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3 TITLE: Root production of hybrid poplars and nitrogen mineralization improve following mounding of
4 boreal Podzols

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32 ABSTRACT

33

34 Successful establishment of fast-growing trees could depend on early root development and the access to
35 belowground resources. Boreal podzolic soils present a distinctive vertical zonation where nutrient
36 availability and the presence of plant roots decline sharply with depth. Mechanical soil preparation that
37 modifies the vertical arrangement of soil layers creates microsites with improved physical conditions, but
38 potentially lower nutrient availability. We compared the vertical distribution of proximal roots of young
39 hybrid poplars in soil layers of mechanically prepared (by mounding) and unprepared microsites. We also
40 evaluated the relationship between root distribution and the availability and mineralization of soil
41 nitrogen. Hybrid poplar roots were less abundant in the surface organic layer of unprepared soils, whereas
42 they proliferated in the buried organic layer of mounds. Total mineralized N was highest in the upper
43 mineral layer of mounds, while it was similar between the buried organic layer of mounds and the
44 unprepared organic layer. Altogether, mounding created conditions conducive to greater soil N
45 mineralization, and greater production and vertical distribution of proximal roots. This possibly provided
46 access to a larger soil volume and greater soil nutrient pools, which may explain the success of mounding
47 in terms of aboveground growth of hybrid poplars.

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49 *Keywords:* hybrid poplar, mechanical soil preparation, nitrogen, Podzol, root distribution.

50 1. INTRODUCTION

51

52 Early root development of the target species is a fundamental factor in the successful establishment
53 of plantations, as it can favour juvenile tree growth and survival (Grossnickle 2005). Indeed, planted
54 seedlings that root well in their first year may experience better growth the following year (Luoranen et
55 al. 2006). However, early root development may be impeded by microsite conditions such as a water-
56 logged (Knapp et al. 2008), dry (Morris and Lowery 1988; Teskey and Hinckley 1981) or compacted soil
57 (Wolken et al. 2010), or competition for belowground resources (Balandier et al. 2007; Löff and Welander
58 2004). One notable way to improve the early root development could be through adequate soil
59 management prior to planting, such as mechanical soil preparation (MSP).

60 MSP creates soil disturbance that can improve microsite conditions by modifying soil texture and
61 soil water regime, increasing soil temperature (Löff et al. 2012), and reducing the levels of both above-
62 and belowground competition (e.g., DesRochers et al. 2004; Nilsson and Örlander 1999). MSP usually
63 has a beneficial impact on tree growth (Örlander et al. 1990). Long-term benefits of MSP on the growth
64 of Scots pines (*Pinus sylvestris*) were observed by Örlander et al. (1996), even though the mechanically
65 prepared soils had much lower C and N content. Similar observations were made regarding the juvenile
66 growth of nutrient-demanding hybrid poplars (Bilodeau-Gauthier et al. 2011).

67 Mounding is a type of MSP whose purpose is “to create elevated planting spots free from water
68 logging and with little vegetative competition” (Löff et al. 2012). It can improve soil drainage and aeration
69 (Londo and Mroz 2001), increase soil temperature (Knapp et al. 2008), and decrease soil bulk density. In
70 water-logged conditions, mounding can improve tree survival and growth (Kabrnick et al. 2005), although
71 in drought-prone conditions it may worsen the effects of soil drought (Hallsby and Örlander 2004). A
72 certain number of studies have shown that mounding benefits the root system of planted trees (Bolte and
73 Löff 2010, with *Quercus robur*; Knapp et al. 2006, with *Pinus palustris*). The decrease in soil bulk
74 density, for instance, generally favors root development and growth, since a looser soil allows easier root
75 penetration (Löff et al. 2012).

76 MSP can also modify the spatial distribution of soil nutrients, for instance by amalgamating
77 nutrients in patches or redistributing the rich top layers into a greater soil volume. Plant root growth may
78 show plastic response to nutrient-enriched soil patches, which may optimize root foraging and efficient
79 acquisition of resources (Hodge 2004). However, there have been very few studies on the response of tree
80 roots to the spatial distribution of soil resources (Hawkins and Metcalfe 2008, with *Pseudotsuga*
81 *menziesii*; Heineman et al. 1999, with *Picea glauca*; Makita et al. 2011, with *Quercus serrate* and *Ilex*
82 *pedunculosa*). Heineman et al. (1999), notably, studied spruces growing on mounds and they analyzed
83 vertically the soil and tree root system. However, they delimited vertical sampling layers based on fixed
84 depth intervals (as did Makita et al. 2011) rather than by soil horizon types as advocated by Strong and La
85 Roi (1988). In this respect, their results cannot be used to identify root foraging strategies with regard to
86 the optimal preference of soil material in which to proliferate.

87 Boreal forest soils (most notably Podzols, Luvisols, and Brunisols/Cambisols; IUSS Working
88 Group WRB 2006; Soil Classification Working Group 1998) present two particular features that create a
89 distinctive vertical zonation and in turn influence plant establishment and development. The first feature
90 is that nutrient availability declines sharply with soil depth (Gastaldello et al. 2007; Paré and Bernier
91 1989), whereas this transition is much less abrupt in other soil types that have an active burrowing
92 macrofauna (Wood et al. 1984). The second distinctive feature of boreal soils is that plant roots mainly
93 colonize the first 15 cm of soil (Strong and La Roi 1983, 1985), which includes the organic layers and the
94 top of the (mineral) B horizon, with roots avoiding or bypassing quickly the Ae horizon when present. In
95 a review on the rooting pattern of boreal trees, Van Rees (1997) indicated that approximately 50% of the
96 fine roots were within the organic layers, while Finér et al. (1997) found more than 80% of all roots in
97 the 5-8 cm thick organic layer and the first 10 cm of the B layer (Strong and La Roi 1985). Brassard et al.
98 (2013) showed for several boreal tree species that the number of fine roots was highest in the surface
99 organic layer and dropped steadily with soil depth; for non-tree fine roots, the pattern was even more
100 skewed towards the organic layer.

101 To better understand the relationships between tree root development and the spatial arrangement of
102 soil layers (and available soil nutrients), we took advantage of a well replicated experimental design with
103 hybrid poplars planted on podzolic soils of the southern boreal forest of Québec, Canada (Bilodeau-
104 Gauthier et al. 2011), where soils either 1) were left unprepared or 2) received MSP by mounding. These
105 two treatments allowed comparing a soil that follows the typical sharp vertical boundaries found in
106 podzolic soils (the unprepared control) with a soil where this spatial pattern was disrupted (the mounding
107 treatment). We chose hybrid poplars because of the generally high nutritional needs of *Populus* species
108 (Paré et al. 2001) and clones (Mitchell et al. 1999), and because they often respond negatively to the
109 presence of competitors (Kabba et al. 2007). Indeed, as shade-intolerant trees, they are known for their
110 sensitivity to aboveground competition for light (Messier et al. 1998). Yet, as pioneer trees, hybrid
111 poplars also seem to be intolerant of belowground competition for nutrients and space (Coll et al. 2007;
112 Messier et al. 2009). Such a demanding tree may fare poorly when planted in soils with a distinctive
113 vertical zonation such as Podzols, unless soil management prior to planting accounts for the soil's
114 particular features and aims at creating improved conditions suited to the tree's needs.

