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12 **Does natural root grafting make trees better competitors?**

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20

21 **Abstract**

22 Natural root grafts (anastomoses) are morphological unions formed between roots of different
23 trees. Common root systems allow translocation of water, nutrients and photosynthesis products
24 between grafted trees, affecting their growth and their physiology. As carbohydrates are
25 redistributed among grafted trees, the formation of a common root system could reduce the
26 negative effect of intraspecific competition for light or soil resources within stands. The aim of
27 this study was to investigate the role of root grafting on intraspecific competition and growth
28 of balsam fir (*Abies balsamea* (L.) Mill). We studied inter-tree relationships in three natural
29 balsam fir stands of the boreal forest of Quebec (Canada) that contained an average 36% of
30 grafted trees. At each stand, ring width and basal area of trees were measured using
31 dendrochronology techniques. We used mixed linear models to test the effect of root grafting
32 and intraspecific competition on annual basal area increment of trees. Trees before grafting had
33 higher growth rates than trees once grafted. Thus, root grafting did not improve tree growth.
34 Growth of grafted trees was more negatively affected by intraspecific competition than growth
35 of non-grafted trees. Thus, grafted trees cannot be considered as better competitors than non-
36 grafted trees. Under high intraspecific competition, growth of larger grafted trees was less
37 affected than that of smaller trees suggesting that they were able to divert resources at their
38 advantage within a union. Our study demonstrated that grafted trees acted on each other's
39 growth and provides support for the idea that grafted trees respond to competition for resources
40 more as a community rather than as individual trees.

41 Key words: Root grafting, *Abies balsamea*, Boreal forest, Competition, Radial growth,
42 Anastomosis.

43

44 **Introduction**

45 When two roots from different trees come into contact, a morphological union can occur by
46 the fusion of their vascular tissues to form a natural root graft (i.e. anastomosis, Graham and
47 Bormann 1966, Mudge et al. 2009). In recent decades, underground networks created by root
48 grafting generated interest in forest ecology as mechanisms of “resource sharing” between trees
49 (McIntire and Fajardo 2014, 2011, Valladares et al. 2015). In addition to their role in facilitating
50 resource acquisition and assimilation, extended common root systems of grafted trees allow
51 resources exchange such as water, nutrients and photosynthates (Fraser et al. 2006, O’Neal and
52 Davis 2015, Klein et al. 2016, Bader and Leuzinger 2019). Since grafted trees may directly
53 share substances and affect each other’s growth, ecological concepts that support the notion of
54 plant individuality and dominance of competition for resources in plant interactions are
55 challenged (Lortie et al. 2004, Brooker 2006, Brooker et al. 2008).

56 While root grafts have been observed worldwide in more than 200 tree species, root grafting
57 has long been considered as a rare or random event and little research has focussed on its
58 ecological significance (La Rue 1952, Graham and Bormann 1966). The role of root grafting
59 was first reduced to a mechanism to improve anchorage and stability in windy environments
60 and waterlogged soils (Rigg and Harrar 1931, Keeley 1988, Basnet et al. 1993). Root grafting
61 was also considered as a vector for diseases because pathogens translocated between grafted
62 trees through sap flow or contact between roots (Epstein 1978, Baric et al. 2008). Over the last
63 twenty years, interest in the role of root grafting on tree growth has grown to explain forest
64 dynamics (Tarroux et al. 2010, McIntire and Fajardo 2011, Adonsou et al. 2016). On the one
65 hand, Tarroux and DesRochers (2011) showed that *Pinus banksiana* radial growth was
66 increased by intraspecific root grafting. Moreover, it was shown that radial growth of grafted
67 *Picea mariana* or *Populus balsamifera* under insect outbreak or unfavorable climatic conditions
68 was improved compared to growth of non-grafted trees, suggesting that root grafting could be

69 an ecological advantage for trees under environmental stresses (Salomón et al. 2016, Adonsou
70 et al. 2016). These results promote the idea that common root systems improve access,
71 redistribution and use of soil resources among grafted trees leading to better growth and
72 survival. This implies that grafted trees do not only compete for resources but can also directly
73 facilitate the growth of their grafted neighbors (Eis 1972, Keeley 1988, Loehle and Jones 1990,
74 McIntire and Fajardo 2011).

