493 seedling emergence or mortality and micro-environmental variables. Results are  
 494 based on the average value of each variable for the highest emergence (late June to  
 495 late July 2014) and mortality (mid-July to mid-August 2015) periods. P-values are  
 496 shown in bold when under the Bonferroni-adjusted significance threshold (p = 0.10/5  
 497 = 0.02). Confidence intervals (CI = 100 - 0.02 = 98%) excluding zero indicate a  
 498 significant linear relationship at 2% probability of error.

|                    | Emergence (2014) |                |         | Mortality (2015) |                        |              |
|--------------------|------------------|----------------|---------|------------------|------------------------|--------------|
|                    | Coefficient      | CI             | P-value | Coefficient      | CI                     | P-value      |
| Herbaceous biomass | -0.538           | -0.863 ; 0.099 | 0.047   | 0.403            | -0.240 ; 0.800         | 0.136        |
| Soil moisture      | 0.297            | -0.350 ; 0.751 | 0.283   | 0.014            | -0.596 ; 0.614         | 0.963        |
| Available light    | 0.185            | -0.170 ; 0.497 | 0.225   | -0.399           | <b>-0.672 ; -0.029</b> | <b>0.013</b> |
| Soil temperature   | 0.164            | -0.191 ; 0.481 | 0.281   | -0.075           | -0.437 ; 0.308         | 0.655        |
| Leaf litter cover  | -0.388           | -0.794 ; 0.256 | 0.153   | -0.138           | -0.670 ; 0.488         | 0.625        |

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 500 with the available light variable ( $r=-0.398$ ,  $p=0.013$ ) during the main mortality period surveyed  
 501 over the duration of the study, in late-season 2015. Diminution of light availability thus

502 corresponded to increased seedling mortality rates for these species at the end of the third  
 503 growing season in the plantations.

504 No significant relationships were identified between the micro-environmental variables and the  
 505 seedling emergences of *P. glauca* and *A. balsamea* during the peak emergence period monitored  
 506 in the 2015 growing season (Table 5). Strength of relationships for moisture conditions was the

507 Table 5. Correlations between *Picea glauca* and *Abies balsamea* seedling emergence  
 508 or mortality and micro-environmental variables. Results are based on average value  
 509 of each variable for the highest emergence (mid-May to mid-June) and mortality  
 510 (mid-July to mid-August) periods in 2015. P-values are shown in bold when under  
 511 the Bonferroni-adjusted significance threshold ( $p = 0.10/5 = 0.02$ ). Confidence  
 512 intervals (CI =  $100 - 0.02 = 98\%$ ) excluding zero (shown in bold) indicate a  
 513 significant linear relationship at 2% probability of error.

|                       | Emergence   |                |         | Mortality   |                |         |
|-----------------------|-------------|----------------|---------|-------------|----------------|---------|
|                       | Coefficient | CI             | P-value | Coefficient | CI             | P-value |
| <i>Picea glauca</i>   |             |                |         |             |                |         |
| Herbaceous biomass    | NA          | NA             | NA      | 0.013       | -0.577 ; 0.595 | 0.962   |
| Soil moisture         | 0.533       | -0.077 ; 0.853 | 0.041   | -0.182      | -0.709 ; 0.475 | 0.533   |
| Available light       | -0.054      | -0.391 ; 0.296 | 0.725   | -0.092      | -0.423 ; 0.261 | 0.549   |
| Soil temperature      | -0.248      | -0.546 ; 0.105 | 0.100   | 0.158       | -0.197 ; 0.477 | 0.299   |
| Leaf litter cover     | 0.230       | -0.124 ; 0.532 | 0.129   | -0.490      | -0.836 ; 0.135 | 0.064   |
| <i>Abies balsamea</i> |             |                |         |             |                |         |
| Herbaceous biomass    | NA          | NA             | NA      | 0.440       | -0.197 ; 0.816 | 0.101   |
| Soil moisture         | 0.500       | -0.122 ; 0.840 | 0.058   | 0.198       | -0.463 ; 0.717 | 0.498   |
| Available light       | 0.016       | -0.330 ; 0.359 | 0.914   | -0.018      | -0.360 ; 0.329 | 0.908   |
| Soil temperature      | -0.144      | -0.465 ; 0.211 | 0.345   | -0.005      | -0.350 ; 0.340 | 0.972   |
| Leaf litter cover     | -0.189      | -0.501 ; 0.166 | 0.214   | 0.118       | -0.503 ; 0.658 | 0.676   |

514  
 515 highest of all micro-environmental variables, both with *P. glauca* ( $r=0.533$ ) and *A. balsamea*  
 516 ( $r=0.500$ ), but p-values (0.041 and 0.058) remained higher than the Bonferroni-adjusted  
 517 significance threshold. Likewise, the correlation analysis did not detect any significant  
 518 associations between the micro-environmental variables and *P. glauca* or *A. balsamea* seedling  
 519 mortality.