115 We undertook root excavations within the aforementioned experimental plantations of hybrid
116 poplars (Bilodeau-Gauthier et al. 2011). The main objective was to compare how the root system of
117 hybrid poplars developed in the different soil layers of the two soil treatments. A secondary objective was
118 to characterize soil nitrogen availability in the different soil layers of the two soil treatments. We
119 hypothesized that the vertical distribution of hybrid poplar roots would reflect the improved soil
120 conditions created by mounding, and that roots would respond to the nitrogen availability in the different
121 soil layers. A previous experiment under controlled conditions had suggested that root development of
122 hybrid poplars was particularly sensitive to soil conditions (Messier et al. 2009), and soil N is the most
123 limiting nutrient in boreal systems (Fisher and Binkley 2000) where N additions were often shown to
124 improve tree growth (Newton and Amponsah 2006). The results should help increase our understanding
125 of the response of hybrid poplar trees to the spatial distribution of soil resources, as well as improve the
126 efficiency of silvicultural treatments such as soil management.

127

128 1. METHODS

129 2.1 Sites and experimental design

130 This study took place among experimental plantations that are described elsewhere in greater
131 details (Bilodeau-Gauthier et al. 2011). Eight formerly forested sites were chosen in the Saguenay–Lac-
132 St-Jean region (southern boreal forest, between 71° 05' and 72° 52' W, and between 48° 08' and 48° 43'
133 N) of the province of Quebec, Canada. Tree species in original stands consisted of balsam fir (*Abies*
134 *balsamea*), trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), white spruce (*Picea*
135 *glauca*), and paper birch (*Betula papyrifera*). Soils are representative of Precambrian Shield settings
136 characterized by coarse acidic soils (soil texture: 70% sand, 25% silt, 5% clay; mean pH of the B horizon
137 = 4.1, SD = 0.2), and are classified as Orthic Ferro-Humic Podzols (Soil Classification Working Group
138 1998). All sites were found on moderate slopes with no apparent waterlogged conditions, thus classified
139 as mesic with a good drainage (volumetric water content: 14% in mounds, 26% in unprepared soil). A
140 description (thickness and depth) of the different soil layers is provided in Table 1, where the unprepared
141 treatment is representative of natural conditions. Mean annual temperature for this region is 2.2°C and
142 mean annual precipitation is 1000 mm (of which 710 mm is rainfall), while mean summer (June-
143 September) temperature is 15.5°C and mean monthly summer precipitation (rainfall) is 107.5 mm
144 (Environment Canada 2009).

145 Following whole-tree harvesting in the summer of 2002, soils were mechanically prepared in the
146 fall of 2003. Two soil treatments were compared: 1) MSP by mounding and 2) a control where the soil
147 was left unprepared. Each treatment covered a 1 ha plot and was repeated at each of the eight sites, hence
148 $n = 8$. The 1 ha plots were further divided into four equal subplots (0.25 ha) where different vegetation
149 control (weeding by brushing) schedules were tested. The data presented here was obtained from the
150 subplot with the most frequent weeding schedule (vegetation controlled once a year during the first 3
151 years). Bare-root, ~ 1 m tall hybrid poplar tree cuttings of the 915319 clone *Populus maximowiczii* ×
152 *Populus balsamifera* (Périnet et al. 2001) were obtained from a nursery operated by the Ministère des

153 Ressources naturelles et de la Faune du Québec at Grande-Piles, QC, Canada. The cuttings were produced
154 in the spring from stool beds in the nursery plantations, and cultivated over the summer in irrigated,
155 fertilized, and weeded soil. This allowed them to develop a substantial root system, which was
156 subsequently groomed in the fall when the cuttings were dormant, a state in which they were kept until
157 shipped to the field the next spring. Bare-root cuttings were hand-planted with a shovel in April 2004 at a
158 depth of 20-30 cm and in straight rows at a spacing of 3×3 m (density = 1100 trees ha⁻¹). The year of
159 planting is hereafter considered as year 1. Tree cuttings were planted on the side of the mound, down to a
160 depth of 20-30 cm so that the rooted end of the tree cutting reached at least the buried organic layer. Trees
161 in the unprepared control were planted at the same depth as those on mounds (when possible, since
162 unprepared soil was not as easily penetrated as the soil of mounds, see Bilodeau-Gauthier et al. 2011).
163 Figure 1 provides a schematic description of mounding and Table 1 illustrates the vertical soil profile of
164 the two treatments.

165 Mounding is a common MSP treatment in Scandinavia and Canada (DesRochers et al. 2004;
166 Örlander et al. 1990; Sutton 1993). For this study, it was done using a backhoe equipped with a 45 cm
167 wide bucket that dug into the soil through the organic layer (also called LFH in the Canadian Soil
168 Classification, or O horizon in the World Reference Base for Soil Classification) and down to a depth of
169 60 cm to retrieve the mineral soil (i.e., the B horizon, which, in the case of Podzols, is visually,
170 physically, and chemically very different from the soil layers located above it: the organic layer composed
171 of organic matter in different states of decomposition, and the Ae horizon enriched in minerals
172 recalcitrant to biochemical weathering such as quartz and muscovite). The mineral soil and the organic
173 layer were then upturned over undisturbed soil nearby to form a mound of about 30 cm in height and 50
174 cm in radius. This mound therefore covered the vegetation that had regenerated after the harvest. The
175 resulting combination of undisturbed and upturned organic material – hereafter referred to as the buried
176 organic layer – found within mounds (Figure 1) was compressed by the mineral soil over it so that it was
177 thinner than the undisturbed organic layer (Table 1). Bilodeau-Gauthier et al. (2011) reported that the
178 upper part of mounds (composed of mineral soil) presented, compared with the upper part of unprepared

179 soils (composed of organic matter), a lower soil bulk density (measured as higher penetrability), lower
180 total soil N concentrations (mounds: mean = 0.8 mg g⁻¹, SE = 0.2; unprepared: mean = 3.4 mg g⁻¹, SE =
181 0.6), and a higher soil temperature (mounds: mean = 14.8°C, SE = 0.9; unprepared: mean = 13.8°C, SE =
182 0.5).

183

184 2.2 Root excavations

185 In July of year 4, 45 three-year-old hybrid poplar trees were randomly chosen in the mounding
186 treatment (24 trees, three per site across the eight sites) and the unprepared control (21 trees, three per site
187 at seven sites, as one site had no usable control). The root system was partly excavated in a non-
188 destructive manner. Digging was done by hand in a 30 cm radius around the base of the trees and down to
189 the cutting end (see maximum rooting depth in Table 1). Such partial excavations allowed us to maintain
190 the tree stability and spatial arrangements of roots. The excavation process exposed all roots that started
191 directly from the poplar cutting itself. These roots are called proximal roots in the literature (Domenicano
192 et al. 2011); one could think of them as main, primary or first-order roots (e.g., Fitter 1986; Rose 1983)
193 that can be of any size and that subsequently branch into several smaller roots.

194 Diameter at the base (at the junction with the cutting, also called the root collar) of every
195 proximal root was measured with an electronic calliper. The use of the proximal root diameter was based
196 on a positive demonstration by Domenicano et al. (2011) that proximal root diameter of hybrid poplars
197 was strongly and linearly related to other root characteristics. These authors undertook complete
198 excavations of root systems and made numerous measurements of root architecture and physiology. They
199 successfully built linear equations ($R^2 = 0.6$ to 0.8 , $P < 0.0001$) linking proximal root diameter to root
200 length, root biomass, and number of root links, thus suggesting that non-destructive, partial excavations
201 were an adequate proxy for total root biomass and architecture. Moreover, they excavated root systems
202 from 2-year-old hybrid poplars of clone types (913313 and 913311, both *P. maximowiczii* × *balsamifera*)
203 that are closely related to the clone used in the present study.