75 Nonetheless, it was also reported that root grafting was an energetically costly process:
76 dendrochronological analyses of root grafts correlated root grafting to a decrease in tree growth
77 during their formation (Tarroux and DesRochers 2011). The same authors also showed that the
78 inheritance of a root system from a removed tree, creates an imbalance between root biomass
79 and leaf area, and thus could negatively impact growth of residual trees (generally the larger
80 one) in thinned *Pinus banksiana* stands (Tarroux et al. 2010).

81 Negative and positive interactions reported between grafted trees support the idea that
82 relationships between grafted trees are non-neutral and can be summarized as: i) facilitation:
83 moderation of biotic and abiotic stress, enrichment of resources or increased access to
84 resources, or ii) parasitism: resources are translocated from the dominant to suppressed trees
85 improving their survival at the expense of the growth of dominant trees. In the case of
86 parasitism, it would also be conceivable that larger trees would take advantage of smaller trees,
87 as larger members of a root complex may be able to, at the expenses of the less vigorous trees,
88 establish gradients that cause water and nutrients absorbed by the communal root system to
89 move primarily to them (Bormann 1962, Wimmmler et al. 2022). Larger trees, with their larger
90 crowns, will transpire more than suppressed trees, creating a stronger sink for water (Bader and
91 Leuzinger 2019, Wimmmler et al. 2022). However, we don't know if grafted trees are differently
92 affected by root grafting according to their size within the union.

93 Competition (i.e. negative interaction between plants through direct interference or indirectly
94 through the exploitation of common resources) is a key process to explain community structure
95 and dynamics in forests worldwide (Kunstler et al. 2016). In forest stands, competition between
96 trees increases with tree size, tree proximity and stand density (Lorimer 1983). Interestingly,
97 the probability of root graft formation also increases with tree size, proximity of trees and stand
98 density, allowing resources translocation and cooperation relationships (Fraser et al. 2005,
99 Tarrow and DesRochers 2010, Gaspard and DesRochers 2020). A relatively high frequency of
100 root grafting in balsam fir (*Abies balsamea* (L.) Mill) stands was reported (36% of grafted trees
101 in three 50 m² stands), where root grafting increased with tree proximity and number of roots
102 per tree (Quer et al. 2020). Balsam fir is known to be a shade tolerant species, growing for
103 prolonged periods of time in dense understory environments without self-thinning (Burns and
104 Honkala 1990, Ruel et al. 2003). Moreover, balsam fir maintains an abundant seedling bank on
105 the ground leading to the formation of very dense stands after disturbances remove canopy trees
106 (Morin and Laprise 1997). Under these conditions of high intraspecific competition for light
107 and soil resources, root grafting might lessen competition effects in dense stands by supporting
108 tree growth through resources sharing and translocation (Loehle and Jones 1990, Lev-Yadun
109 2011). We thus undertook this study in order to better understand the ecological significance of
110 root grafting in balsam fir stands under high intraspecific competition. In order to demonstrate
111 if root grafting could alleviate the negative effects of intraspecific competition on balsam fir
112 tree growth, we developed mixed linear models estimating the role of root grafting and
113 intraspecific competition on balsam fir growth. After selecting the “best” model to predict tree
114 growth, we studied interactions between root grafting and intraspecific competition to further
115 explore their relationships. Our main hypotheses were: (i) intraspecific root grafting improves
116 growth of grafted balsam fir trees; (ii) intraspecific competition reduces growth of grafted
117 balsam firs; (iii) root grafting alleviates the negative effects of intraspecific competition on

118 balsam fir growth, (iv) trees are differently affected by root grafting according to their
119 respective size within the union.