520 **4 Discussion**

521 4.1 Nurse tree effect on the understory micro-environment

522 Young plantations of fast-growing trees on waste rock slopes rapidly exerted control over the  
523 understory conditions, in accordance with our first hypothesis. The micro-environment-  
524 modifying capacity of the nurse tree cover was observed for all understory parameters studied.  
525 However, the relationships between tree density and environmental conditions were often  
526 quadratic, indicating concurrent underlying mechanisms. The development of an overstory  
527 structure quickly reduced light availability in the young plantation understories, thereby driving  
528 changes in other micro-environment attributes. Stronger shading effect associated with denser  
529 hybrid poplar spacings likely contributed to decreasing herbaceous biomass –largely attributable  
530 to shade-intolerant species– along the density gradient. Light is often the most limiting resource  
531 affecting understory plant establishment and growth (Strengbom *et al.* 2004; Hart & Chen 2006).  
532 Conversely, light conditions can be modified by the understory vegetation, which in turn  
533 becomes a structural layer affecting the micro-environment (Burton & Bazzaz 1991; Hart &  
534 Chen 2006). Increased overstory light transmission is therefore frequently counterbalanced by  
535 increased light interception from the understory vegetation layer (Constabel & Lieffers 1996;  
536 Messier *et al.* 1998). In the plantations, the stronger structuring role played by the herbaceous  
537 cover under the widest spacing level and the control treatment without nurse tree was noticeable  
538 not only for available light at ground level, but also for other micro-environmental parameters,  
539 such as soil temperature and leaf litter cover. In other words, increased herbaceous biomass  
540 translated into a stronger contribution to light and heat interception and to litterfall.

541 The influence of a tree cover on surface soil moisture is known to be generally positive because  
542 of a reduced soil-to-air vapour pressure gradient and decreased wind movement, resulting in less  
543 evaporation from the soil surface (Geiger 1965; Burton & Bazzaz 1991; Man & Lieffers 1999).  
544 Nonetheless, a significant decrease in moisture content was recorded during the drier second half  
545 of summer 2015 under the 1x1-m cover compared to the 2x2-m cover, while the relationship  
546 between poplar density and moisture content switched from positively linear to quadratic.  
547 Competition for water on drought-prone sites like waste rock slopes may thus negate the  
548 facilitative effect of the nurse shelter at high densities (Dordel 2009). Moreover, fast-growing  
549 nurse trees may deplete soil water resources more rapidly than slower-growing species  
550 (Govindarajan *et al.* 1996, McIntyre *et al.* 1997). Rosenberg *et al.* (1983) noted that a fast-  
551 growing canopy can reduce soil moisture availability when transpiration rates exceed  
552 evaporation rates from bare soil. Thus, the trend observed in the plantations –that already started  
553 to appear in mid-summer 2014– likely reflected an offset of the beneficial tree cover shading  
554 effect by a transpiration effect for the highest planting density.

#### 555 4.2 Nurse tree effect on forest tree seedlings

556 Our results partly support the hypothesis that planting of fast-growing nurse trees would benefit  
557 forest tree seedling performances (Lugo 1997; Parrotta *et al.* 1997) compared to bare soil, but  
558 indicate that facilitation and competition were driven by differential response patterns among  
559 species. The densest cover treatment (1x1m) promoted the highest emergence rates for *P. glauca*  
560 and *A. balsamea* seedlings. Sheltered conditions also improved the emergence of *Salicaceae*  
561 seedlings, while higher emergence rates were observed under the 2x2-m spacing treatment. The  
562 emergence patterns observed may compare with data collected in forested environments. For  
563 example, McLaren & Janke (1996) found *A. balsamea* emergence to increase as a function of

564 tree cover in *Populus tremuloides*-dominated stands. Similarly, Calogeropoulos *et al.* (2004)  
565 observed greater *A. balsamea* emergence in partial cuts than in clearcut treatments in their study  
566 on the effects of harvest intensity. Sheltered sites were also noted to produce more germinants  
567 than open sites for earlier-successional tree species (Burns & Barbara 1990). Nonetheless,  
568 *Salicaceae* seedling mortality rates increased along the hybrid poplar density gradient during the  
569 final year of sampling (2015), likely pointing to an increasing exclusion of these species in the  
570 plantations, typical colonizers of more open habitats (Burns & Barbara 1990; Peterson &  
571 Peterson 1992).