204 The depth (from the soil surface) at which a proximal root was located was noted with a
205 measuring tape. The fact that the hybrid poplar cuttings were planted deep into the soil, as well as their
206 capacity to produce roots from the whole length of the cutting that is belowground and not just the
207 already-rooted bottom end, meant that proximal roots extended relatively horizontally from the cutting –
208 at least in the 30-cm radius area that was sampled –, which simplified the identification of the soil layer
209 which was explored. Thickness and location of the organic and mineral soil layers were also noted for
210 every tree (which was made possible by the clear visual horizonation of Podzols) to later build an average
211 vertical soil profile for each treatment (Table 1). After measurement, the soil was gently filled back in to
212 cover the roots. Total stem height and annual shoot lengths of the 45 excavated trees were measured with
213 a measuring pole and tape. Stem diameter was measured with an electronic calliper, at mid-breast height
214 (65 cm from the ground) because some trees were too short to allow measuring at the standard height of
215 1.3 m.

216 For every tree, the sampled proximal roots were subsequently classified by diameter (0-2, 2-10,
217 11-20, and 21-30 mm) and by the soil horizon in which they were found. Roots will thereafter be mainly
218 referred to according to their diameter class, rather than to other common terms like “fine roots” or
219 “coarse roots”. Such terms imply that the function of said roots is known, which is not necessarily the
220 case since the link between root diameter and function may vary between species. Calculations were
221 made for average diameter of proximal roots per tree, number of proximal roots per tree and per diameter
222 class, and absolute number of proximal roots per soil layer (organic and mineral soil). The relative
223 abundance of roots per cm of soil depth was obtained by dividing the absolute number of roots per tree
224 per soil layer by the average thickness of the soil layer. The ratio of tree height over root surface (this
225 denominator being the product of average root diameter and total number of roots of a tree), thereafter
226 referred to as the height:root ratio, was also computed.

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2.3 Soil analyses

In situ soil incubations served in assessing potential net N mineralization. To this end, nitrate (NO_3) and ammonium (NH_4) concentrations were compared between the start and the end of 6-week (from the beginning of July to mid-August) *in situ* incubations undertaken at two (for the unprepared control) or three (for the mounding treatment) different soil depths, i.e., 0-15 cm, ~20 cm, and for mounds also ~30 cm. Soil samples were taken at a distance of 30 cm from the base of three trees per soil treatment at each site (overall: 45 trees, 114 incubations, $n = 8$ for mounding and 7 for the control). These trees were not the same that were excavated for root measurements. The 0-15 cm incubations were conducted in year 4 with 20 cm long and 5.8 cm wide closed-top PVC tubes as described in Raison et al. (1987) and Brais et al. (2002). The initial soil samples were obtained by inserting the tubes into the surface soil and taking back this volume of soil immediately to the laboratory. At the same time and at the same distance from the tree, but not in the exact same spot, other tubes of equal dimensions were inserted into the soil and left in place for the 6-week duration. The ~20 and ~30 cm incubations were done in year 5 at the same distance from the same trees that were used for tubes. Initial soil samples were obtained by extracting with a soil auger about 1 kg of soil material from each depth. Final soil samples were obtained by extracting a similar quantity of soil at the same depths, placing it in polyethylene bags and burying it back in the holes under the soil material that had been taken out (note that the ~20 and the ~30 cm incubations were not placed directly one above the other). Bags were tightly closed to prevent leaching induced by percolating waters (Brais et al. 2002). Soil incubations provide an estimate of the soil potential for net N mineralization. Being mostly closed to outside influences that could alter nutrient concentrations (e.g., water flow, root uptake), yet subjected to *in situ* temperature conditions, incubations constitute a snapshot of the activity of the microorganisms that degrade soil organic matter, which releases N into inorganic forms more readily accessible to plants (mostly NH_4 , in the type of soils studied here) during the most active period of the year. For all tube and bag soil samples, NH_4 and NO_3 were extracted from

252 fresh soil with 2M KCl (Maynard et al. 2007) and analyzed by flow injection analysis and ion
253 chromatography (FIA; Lachat Instruments, Milwaukee, WI).

254 Potential nitrogen mineralization was calculated as the difference in the inorganic N
255 measurements between the final and initial incubations. The amount of mineralized N was further
256 estimated for the total soil volume. This volume differed between the two treatments. It was schematically
257 represented as a cylinder with a 50-cm radius surface area (the size of a mound) and a length
258 corresponding to the location of the deepest proximal root (see Table 1). From the vertical soil profiles, it
259 was possible to calculate a volume for each soil layer. The density of the mineral layers was obtained
260 from the calculations of Saxton et al. (1986), using a soil texture of 70% sand, 25% silt, and 5% clay (data
261 taken from Bilodeau-Gauthier et al. 2011); this was done because the mineral soil was often too rocky in
262 those sites and our standard method of using a small sample tube of known volume was not feasible. The
263 density of the organic layer was derived from surface soil samples taken in plots of the unprepared control
264 with incubation tubes of known dimensions (in these plots, the tube samples were mostly comprised of
265 organic soil material). By combining the total volume of soil per layer with the density of each layer, a
266 total mass of soil per layer was calculated. Afterwards, N values per soil mass unit were related to total
267 mass of soil per layer to provide a total quantity of N for the whole soil profile.

268 In addition, soil concentrations of NO_3 and NH_4 were assessed in year 5 with ion-exchange resins
269 (Plant Root Simulators, or PRSTM-probes, Western Ag Innovations, Saskatoon, SK, Canada). The ion-
270 exchange resin of these probes is a thin membrane (1.5 cm \times 5.5 cm in surface area) contained in a small
271 plastic probe (3 cm \times 15 cm) that can be inserted into the soil with little disturbance. Resins were
272 vertically installed at three soil depths, i.e., 0-5 cm, ~20 cm, and ~30 cm, during the same 6 weeks and at
273 the base of the same trees as the incubations. During the burial period, the resins continuously adsorb soil
274 nutrient ions that are flowing to the probe through the soil solution. The amounts of nutrients trapped by
275 the resin represent the nutrient supply rate from freely flowing water to a specific soil location within the
276 soil profile during a specific burial time period. It is a dynamic measure of ion fluxes in the soil over time,
277 rather than a static measurement at a particular point in time like more conventional extraction methods

278 (Qian and Schoenau 2002). Several previous studies in agronomy and forestry have successfully used
279 PRSTM-probes to assess soil nutrient availability (e.g., Adderley et al. 2006; Moukoumi et al. 2012).

280 Soil temperature was assessed with data-logging temperature sensors (Maxim Integrated
281 Products, Sunnyvale, CA, USA) placed at the base of 15 trees from two out of the eight sites (9 trees on
282 mounds, 6 trees in unprepared soils). Soil temperature was measured at depths of 2, 10 and 20 cm every 2
283 hours from the beginning of June to the end of October during year 4. A previous study on the same
284 research sites (Bilodeau-Gauthier et al. 2011) had reported soil temperature values (see section 2.1) taken
285 with a hand-held thermometer probe covering the same soil depth and over the same months, but only
286 during the day.