120

121 **Material and methods**

122 *Study sites*

123 This study was conducted in Abitibi-Témiscamingue, north-western Quebec, in the balsam fir-
124 white birch (*Betula papyrifera* Marsh.) bioclimatic domain of the boreal forest (Grondin et al.
125 1996). The first site (S1) was located near the Lake Duparquet Research and Teaching Forest
126 (48°52'21.6"N, 79°46'53.0"W), the second site (S2) was located near Kinojévis teaching forest
127 (48°18'26.1"N, 78°84'63.7"W) and the third site (S3) was located near the Harricana teaching
128 forest training center (48°76'27.8"N, 77°77'93.3"W). All sites were on heavy clayey soils (at
129 least 60% of clay) associated to post Wisconsinan glaciolacustrine deposits (Vincent and Hardy
130 1977, Agriculture Canada Expert Committee on Soil Survey 1987). From 1981 to 2010, mean
131 daily temperature in this region was 1.5 °C with a mean of 2366 degree-days above 0 °C and
132 annual total precipitation averaged 929 mm (253 mm of snow and 675 mm of rain)
133 (Environment Canada 2019). To be selected, sites had to be monospecific, naturally
134 regenerated, mature (> 30 years old) and healthy balsam fir stands. Site areas were
135 approximately 50 m² and included a minimum of 15 living trees. Stand density ranged from
136 6000 stems ha⁻¹ to 14200 stems ha⁻¹. Prior to this study, hydraulic excavation and
137 dendrochronological analyses of the root systems of each tree were carried out to determine
138 frequency of root grafting, age of trees and grafts, as well as the distance between trees (see
139 Quer et al. 2020 for further details). Stand age ranged from 39 to 74 years old. Percentage of
140 grafted trees and number of grafts per tree was similar between stands, corresponding
141 respectively to 36% (± 2.86 SE) and 1.30 (± 0.03 SE). Mean graft age was 13.57 years (± 0.98
142 SE) (Quer et al. 2020) (Table 1).

143 *Tree radial growth analyses by tree ring width series measurement*

144 Field work was performed in summer 2017. At each site, all trees were felled with a chainsaw
145 and cross-sectional disks were collected at ground level (0 m). Cross-sectional disks were air
146 dried and sanded (80-400 grit) to reveal growth rings. Tree ring widths series were measured
147 on cross-sectional disks from the stem base using a Velmex “TA Unislide” measurement system
148 with ACU-Rite linear encoder and QC10V digital readout device (Velmex, Inc., Bloomfield,
149 New York) interfaced with Measure J2X (Version 5.0x) ring-reading software (Project J2X,
150 Voortech Consulting, Holderness, NH). Ring-width series were measured with 0.001 mm
151 precision along two rays per wood disk when possible (i.e. when the rings were clearly visible)
152 and visually cross-dated. To obtain a single series per tree, chronologies were averaged for each
153 tree when two of them were available. A total of 110 tree ring width series were obtained.

154 Tree age and stem size increasing over time promotes a decline of tree ring width along cross-
155 sectional radius. To avoid this biological trend, we converted tree ring width series into basal
156 area increment (BAI) to calculate annual tree growth (Biondi and Qeadan 2008) following
157 equation (1) :

158
$$BAI_t = \pi R_t^2 - \pi R_{t-1}^2 \quad (1)$$

159 Where R_t is the stem radius at year t and R_{t-1} is the stem radius at year $t-1$.

160 In order to include a minimum of 30 tree ring width measurements per year, we used only the
161 data of tree growth for the last 60 years. Due to the inaccuracy of tree ring width measurement
162 during the first years of growth, we decided to not take into account the first 5 years of growth
163 of each tree in the data analysis.

164 *Intraspecific competition measurements by using competition indices*

165 Intraspecific competition between trees was estimated using distance-independent (BAL: Basal
166 area of the Larger tree) and distance-dependent (HEG: Hegyi competition index) competition

167 indices. The first index (BAL) was developed by Wykoff et al. (1982) and corresponds to the
168 sum of the of the basal area of neighbor trees that are larger than the subject tree:

169
$$BAL = \sum_{\substack{j=1 \\ j \neq i \\ R_j > R_i}}^n \pi R_j^2 \quad (2)$$

170 With R_i = Radius of the subject tree i ; R_j = Radius of the competing tree j . The second index
171 (HEG) was developed by Hegyi (1974) and corresponds to the sum of the ratios of diameters
172 of a subject tree and its competitors, weighted by the distance from the subject tree. To integrate
173 tree growth variability over time we replaced tree diameter by tree basal area in the next
174 formula:

175
$$HEG = \sum_{j=1}^n \frac{BA_j / BA_i}{Dist_{ij}} \quad (3)$$

176 Where: HEG = Hegyi competition index; BA_i = Basal area of the subject tree i ; BA_j = Basal
177 area of the competing tree j ; $Dist_{ij}$ = distance between trees i and j ; n = total number of
178 competitors. In order to determine the radius around the subject tree in which there are potential
179 competitors, we calculated competition indices (HEG) for 10 trees in each site for 10 years and
180 for different values of radii (from 1 to 9 m). We then considered that each tree found in a radius
181 of 6 m or less around the subject tree was a potential competitor (Supporting information, Figure
182 S1). As HEG integrates basal area, it measures symmetric competition (i.e. competitors share
183 resources in proportion to their size) and it is often associated to competition for belowground
184 resources (Pretzsch and Biber 2010). BAL only integrates basal area of larger neighbor trees
185 and measures symmetric and asymmetric competition (i.e. large competitors capture a
186 disproportionate share of contested resources over smaller competitors) thus it reflects
187 competition for belowground resources but also for light (Weiner 1990, Connolly and Wayne
188 1996, Freckleton and Watkinson 2001).