572 The light-water model proposed by Holmgren *et al.* (1997) suggests that facilitation occurs when  
573 the improvement of plant-water relationships under the canopy exceeds the costs of decreased  
574 light availability, hence hinting at the potential of nurse plantations on drought-prone slopes,  
575 especially for shade-tolerant species. Our correlation analysis using a conservative significance  
576 threshold did not allow to clearly pinpoint the determining micro-environmental variables for  
577 seedling emergence. Nonetheless, the highest emergence rates for both *A. balsamea* and  
578 *P. glauca* coincided with the highest soil moisture contents found during the peak emergence  
579 period (mid-May to mid-June 2015), while moisture levels increased with plantation density.  
580 Greater emergence for *Salicaceae* species also occurred under the spacing treatment associated  
581 with the highest soil moisture content values during the 2014 emergence period, i.e. the 2x2-m  
582 spacing treatment. If soil moisture is known to be the most limiting factor for the germination of  
583 boreal tree species (Greene *et al.* 1999), light availability emerged as a driving factor of  
584 *Salicaceae* species abundance as soon as during the third growing season of the plantations.  
585 Decrease in understory light already became limiting for the survival of these shade-intolerant

586 species, whose germinants lacking endosperm are more dependent on rapidly establishing  
587 photosynthetic leaf area to support development (Karrenberg *et al.* 2002).

588 Results for *Salicaceae* species showed that facilitation and competition mechanisms not only  
589 differ among plantation densities, but also change as plantations continue to develop and as  
590 seedlings grow. Pickett *et al.* (1987) remarked that early facilitation of a colonizer by a nurse  
591 plant often gives way to inhibition as the colonizer matures. Competition for light under denser  
592 cover started to outweigh facilitation and exerted a detrimental effect for *Salicaceae* seedlings in  
593 2015. In this context, later-successional species such as *A. balsamea*, more sensitive to soil  
594 moisture than light limitations (Lieffers & Stadt 1994; Landhäusser & Lieffers 2001), may be  
595 better equipped to take advantage of opportunities in the understory. Nonetheless, the decrease in  
596 moisture content recorded at the end of the survey under the densest hybrid poplar spacing  
597 treatment suggests that their influence on soil water resources may become increasingly  
598 competitive over the next growing seasons, and compromise their nursing potential in the longer  
599 term.

#### 600 4.3 Hydroseeded cover effect on forest tree seedlings

601 In accordance with our third hypothesis, the competitive effect exerted by the hydroseeded  
602 herbaceous cover limited seedling emergence and increased seedling mortality, although not all  
603 forest tree species were influenced in the same way. Dense herbaceous covers are known to  
604 reduce seedbed receptivity, especially for small-seeded species like poplars and willows,  
605 characterized by smaller radicles with limited ability to reach soil resources (Greene & Johnson  
606 1998; Hesketh *et al.* 2009). Although we could only document the detrimental effect of the  
607 hydroseeded cover treatment on pioneer *Salicaceae* seedling emergence, we do not conclude that

608 the hydroseeded cover would not affect the emergence of larger-seeded *P. glauca* and  
609 *A. balsamea* originating from seed rain. Our sowing method with direct positioning of seeds onto  
610 the mineral soil may have inflated emergence occurrences. Previous studies noted for instance  
611 that abundant herbaceous vegetation inhibits spruce regeneration: dense growth may intercept  
612 seeds before they reach the ground (Eis 1981), while germinants that do reach the soil are more  
613 easily shaded out, smothered by dead foliage or outcompeted for soil water (Coates *et al.* 1994).  
614 Increase in mortality rates in hydroseeded plots were, however, only registered for *A. balsamea*  
615 seedlings, which may be somewhat surprising given that fir seeds are four times larger than  
616 white spruce seeds and usually lead to more resistant seedlings able to develop their root system  
617 more rapidly (Bakuzis & Hansen 1965). Nonetheless, this result may reflect the difficulty for  
618 slower-growing seedlings to compete against aggressive herbaceous species in more open  
619 environments.

620 The understory vegetation can both act as a driver of tree succession (Hart & Chen 2006) and be  
621 determined by overstory structure (De Grandpré *et al.* 1993). The negative relationship between  
622 hybrid poplar cover and herbaceous biomass monitored in the young plantations suggests that the  
623 increasingly dense tree cover will eventually shade out the light-demanding (naturally  
624 established or hydroseeded) ground cover vegetation. Therefore, the competitive effect of the  
625 hydroseeded cover on seedlings may weaken as the plantations mature.