287

288 2.4 Statistical analyses

289 Roots and soil data were compared between mounding and the unprepared control, as well as
290 between the different soil layers; roots were further compared between root diameter classes. In order to
291 illustrate the differences between all categories and combinations of variables, and because the soil
292 treatment \times soil layer interaction was incomplete (since mounding had three different soil layers while
293 unprepared had two), we combined the soil treatments with the soil layers to produce a meta-variable with
294 five levels (mound/upper-mineral, mound/organic, mound/lower-mineral, unprepared/organic,
295 unprepared/mineral); for the roots data, this meta-variable further included the diameter classes (hence, a
296 total of 20 levels). The meta-variable served as the fixed effect in mixed analyses of variance. The
297 random variables consisted in plot (2 plots per site, each plot being in effect a soil treatment and
298 containing 3 trees) nested in site (8 levels), which allowed to model the hierarchical design and thus use
299 data from all sampled trees. Probability levels were resolved by Restricted Maximum Likelihood
300 (REML; see Searle et al. 1992; Wolfinger et al. 1994). Data were also submitted to post hoc Tukey-
301 Kramer HSD tests. Finally, non-parametric Spearman's rank correlations were conducted between root,
302 stem, and soil characteristics for the 45 excavated trees. All statistical analyses used a confidence level of
303 $\alpha = 0.05$ and were conducted using R 3.0.0 (R Development Core Team 2013).

304

305 3. RESULTS

306 3.1 Roots across the whole soil profile

307 When looking at all proximal roots across the whole soil profile of a tree, results showed that
308 trees growing on mounds had a greater total number of proximal roots per tree compared with unprepared
309 soils (respectively 35, SE = 2, and 25, SE = 2, at $P = 0.006$), but that the average root diameter was
310 similar between the two treatments (respectively 5.1 mm, SE = 0.4, and 4.6 mm, SE = 0.4, at $P = 0.4$).
311 Differences between soil treatments were also found among the different root diameter classes. Across the
312 whole soil profile, the number of proximal 0-2 mm diameter roots did not differ between mounds and
313 unprepared soils, whereas the number of proximal roots greater than 2 mm diameter was significantly
314 greater in mounds (Table 2).

315

316 3.2 Roots across different soil layers

317 The most striking distinction between the two soil treatments was provided by the relative
318 abundance of proximal roots (i.e., the number of proximal roots per cm of soil depth, used as a relative
319 measurement of root density per soil layer) in the various soil layers (Figure 2 and Table 3). The 0-2 mm
320 root diameter class in the buried organic layer of mounds had the highest relative abundance of all root
321 diameter classes across all soil layers, except for the 0-2 and 2-10 mm classes of the unprepared mineral
322 layer (Figure 2). For all treatments and layers, small roots (0-2 and 2-10 mm in diameter) were more
323 numerous than large roots (11-20 and 31-20 mm), both in relative abundance (Figure 2) and in absolute
324 numbers (Table 2).

325 Within the upper and lower mineral layers of mounds, the 0-2 and 2-10 mm diameter classes had
326 similar relative abundances; between these two layers, the 2-10 mm classes were similar, but the 0-2 mm
327 class had a higher relative abundance in the lower mineral layer (Figure 2). It must be noted, however,
328 that the upper mineral was twice as thick as the lower mineral, which means that the absolute number of
329 roots was actually higher in the upper mineral layer (data not shown). In unprepared soils, the mineral

330 layer presented the highest relative abundance of proximal roots from all diameter classes but the largest
331 (21-30 mm). Within each unprepared layer, the 0-2 and 2-10 mm diameter classes showed similar relative
332 abundances (Figure 2).

333 The comparison of soil layers of similar material between the two treatments shows that proximal
334 roots in the 0-2 mm diameter class had a higher relative abundance in the buried organic layer of mounds
335 compared with the surface organic layer of unprepared soils. On the other hand, the underlying mineral
336 layer of unprepared soils presented a higher relative abundance of proximal roots in the 0-2 and 2-10 mm
337 diameter classes compared with the upper mineral layer of mounds, but similar relative abundances
338 compared with the lower mineral layer (Figure 2).

339

340 3.3 Soil nitrogen and temperature

341 The ion-exchange resins installed at three different soil depths provided comparison between soil
342 treatments regarding inorganic soil N availability, i.e., $[\text{NH}_4+\text{NO}_3]\text{-N}$ (Figure 3a). At depths of 0-5 cm
343 and ~20 cm, significantly higher values were found in the unprepared soils, more than two-fold the values
344 observed in the mounds. Within a given treatment, N concentrations did not differ between depths, with
345 the exception of mounding where significantly higher concentrations were observed at the ~30 cm depth.
346 This depth was not sampled in the unprepared soils.

347 Potential net N mineralization was derived from the *in situ* incubations (Figure 3b). At 0-15 cm,
348 the two soil treatments did not differ in net mineralized N over the 6-week period. At ~20 cm, net
349 mineralized N was significantly higher in mounds compared with unprepared soils. In the latter, net
350 mineralized N was significantly higher at 0-15 cm compared with ~20 cm. Conversely, in mounds, there
351 was no significant difference in net mineralized N between 0-15 cm and ~20 cm, but it decreased
352 significantly at ~30 cm. The calculation of total levels of net mineralized N in the soil rooting volume
353 (Figure 3c) revealed that the upper mineral layer of mounds contained significantly more mineralized N
354 than all other soil layers, thanks to its thickness and volume (Table 1). Within unprepared soils, greater

355 amounts of total net mineralized N were found in the surface organic layer compared with the underlying
356 mineral layer.

357 Soil temperature measured with data loggers was overall not significantly different between
358 mounds and unprepared soils. However, when focusing on the three summer months (June to August) and
359 discriminating for day and night temperatures, it was revealed that soil temperature at night was
360 significantly higher in mounds (Table 4).

361

362 3.4 Above- vs belowground growth

363 The average total tree height in mounds was significantly greater than in unprepared soils (Table
364 5). Diameter at mid-breast height (mid-DBH) showed a similar difference. Estimated height:root ratio
365 was significantly lower for trees on mounds compared with those in unprepared soils. Correlations
366 between root, stem, and soil characteristics were tested for the 45 excavated trees (Table 6). Total number
367 of proximal roots per tree was significantly correlated to the stem characteristics of tree height and mid-
368 DBH. Tree height was also a strong determinant of the number of roots in all diameter classes. Mid-DBH
369 was positively correlated to the number of roots per diameter classes, although the coefficients were
370 greater for larger diameter roots (11-20 and 21-30 mm). Only these larger roots were significantly, and
371 positively, correlated to soil temperature. Soil N characteristics did not correlate significantly to root
372 variables. The height:root ratio was not correlated to any variable (data not shown).

373

374 4. DISCUSSION

375 4.1 Root growth in different soil layers

376 This study provided information on the distribution of proximal roots in various soil layers within
377 a hybrid poplar's immediate soil environment (30 cm radius around the base of the tree). This may hint at
378 the preferential use of different soil material types in the early stages of the root system development, but
379 it may not represent soil exploration beyond that area or in later years. One highlight of the results was the
380 greater number of proximal roots of the 0-2 mm diameter class produced per cm of soil depth in the

381 buried organic layer of mounds compared with the surface organic layer of unprepared soils (Figure 2),
382 despite the fact that the buried organic layer showed lower resin-adsorbed N (Fig. 3a). The ratio of root
383 production relative to resin-adsorbed N was thus much greater for hybrid poplars planted in mounds. In
384 addition, given that the buried organic layer of mounds represented a lower proportion of the whole
385 vertical soil profile than did the surface organic layer of unprepared soils, this preference suggests an
386 advantage (e.g., improved nutrition) provided by mounding and by the burial of the organic layer (see
387 next section on soil N).