189 *Statistical analyses*

190 Statistical analyses were done using R software version 4.0.3 (R core team 2019).
191 Considering grafted trees, for a same tree, years of growth were annotated BG for years of
192 growth before grafting and G for years of growth once tree was grafted; for non-grafted trees:
193 years of growth of a non-grafted trees were annotated NG.
194 In order to test the effects of intraspecific competition (i.e. HEG and BAL) and root grafting
195 status (i.e. BG, G and NG) on *Abies balsamea* tree growth (i.e. BAI), we developed linear mixed
196 effect models (LMER, packages “lme4” and “lmerTest”, Bates et al. 2020, Kuznetsova et al.
197 2020). Data were log-transformed to satisfy linearity and normality of the residuals assumptions
198 using the “LogSt” function formulated to taking into account null values (i.e. HEG, BAL,
199 package “DescTools”, Signorell et al. 2020). Site, year and individual (i.e. tree) were considered
200 as random factors for the intercept. The Model equation was as follows:

$$201 \log(BAI_{i,t}) = \beta_0 + \beta_1 \log(BA_{i,t-1}) + \beta_2 \log(CI_{i,t}) + \beta_3 \text{Status}_{i,t} + b_1 + b_2 + b_3 + e \quad (4)$$

202 with $BAI_{i,t}$ the Basal Area Increment of tree i at year t , $BA_{i,t-1}$ the Basal area of tree i at the
203 previous year ($t-1$), $CI_{i,t}$ the Competition Index (i.e. HEG or BAL) of tree i at year t , the graft
204 Status (i.e. BG, NG and G) of the tree i at the year t , b_1 , b_2 and b_3 the random effects estimated
205 for the intercept with respectively trees, years and sites as grouping factors and e the residual
206 error. β_0 , β_1 , β_2 , β_3 were the fixed effect parameters. As tree growth is strongly influenced by
207 their size (MacFarlane and Kobe 2006), BA was included to the model in order to integrate the
208 effect of tree size on annual tree growth.

209 All combinations of random effects (trees, sites and years) on the intercepts were tested by
210 adding or nesting them together but preliminary analysis revealed that the models better
211 performed by integrating the three effects additionally. Models including all the possible
212 combinations of independent variables (CI, status and BA) were compared based on the second-
213 order Akaike Information Criterion (AICc) using the “aictab” function (package
214 “AICcmodavg”, Mazerolle 2020). Marginal and conditional r-squared (reporting proportions

215 of variance explained by the fixed factor and by the fixed and the random factors, respectively)
216 were calculated and used to quantify model performance (function “r.squaredGLMM”, package
217 “MuMin”, Barton 2020). ANOVAs were used on the selected models to test the global effect
218 of the categorical variables on BAI. Interactions between competition index (i.e. HEG or BAL)
219 and root grafting status (i.e. NG or G) were then tested on the best performing model using the
220 same method. Effect plots of the selected model were represented graphically using the R
221 package “effects” (Fox et al. 2020). For each model, normality of the residuals and
222 multicollinearity of the explanatory variables were tested using Shapiro-Wilk test and the
223 Variance Inflation Factor. We used this modeling approach: (i) on the data from the BG and G
224 trees to test if root grafting improved tree growth once grafted, (ii) on data from G and NG trees
225 to determine if root grafting alleviated the negative effect of competition on growth.
226 To investigate if the growth of grafted trees was differently affected according to their size
227 within a union by root grafting and intraspecific competition, we replaced the independent
228 variable Status with Size in our models. The smallest trees within a union were annotated S and
229 the larger L.