626 4.4 Forest-like recruitment rates?

627 It was suggested that the rapid redevelopment of a tree cover could accelerate the return of  
628 conditions beneficial to the regeneration of forest tree seedlings (Carnevale & Montagnini 2002;  
629 Boothroyd-Roberts *et al.* 2013). Under the densest tree cover treatment, recruitment success rate



630 for *A. balsamea* first-year seedlings averaged 5%. This compares to results (4-4.5%) found in  
631 studies realized in aspen (*Populus tremuloides Michaux*)-dominated stands for seedlings less  
632 than two years old (McLaren & Janke 1996; Calogeropoulos *et al.* 2004). Regardless of tree  
633 cover treatment, recruitment success rate for *P. glauca* was higher (~10%) than for *A. balsamea*,  
634 and surprisingly high compared to studies in forested environment (2-4%) (Purdy *et al.* 2002;  
635 Simard *et al.* 2003; Calogeropoulos *et al.* 2004; Wang & Kembal 2005). Although success rates  
636 of first-year seedlings may be promising, our sowing method could again limit the interpretation  
637 of our results –especially for smaller-seeded *P. glauca* seedlings, more dependent on seedbed  
638 receptivity–, since seed positioning in tiny furrows may have positively biased emergence rates.  
639 Concordantly, success rates in control plots without nurse trees remained relatively high for both  
640 *A. balsamea* (>3%) and *P. glauca* (~9%).

641 Results from the natural colonization survey showed that *A. balsamea* (2%) and *P. glauca* (10%)  
642 seedlings accounted for a small proportion of colonizing seedling abundance after three growing  
643 seasons. This translates into a rather marginal density of 0.02 and 0.10 seedlings per m<sup>2</sup>  
644 respectively for each species. While context-dependent and based on a limited period of time,  
645 these results may suggest that seed availability for species most likely to benefit from the  
646 understory conditions could be unreliable on uphill rock slopes. White spruce seeds are known to  
647 disperse up to 300 m (Sims *et al.* 1990), but as low as 7, 4 and 0.1% of them generally reach 50,  
648 100 and 200 m (Nienstaedt & Zasada 1990). The distance is even smaller for the heavier fir  
649 seeds, many of which fall with their scales near the parent tree (Sims *et al.* 1990). Consequently,  
650 since successful seedling recruitment requires sufficient availability of seeds, management  
651 practices may have to include seeding work depending on the vicinity of seed bearers and site  
652 topography.

653 **5 Conclusion**

654 Natural processes such as succession provide a framework for the implementation of sustainable  
655 restoration practices. Plantations may act as accelerators of natural succession through rapid  
656 canopy re-establishment. Compared to the traditional anti-erosion treatment, results in the young  
657 plantations of hybrid poplars suggest that fast-growing plantations rapidly provide opportunities  
658 for the early establishment of later-successional boreal tree seedlings in waste rock slopes. This  
659 novel assemblage (Hobbs *et al.* 2006) relying on a semi-exotic tree species accelerated canopy  
660 redevelopment and already exerted a structural influence on the forest tree recruitment conditions  
661 in the first years after planting. Nonetheless, soil moisture monitoring results may imply that  
662 influence on soil water resources will become increasingly competitive as fast-growing hybrid  
663 poplars continue to develop.

664 Waste rock pile topography, characterized by erodible slopes, increases the importance of rapid  
665 tree establishment. Hybrid poplars have the advantage of growing more quickly than other nurse  
666 tree species available for reclamation (Guy & Bateman 1989). However, high soil water  
667 consumption may compromise longer-term nursing potential of hybrid poplars in waste rock  
668 slopes where competition for limited resources, such as water, may be severe.

669 **Acknowledgements**

670 This study was funded by the Natural Sciences and Engineering Research Council of Canada  
671 (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT) and the  
672 Canadian Malartic Partnership. The authors are indebted to the research technician and  
673 undergraduate students who have contributed to the collection of field data, namely Avril Jobin,  
674 Yoan Goudreau, Charles Frenette-Vallières, Sara Gervais, Paulo-Bernardo Neves-E-Castro,

675 Antoine Beaulieu, Maguelonne Rajot and Liam Boivin. We are also grateful to Brian Harvey,  
676 Guy LaRocque, Yves Bergeron and Jean-François Boucher for providing valuable comments.