388 This study also revealed enhanced colonization of the whole soil environment by hybrid poplar
389 roots in mounds. Compared with trees planted in unprepared soils, trees on mounds produced a greater
390 number of proximal roots, particularly larger roots. This is to be expected of trees with larger
391 aboveground biomass, since large roots serve as anchorage (Coutts 1987). Yet, a proximal root branches
392 into several additional, smaller roots, as reported by Domenicano et al. (2011) who showed that proximal
393 root diameter was positively related to total root biomass and length. Hence, the larger proximal roots
394 observed in mounds are also indicative of a generally more extensive root system.

395 Mounds likely provided advantageous conditions for root development, because of a higher soil
396 temperature or lower soil bulk density (reported by Bilodeau-Gauthier et al. 2011) or other typical
397 benefits of mounding mentioned in the literature (Löf et al. 2012). The present study showed that
398 nighttime soil temperatures were particularly higher in mounds compared with unprepared soils, while
399 daytime temperatures were comparable. The mounding process also possibly modified the
400 physicochemical conditions of the buried organic layer due to the compaction of the organic matter
401 (usually of low density and large pore size), therefore improving soil water holding capacity and aeration.
402 These modifications, in turn, might have stimulated microbial activity and favoured mineralization of
403 organic matter (see next section on soil N). Another benefit of the mound might have been to favour
404 greater adventitious root formation – which is known to frequently occur in *Populus* species (Stettler et al.
405 1996) – along the whole length of the cutting and not only at its bottom end (where the roots formed at
406 the nursery are found). Indeed, because of the looser soil of mounds, poplar cuttings may have been

407 planted slightly deeper than in unprepared soils; consequently, a greater portion of the stem would have
408 been in contact with the soil and might have produced a larger number of new adventitious roots.

409 Proximal roots from the 0-2 mm diameter class were found in equivalent numbers in mounds and
410 unprepared soils. Yet in mounds they were mainly located in the buried organic layer. This layer may
411 have offered more favourable conditions than the surface organic layer of unprepared soils: i) aeration
412 may have been improved when this buried layer was somewhat compressed by the mounding process; ii)
413 temperature may have been higher due to its position within the mound and its proximity with the warm
414 upper mineral soil; iii) it may have contained fewer live roots from competing species, since these were
415 buried and possibly killed during mound formation, which is a typical benefit of mounding, coherent with
416 our field observation of a slow re-colonization of mounds by competing vegetation and also with previous
417 studies reporting lowest vegetation covers on mounds, e.g., Knapp et al (2008); and iv) present results
418 show that net N mineralization was high. In contrast, in unprepared soils, proximal roots in the 0-2 and 2-
419 10 mm diameter classes were found more in the mineral layer, even though nitrogen mineralization was
420 much lower in that layer compared with the surface organic layer, which suggests the unprepared mineral
421 layer offered some other benefits to poplar roots.

422 Most plant species growing on boreal soils produce the majority of their roots in the surface
423 organic layer or at the organic: mineral boundary (Brassard et al. 2013; Finér et al. 1997; Van Rees 1997);
424 yet hybrid poplars in the unprepared soils of this study followed an opposite trend, with roots preferably
425 growing in the underlying mineral layer despite its slower nitrogen dynamics. Previous studies have
426 shown that the vertical distribution of fine roots may influence the outcome of competition between
427 species, for instance by increasing the level of competition when species exhibit a similar root distribution
428 (Bauhus et al. 2000). Species that are sensitive to root competition, e.g., pioneer tree species such as
429 *Populus*, would therefore tend to avoid such a situation, a strategy called ‘competition avoidance’
430 (Novoplansky 2009) or ‘root segregation’ (Schenk et al. 1999). Hybrid poplars were shown to be
431 sensitive to root competition (Coll et al. 2007), and even to avoid competing roots of other plant species
432 (Messier et al. 2009). However, since competing roots were not directly quantified in this study, the

433 results cannot clearly determine whether such a response to competition could have played a role in the
434 advanced colonization by fine roots of the buried organic layer in mounds compared with the surface
435 organic horizon of unprepared soils.

436

437 4.2 Soil nitrogen

438 The estimates of N mineralization obtained from *in situ* incubations indicated that concentrations
439 of mineralized N in the surface layers of mounds and unprepared soils were equivalent. However, the
440 unprepared soils experienced a stark decrease in net N mineralization with depth, whereas it remained
441 similar between the surface mineral horizon and the buried organic layer of mounds (Figure 3b). This
442 suggests that the disturbed soil conditions induced by mounding were at least as adequate, if not better as
443 those of undisturbed soil to promote the release of N to tree roots via mineralization. A previous study
444 done at the same sites showed that mounds had lower total C and N concentrations in the surface soil
445 compared with unprepared soils (Bilodeau-Gauthier et al. 2011). If one were to compare net N
446 mineralization (from incubation tubes, Figure 3b) with total N concentrations (see section 2.1), N
447 mineralization in the upper mineral layer of mounds would represent a strikingly large part of total soil N,
448 over 22%, whereas it would remain at 2 to 3% in unprepared soils. Moreover, when considering the
449 volume occupied by each soil layer, the total amount of mineralized N in the upper mineral layer of
450 mounds was strikingly higher than in all other soil layers (Figure 3c), thus pointing to the potential
451 importance of this layer for nitrogen supply. In comparison, the buried organic layer, because of its
452 thinness, had lower total net mineralized N than the upper mineral layer (Figure 3c), even though they had
453 similar mineralization rates (Figure 3b). Nonetheless, the buried organic layer of mounds was not
454 different from the unprepared organic layer, both in net and total mineralized N. Faster mineralization is
455 important for tree nutrition during a given stand rotation, although it also raises the question of whether it
456 could lead to long-term depletion of nutrient reserves (Örlander et al. 1996).

457 Because the upper mineral layer of mounds occupies a large volume, it appears to be the greatest
458 contributor to total net mineralized N in mounds; meanwhile, for unprepared soils it is the organic layer

459 that contributes the most. Since the total rooting volume is much larger in mounds, it would translate into
460 greater total amounts of net mineralized N, all soil layers combined, compared with unprepared soils. This
461 suggests that, even though N mineralization rates were at best comparable, and for some layers even
462 lower, in mounds compared with unprepared soils, trees planted in mounds had access to greater nutrient
463 pools thanks to soil conditions that favoured early root growth. Previous studies have similarly shown that
464 MSP can favour tree development by favouring the exploration by roots of a large soil volume (Nadeau
465 and Pluth 1997; Nordborg et al. 2006; Ross and Malcolm 1982).

466 Contrarily to the incubation results, the amounts of soil NH_4 and NO_3 adsorbed onto ion-exchange
467 resins suggested that the soil N supply in unprepared soils was more than two-fold that in mounds, for all
468 soil layers (Figure 3a). However, values from ion-exchange resins are affected by many microsite
469 conditions. First, the ions absorbed by plant roots cannot be captured by the resin membrane. As hybrid
470 poplar trees on mounds developed a larger biomass and a much larger root system than on unprepared
471 soils, they may have been more efficient at absorbing available forms of N. Another possible explanation
472 for the lack of concordance with incubations results is that the resins on mound may have lost their
473 efficiency in capturing nutrients as they experienced desiccation due to summer drought conditions
474 (Kjønaas 1999), and subsequent nutrient flows may have been underestimated in mounds.