230

231 **Results**

232 *Does root grafting improve tree growth?*

233 Between the four single variable models tested, the one including BA (i.e. tree size) better
234 explained BAI (i.e. tree growth) than the one including root grafting status (68.6% of variance
235 explained for models including BA *versus* 10.2% for model including Status, Table 2) and the
236 two including competition indices (i.e. BAL or HEG, 17.7% and 49.7% of variance explained
237 for models including BAL and HEG respectively, Table 2). Thus, tree size better predicted tree
238 growth than root grafting and intraspecific competition. After the addition of the BA (i.e., tree
239 size) to the three previous models, the percentage of variance explained was similar between
240 models (71.1% on average, Table 2). However, when adding BA, the model selected with the
241 AICc included HEG rather than BAL (Table 2). The results showed that, considering grafted
242 and future grafted trees, a competition index reflecting only symmetric competition (i.e. HEG)
243 better explained BAI than a competition index integrating both symmetric and asymmetric
244 competition (i.e. BAL). The best model explaining BAI according to AICc included HEG
245 competition index, tree grafting status (Status) and BA (73.9% of the variance was explained,
246 Table 2). Year, site and tree random effects explained 16.7% of the remaining variance. We
247 also studied the interaction between intraspecific competition and tree root grafting status, but
248 the interaction was not significant and only the additive models were retained.

249 Tree grafting status (i.e. Status), intraspecific competition (i.e. HEG) and tree size (i.e. BA)
250 significantly affected annual radial growth of trees (i.e. BAI, LMER, $P < 0.001$, Table 3 and
251 Fig. 1). Grafted trees (i.e. G) exhibited 0.40 mm^2 lower BAI than the average BAI of future
252 grafted trees (i.e. BG, Table 3 and Fig. 1c). HEG had a negative effect on BAI (Table 3 and
253 Fig. 1a), where a 1% increase in HEG induced a 0.65% reduction in BAI. Tree growth (i.e.
254 BAI) increased with tree size (i.e. BA, Table 3). From 0 to 400 cm^2 , tree growth (i.e. BAI)

255 strongly increased with size of trees (i.e. BA) but beyond 400 cm² tree growth was only slightly
256 affected by tree size (Table 3 and Fig. 1b).

257 *Does root grafting alleviate the negative effect of intraspecific competition on annual*
258 *tree growth?*

259 BA (i.e. tree size) was also the best variable to explained BAI (i.e. tree growth) of grafted trees
260 and non-grafted trees (55.7% of variance explained for the single variable model, Table 4).
261 However, when adding BA, the model selected with the AICc included BAL rather than HEG
262 (Table 4). Thus, considering grafted and non-grafted trees, a competition index integrating both
263 symmetric and asymmetric competition (i.e. BAL) better explained BAI than a competition
264 index reflecting only symmetric competition (i.e. HEG).

265 Considering only models without interactions, the best model explaining BAI according to AIC
266 included BAL competition index, tree grafting status (Status) and BA (68.7% of the variance
267 was explained, Table 4). Year, site and tree random effects explained 23.2% of the remaining
268 variance.

269 After testing the interactions between the selected explanatory variables, we found that the
270 model including an interaction between tree grafting status and BAL was considered as better
271 than the one without interaction according to the AICc (Tables 4). Fixed effects explained
272 69.9% of the variance and random effects explained 22.2% of the remaining variance.

273 Tree grafting status (i.e. Status), intraspecific competition (i.e. BAL) and tree size (i.e. BA)
274 significantly affected annual radial growth of trees (i.e. BAI, LMER, $P < 0.001$, Table 5 and
275 Fig. 2). Grafted trees (i.e. G) had 1.98 mm² greater BAI than the average BAI of non-grafted
276 trees (Table 5 and Fig. 2b). BAL had a negative effect on BAI (Table 5 and Fig. 2b), where a
277 1% increase in BAL induced a 0.18% reduction in BAI. Tree growth (i.e. BAI) increased with
278 tree size (i.e. BA, Table 5). From 0 to 400 cm², tree growth (i.e. BAI) strongly increased with
279 size of trees (i.e. BA) but beyond 400 cm² tree growth was only slightly affected by tree size

280 (Table 5 and Fig. 2a). Considering interactions within the model, BAL had a strong negative
281 effect on BAI once trees were grafted (Table 5 and Fig. 2b). BAI of grafted trees was higher
282 than BAI of non-grafted trees (i.e. BAI of G > BAI of NG) for BAL values ranging from 0 to
283 2000. When BAL was higher than 6000, BAI of grafted trees decreased below that of non-
284 grafted trees (i.e. BAI of G < BAI of NG) meaning that under high BAL, BAI of grafted trees
285 was lower than BAI of non-grafted trees.