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967

## Appendix A

968

969 List of herbaceous species inventoried during the 2<sup>nd</sup> and 3<sup>rd</sup> growing seasons in the hybrid

970

poplar plantations

971

| <b>Common name</b>            | <b>Scientific name</b>  |
|-------------------------------|---|
| Alsike clover                 | <i>Trifolium hybridum</i> Linnaeus  |
| Bull thistle                  | <i>Cirsium vulgare</i> (Savi) Tenore  |
| Canada goldenrod              | <i>Solidago canadensis</i> Linnaeus   |
| Canada thistle                | <i>Cirsium arvense</i> (Linnaeus) Scopoli   |
| Coltsfoot                     | <i>Tussilago farfara</i> Linnaeus   |
| Common dandelion              | <i>Taraxacum officinale</i> F.H. Wiggers  |
| Common kochia                 | <i>Bassia scoparia</i> (Linnaeus) Voss  |
| Common lamb's-quarters        | <i>Chenopodium album</i> Linnaeus   |
| Common mullein                | <i>Verbascum thapsus</i> Linnaeus   |
| Common plantain               | <i>Plantago major</i> Linnaeus  |
| Common timothy                | <i>Phleum pratense</i> Linnaeus   |
| Common yarrow                 | <i>Achillea millefolium</i> Linnaeus  |
| Curled dock                   | <i>Rumex crispus</i> Linnaeus   |
| Field sow-thistle             | <i>Sonchus arvensis</i> Linnaeus subsp. <i>arvensis</i>                             |
| Fireweed                      | <i>Chamaenerion angustifolium</i> (Linnaeus) Scopoli<br>subsp. <i>angustifolium</i> |
| Garden bird's-foot trefoil    | <i>Lotus corniculatus</i> Linnaeus  |
| Grass-leaved goldenrod        | <i>Euthamia graminifolia</i> (Linnaeus) Nuttall                                     |
| Heart-leaved aster            | <i>Symphotrichum cordifolium</i> (Linnaeus) G.L. Nesom                              |
| Horsetail sp.                 | <i>Equisetum</i> sp.  |
| Large-leaved aster            | <i>Eurybia macrophylla</i> (Linnaeus) Cassini                                       |
| Narrow-leaved blue-eyed-grass | <i>Sisyrinchium angustifolium</i> Miller  |
| Orange hawkweed               | <i>Pilosella aurantiaca</i> (Linnaeus) F.W. Schultz & Schultz<br>Bipontinus         |
| Oxeye daisy                   | <i>Leucanthemum vulgare</i> Lamarck   |
| Red clover                    | <i>Trifolium pratense</i> Linnaeus  |
| Red fescue                    | <i>Festuca rubra</i> Linnaeus subsp. <i>rubra</i>                                   |
| Red raspberry                 | <i>Rubus idaeus</i> Linnaeus  |

|                         |   |
|-------------------------|---|
| Reed canarygrass        | <i>Phalaris arundinacea</i> Linnaeus            |
| Rough cinquefoil        | <i>Potentilla norvegica</i> Linnaeus            |
| Rough-stemmed goldenrod | <i>Solidago rugosa</i> Miller                   |
| Sedge sp.               | <i>Carex</i> sp.                                |
| Smartweed sp.           | <i>Persicaria</i> sp.                           |
| Tufted vetch            | <i>Vicia cracca</i> Linnaeus                    |
| White clover            | <i>Trifolium repens</i> Linnaeus                |
| White sweet-clover      | <i>Melilotus albus</i> Medikus                  |
| Wild strawberry         | <i>Fragaria virginiana</i> Miller               |
| Yellow sweet-clover     | <i>Melilotus officinalis</i> (Linnaeus) Lamarck |

## Appendix B

974

975

976 List of naturally established woody (tree and arborescent shrub) species inventoried during the  
 977 2<sup>nd</sup> and 3<sup>rd</sup> growing seasons in the hybrid poplar plantations

978

| <b>Common name</b>    | <b>Scientific name</b>                  |
|-----------------------|---|
| American mountain-ash | <i>Sorbus americana</i> Marshall        |
| Balsam fir            | <i>Abies balsamea</i> (Linnaeus) Miller |
| Balsam poplar         | <i>Populus balsamifera</i> Linnaeus     |
| Bebb's willow         | <i>Salix bebbiana</i> Sargent           |
| Black spruce          | <i>Picea mariana</i> (Miller) BSP       |
| Paper birch           | <i>Betula papyrifera</i> Marshall       |
| Pin cherry            | <i>Prunus pennsylvanica</i> Linnaeus f. |
| Prairie willow        | <i>Salix humilis</i> Marshall           |
| Pussy willow          | <i>Salix discolor</i> Muhlenberg        |
| Red-osier dogwood     | <i>Cornus sericea</i> Linnaeus          |
| Trembling aspen       | <i>Populus tremuloides</i> Michaux      |

979