475 The upturning of mineral soil to create the mound resulted in warmer and less compacted soil
476 (Bilodeau-Gauthier et al. 2011), which is typical of mounding (Örlander et al. 1990; Sutton 1993). The
477 increased temperature in mounds probably generated favorable conditions for the decomposition of the
478 organic material within the buried organic layer and for the mineralization of N, by increasing the activity
479 of microorganisms that transform organic N into mineral forms available for plant root uptake (Leirós et
480 al. 1999). In addition, the burial of the organic layer may have compacted this otherwise much aerated
481 organic material, which may have created better conditions for both soil N mineralization and root
482 exploration. Also pointing to possibly favorable conditions of N mineralization are the available N
483 amounts (as registered by ion-exchange resins) in the lower mineral layer of mounds, which were higher
484 than the amounts in the overlying layers. This could reflect mineralized and newly available N from the

485 buried organic layer that would have leached down the soil profile. It suggests that the organic layer could
486 contribute to enriching the underlying mineral soil with N (and that, whether the organic material is
487 buried or not, since the two unprepared layers also had similar resin-adsorbed N values). Nordborg et al.
488 (2003) reported that net N mineralization was higher for MSP treatments that retained the organic layer in
489 the planting microsite than when it was removed. They also showed that net N mineralization was
490 positively correlated to root growth and N uptake. Therefore, it is possible that the hybrid poplars growing
491 on mounds in the present study also took up more N. Similarly, in a study on MSP used for reforestation
492 of *Pinus halepensis* in semiarid parts of Spain, Barberá et al. (2005) suggested that burying organic matter
493 under furrows (rather than at the soil surface) may have contributed both to improve soil moisture
494 conditions (as organic matter retained water) and to increase nutrient mineralization and availability (by
495 favouring root access to nutrients), which might have led to better tree performance.

496

497 4.3 Hybrid poplar growth

498 Contrary to expectations, the height:root ratio was lower for hybrid poplars planted on mounds
499 compared with those in unprepared soils. These results do not concur with previous work suggesting that
500 smaller (or slower-growing) plants normally allocate more biomass to roots to obtain limiting nutrients
501 (Cahill 2003), but they are in line with Pennanen et al. (2005) who found no increase in aboveground
502 growth for 2-yr-old Norway spruces planted on mounds, but much greater root growth compared with
503 trees in unprepared soils. In our study, a lower height:root ratio for hybrid poplars on mounds compared
504 with unprepared plots did not proceed at the expense of stem growth. Indeed, the trees on mounds were
505 actually taller than those in unprepared soils, suggesting that the larger root system that developed in
506 mounds may have provided access to more available resources, and in turn actually increased the
507 aboveground growth of hybrid poplars. In addition, if belowground competition was potentially higher in
508 unprepared soils, then the smaller root system and higher height:root ratio of trees growing in unprepared
509 soils might hint at some form of avoidance of the densely populated surface organic layer.

510 When planted in favorable conditions, juvenile hybrid poplars can easily outgrow other woody
511 species and thus efficiently acquire light. However, newly planted trees often face harsh competition from
512 herbaceous species, notably grasses, whose negative effect stems mainly from belowground competition
513 (Collet et al. 2006). As such, early soil treatments such as mounding are very efficient for these species,
514 which then require less control of the competing vegetation in subsequent years. Bolte and Löff (2010)
515 thus suggested that mounding in *Quercus robur* plantations could offer an interesting alternative to
516 herbicides, a suggestion that could be extended to other labour-intensive, time-consuming, or potentially
517 environmentally-damaging vegetation control methods, or to mechanical methods involving intensive top
518 soil displacements.

519 It is nevertheless conceivable that slower-growing species would respond differently to such
520 management strategies. For instance, Boateng et al. (2009) showed that spruce (*Picea glauca*), which in
521 the absence of silvicultural treatments was physically overtopped by vegetation, benefited more from
522 lasting reductions in tall shrub and aspen abundance (i.e., increased light availability) than from early
523 effects of mechanical soil preparation on the rooting microsite. Nevertheless, Cortini and Comeau (2008)
524 observed that 11 to 13-year-old spruces were affected by surrounding woody shrubs in competition for
525 light, but that herbaceous plants also had a detrimental impact on the growth of these trees via root
526 competition, because of the spruces' shallow root system that put them in direct contact with herbaceous
527 plant roots.

528

529 5. CONCLUSION

530 By burying the organic layer under a quantity of mineral soil, and thereby modifying the vertical
531 arrangement of soil layers, mounds provided several nutritional and environmental advantages over
532 unprepared soils. The advantages that were emphasized by this study focused on root distribution and
533 nitrogen dynamics: First (1) the mounding process had positive effects on the net N mineralization,
534 notably in the upper mineral layer of mounds (whereas the underlying mineral layer of unprepared soils
535 had low N mineralization rates); Second (2) the burial of the organic layer that resulted from mounding

536 seem to have benefited early root development, since this buried organic layer was extensively explored
537 by the proximal roots of hybrid poplars; Third (3) proximal roots were overall more abundant in the
538 mounds compared with unprepared soils, exploring a larger soil volume and thus accessing a larger
539 nutrient pool (the total net mineralized N). Hence, our results suggest that mounding creates microsite
540 conditions that favour N dynamics and early root development, which in turn enhances the aboveground
541 growth of the planted trees.

542 This research has confirmed that the roots of fast-growing hybrid poplars, and likely other
543 pioneer trees, are responsive to the spatial arrangement of soil layers and resources. This response may be
544 explained in part by the sharp vertical zonation of podzolic boreal soils. Therefore, our results are likely
545 to apply to soils showing a strong zonation, to soils devoid of a macrofauna mixing the soil layers, and to
546 trees with a root system sensitive to soil conditions, for example fast-growing, shade-intolerant species.
547 Soil management that aims at inducing a vertical rearrangement of soil layers in tree plantations may thus
548 improve access to soil resources and optimize aboveground growth for fast-growing pioneer trees.

549

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Table 1. Typical vertical soil profiles of the two soil treatments (mechanical soil preparation by mounding, and the unprepared control) describing the soil layer types and their thickness. Soil layers are presented from top to bottom in the table as they are found from the soil surface down to deeper horizons in the tree's immediate soil environment.

Soil layer	Thickness (cm)	SE
Mounding		
Upper mineral *	16.0	1.9
Buried organic layer	7.5	0.6
Lower mineral	7.8	2.2
Max. depth reached by roots †	31.3	2.4
Unprepared		
Surface organic layer	10.8	1.3
Lower mineral	10.5	1.9
Max. depth reached by roots	21.3	1.4

* The upper mineral layer in the tree's immediate environment is not as thick as the highest point of the mound since the tree is planted on its side.

† Maximum depth reached by roots corresponds to the deepest location of a root as observed in the field root excavations ($n = 8$).

Table 2. Mean number of proximal roots per tree in mounds compared to unprepared soils, all soil layers combined but for different root diameter classes.

	Nb. roots tree ⁻¹ *	SE †	P-value ‡
All diameter classes			
Mounding	35.0	2.3	0.006
Unprepared	25.5	2.5	
0-2 mm			
Mounding	16.8	1.9	0.25
Unprepared	13.6	2.0	
2-10 mm			
Mounding	12.2	0.9	0.054
Unprepared	9.6	0.9	
11-20 mm			
Mounding	4.9	0.3	<.0001
Unprepared	2.0	0.3	
21-30 mm			
Mounding	0.96	0.2	0.001
Unprepared	0.095	0.2	

* Root numbers are means per tree from 24 (mounding) and 21 (unprepared) excavated hybrid poplars at 8 sites.

† SE = standard error.

‡ P-values were produced by mixed analyses of variance comparing mounding with unprepared soil.

Table 3. Detailed results of the mixed ANOVA comparing roots and soil data by soil treatment and soil layer.

Analyzed variable	Source of variation *	df	SSE	MSE	% variance †	F-value	P-value
Number of roots							
Fixed effects							
	Soil treatment & layer & diameter class	19	44.79	2.357	92.9	13.04	< 0.0001
Random effects							
	Site	7	2.254×10 ⁻¹¹	3.220×10 ⁻¹²	1.27×10 ⁻¹⁰		
	Plot	133	1.265	0.009515	0.375		
	Residuals	296	50.60	0.1709	6.74		
	Total	455					
Resin-adsorbed N							
Fixed effects							
	Soil treatment & layer	4	0.005158	0.0012894	94.4	17.28	< 0.0001
Random effects							
	Site	7	2.270×10 ⁻¹²	3.243×10 ⁻¹³	2.37×10 ⁻⁸		
	Plot	28	0.0004850	1.732×10 ⁻⁵	1.29		
	Residuals	72	0.004274	5.937×10 ⁻⁵	4.35		
	Total	111					
Net mineralized N							
Fixed effects							
	Soil treatment & layer	4	0.0875	0.021876	76.8	3.355	0.0125
Random effects							
	Site	7	5.663×10 ⁻¹²	8.090×10 ⁻¹³	2.84×10 ⁻⁹		
	Plot	28	0.01700	0.0006073	2.13		
	Residuals	72	0.4320	0.00600	21.1		
	Total	111					
Total net mineralized N							
Fixed effects							
	Soil treatment & layer	4	1589	397.1	86.6	6.516	< 0.0001
Random effects							
	Site	7	19.40	2.771	0.604		
	Plot	28	95.19	3.40	0.741		
	Residuals	72	3980	55.28	12.1		
	Total	111					

* Soil treatment & layer = a meta-variable with 5 levels, created by combining “soil treatment” (mounding, unprepared) with “soil layer”. For roots, it also included diameter class. See Data analysis, in Methods.

† The % variance is the proportion of the total variance provided by a given source of variation.

Table 4. Soil temperature measured continuously with data-logging sensors during June-August.

	Mean *	SE †
Soil temperature (°C), overall		
Mounding	15.4	2.4
Unprepared	14.5	1.8
P-value	0.15	
Soil temperature (°C), Day ‡		
Mounding	15.8	3.1
Unprepared	15.6	1.8
P-value	0.56	
Soil temperature (°C), Night ‡		
Mounding	15.1	1.6
Unprepared	13.4	1.3
P-value	0.006	

* Mean = average value for three depths (2, 10, and 20 cm) from 15 trees at two sites.

† SE = standard error.

‡ Day = 07:00 to 19:00, Night = 21:00 to 05:00.

Table 5. Aboveground measurements for 3-yr-old hybrid poplars in the two soil treatments.

		Mounding	Unprepared
Height, cm	mean	273	171
	SE †	18	17
	P-value	<0.0001	
mid-DBH, mm *	mean	27.8	14.7
	SE	3.7	1.6
	P-value	<0.0001	
height:root	mean	1.5	2.7
	SE	0.3	0.3
	P-value	0.015	

* mid-DBH = diameter at breast height taken 65 cm above the ground.

† SE = standard error.

Table 6. Correlations on rank (Spearman's rho, ρ) between root characteristics (per tree) and other soil and tree variables.

Variable 1	Variable 2	Spearman's Rho	Prob> Rho
Nb. of proximal roots	Mid-DBH *	0.4862	0.0007
	Total tree height	0.5598	<.0001
Average proximal root diameter	Mid-DBH	0.2318	0.1255
	Total tree height	0.1799	0.2371
	Soil temperature	0.1043	0.4952
	Net mineralized N	-0.5766	<.0001
Shoot: root ratio	Net mineralized N	-0.3006	0.0448
Nb. of proximal roots in diameter class			
0-2 mm	Total tree height	0.3591	0.0154
	No. of proximal roots per tree	0.8548	<.0001
2-10 mm	Mid-DBH	0.3006	0.0448
	Average proximal root diameter	0.3161	0.0344
	Total tree height	0.3723	0.0118
	No. of proximal roots	0.6934	<.0001
11-20 mm	Mid-DBH	0.7710	<.0001
	Total tree height	0.6800	<.0001
	Soil temperature	0.7881	<.0001
21-30 mm	Mid-DBH	0.6605	<.0001
	Total tree height	0.6333	<.0001
	Soil temperature	0.5405	0.0001
	Resin-adsorbed N	0.3447	0.0204

* Mid-DBH: diameter at breast height taken 65 cm above the ground.

FIGURE CAPTIONS

Figure 1. Schematic representation of the mounding process (inspired by Sutton 1993). 1) A portion of the undisturbed soil – covered with competing herbaceous and woody vegetation – is dug out; 2) the dugout soil material is inverted; and 3) placed nearby over the undisturbed organic layer, thus covering and killing the competing vegetation. The tree is planted on the hillside of this mound.

Figure 2. Number of hybrid poplar proximal roots per cm of soil depth per tree, among four root diameter classes, for the two soil treatments (mounding, unprepared), and for different soil layers. Values are means across eight sites and error bars are standard errors. Depth and thickness of soil layers are based on measurements of the vertical soil profile made during root excavations. Different letters indicate a significant difference at $\alpha = 0.05$ between bars (each bar of the graph is a combination of soil treatment \times soil layer \times diameter class, and all combinations are compared at the same time).

Figure 3. Different aspects of soil N dynamics by soil treatment (mounding, unprepared) and soil layer (identified by depth and soil material). A) Concentrations (g m^{-2}) of total inorganic N, i.e., $[\text{NH}_4+\text{NO}_3]\text{-N}$, adsorbed onto ion-exchange resins. B) Net mineralized N per soil unit mass (g kg^{-1}). Values come from 6-week *in situ* burials (A) or incubations (B). C) Total net mineralized N (g) in the rooting volume. This volume was estimated for a cylindrical soil volume of fixed surface area (a circle of 50-cm radius around the tree) and a depth determined by the position in the soil profile of the deepest proximal roots (see Table 1 for depths and thickness of soil layers). Values are means across eight sites and error bars are standard errors. Different letters indicate a significant difference at $\alpha = 0.05$ between bars (each bar is a combination of soil treatment \times soil layer, and all five combinations are compared at the same time in a given graph).

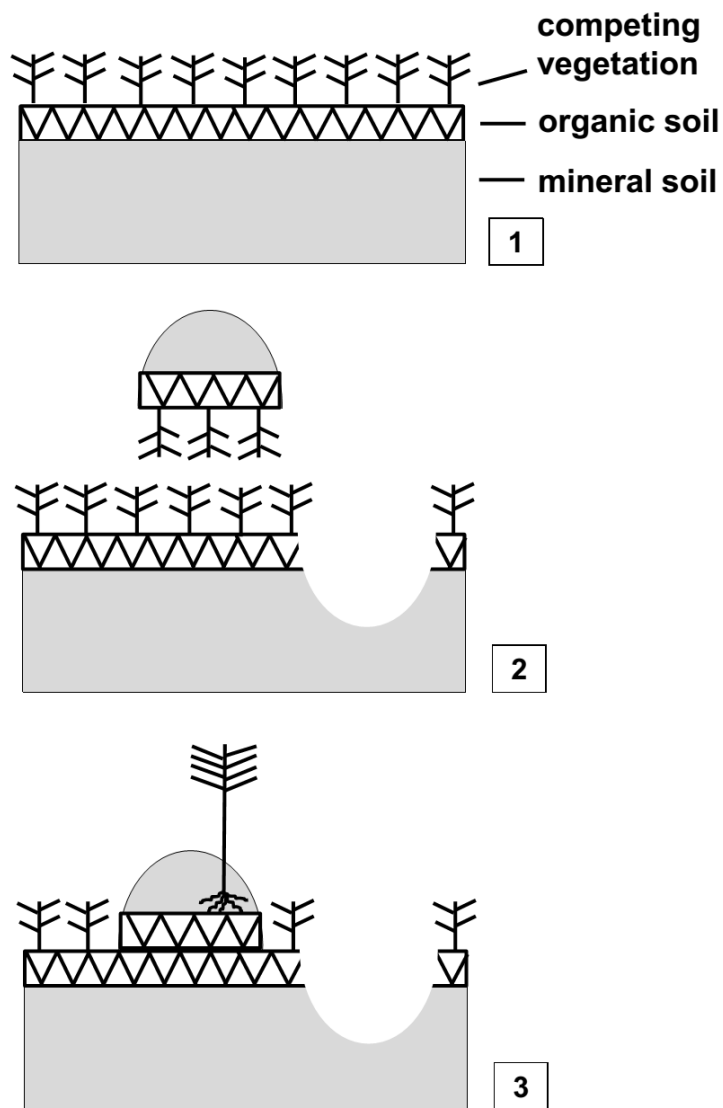


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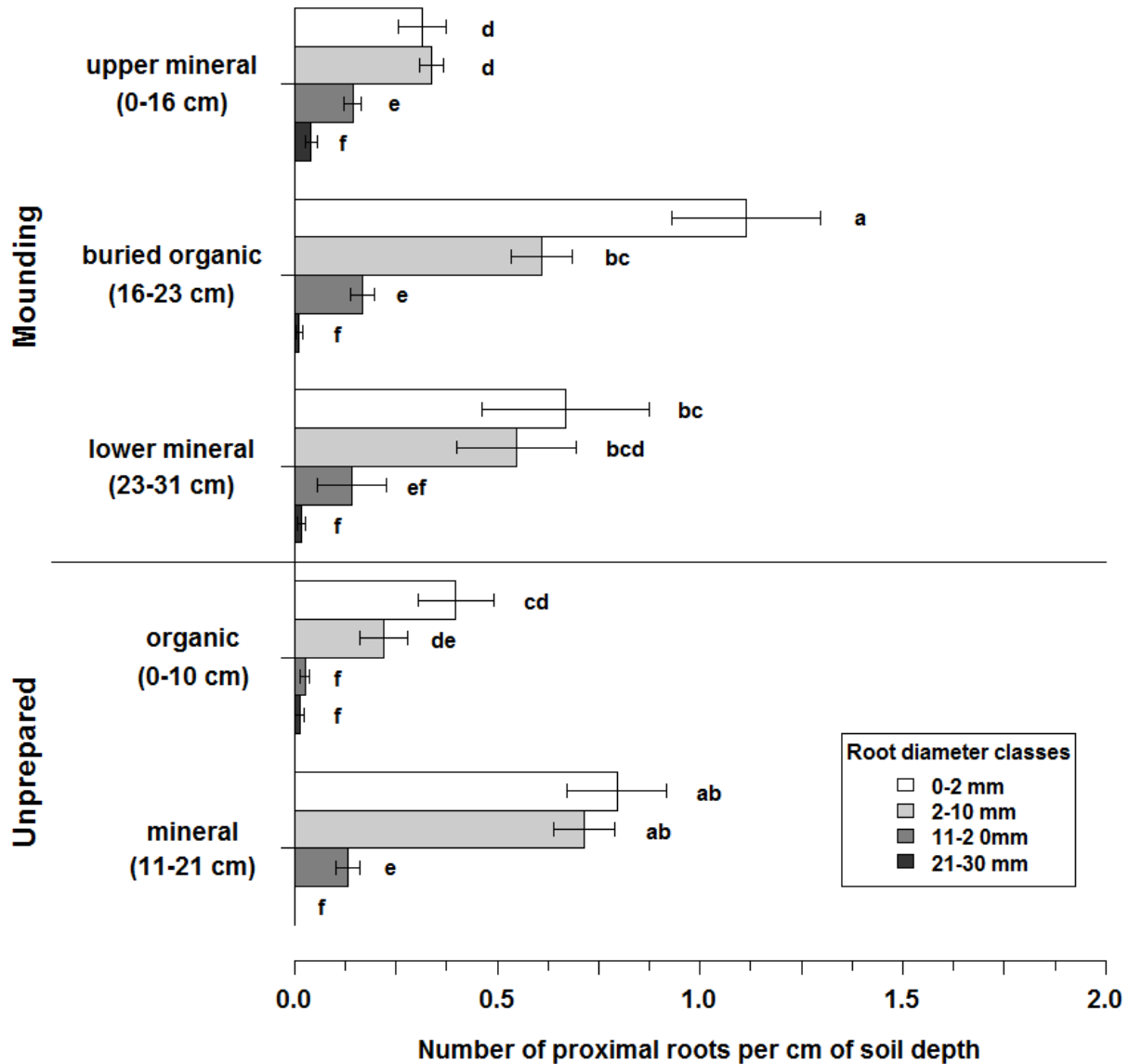


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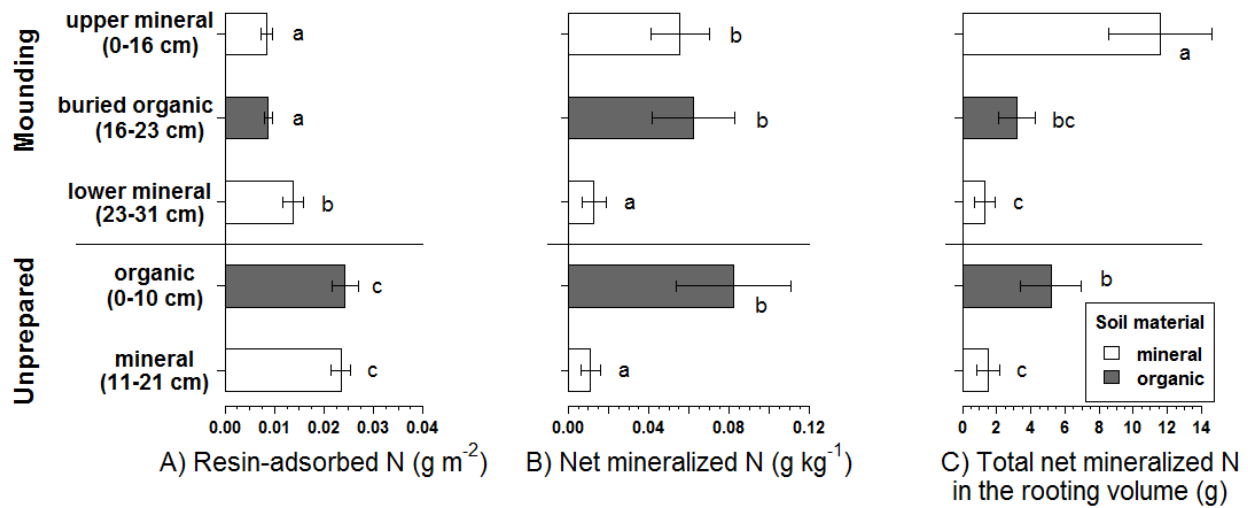


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