286 *Does tree size within a union modify the effect of root grafting and competition on*
287 *annual tree growth?*

288 Considering grafted trees, the best model explaining BAI according to AIC included BA and
289 the interaction between size of trees within a union (Size) and BAL competition index (69.8%
290 of the variance explained, Table 6). Year, site and tree random effects explained 24.1% of the
291 remaining variance. BAL had a strong negative effect on BAI of grafted trees but this effect
292 was modulated according to size of trees within unions (Table 7 and Fig. 3b). BAI of smallest
293 grafted trees was higher than BAI of largest grafted trees (i.e. BAI of S > BAI of B) for BAL
294 values ranging from 0 to 1000. When BAL was higher than 4000, BAI of smallest grafted trees
295 decreased below that of largest grafted trees (i.e. BAI of S < BAI of B) meaning that under high
296 BAL, BAI of smallest grafted trees was lower than BAI of largest grafted trees.

297

298 **Discussion**

299 This study is the first to evaluate the interaction effect between root grafting and
300 intraspecific competition on tree growth. Our results showed that intraspecific competition
301 decreased tree growth, and that growth reduction was more pronounced for grafted trees. We
302 thus reject our hypothesis that root grafting makes trees better competitors than non-grafted
303 trees.

304 Future grafted trees had better growth rate than trees that would never form root grafts,
305 suggesting that they were the most productive trees within a stand (Table 3, Figure S2). Several

306 studies have shown that root grafting primarily occurs between larger trees within a stand
307 (Gaspard and DesRochers 2020, Tarroux and DesRochers 2010). To explain this effect, it had
308 been suggested that roots of larger trees have more chance to cross and fuse (Armson and Van
309 Den Driessche 1959, Reynolds and Bloomberg 1982).

310 Moreover, common root systems established between grafted trees are known to increase the
311 coverage area of roots, thus increasing stand efficiency to exploit soil resources and increase
312 growth rates of trees (Bormann 1966, Loehle and Jones 1990, Basnet et al. 1993, Tarroux and
313 DesRochers, 2011). However, we showed that once trees grafted, their growth decreased (Fig.
314 2c). Tarroux and DesRochers (2011) demonstrated that growth of *Pinus banksiana* trees
315 decreased during the time that root grafts were forming, suggesting that root grafting is an
316 energetically costly process (Bormann, 1966; Loehle and Jones, 1990). However, reduction in
317 Jack pine growth lasted from 5 to 10 years after graft formation (Tarroux and DesRochers,
318 2011) while we observed a much longer reduction in growth once our trees grafted (mean graft
319 age was 14 in the studied stands [Quer et al. 2020]). It would be relevant to study older stands
320 to test if this growth reduction persists over time (e.g. after 10, 20 or 30 years of root grafting).

321 We showed that once trees grafted, there was a negative effect of root grafting with intraspecific
322 competition, while non-grafted trees were less affected by intraspecific competition (Fig. 2b).

323 Considering models on grafted and non-grafted trees, the better performance of BAL
324 competition index in our model reflected that both asymmetric (i.e. competition for light) and
325 symmetric competition (i.e. competition for soil resources, Wykoff et al. 1982, Schwinning and
326 Weiner 1998) negatively affected balsam fir growth (Tables 5, Fig. 2b) even if (i) balsam fir is
327 a shade tolerant species with a strong crown morphological plasticity adapted to dark
328 environments (Baker 1949, Duchesneau et al. 2001) and (ii) soil resources could be directly
329 redistributed among trees through root grafting. The Hegyi competition index was nevertheless
330 selected as the best predictor of BAI for the single variable models (Table 4). The BAL

331 competition index was then selected as the best predictor of BAI for the two or three variables
332 models (Table 4). Once basal area of trees was included into the models, the BAL competition
333 index performed better than the Hegyi competition index to explain BAI (Table 4), suggesting
334 that the part of model variance explained by Hegyi competition index was mainly due to the
335 fact that it integrated tree size. As the Hegyi competition index also includes distance between
336 trees, our results suggest that tree proximity was not an important predictor of tree growth and
337 intraspecific competition. This was confirmed by the fact that the best model selected to explain
338 tree growth included BAL, a distance-independent competition index. This suggests that
339 competition between trees was more driven by tree size than by tree proximity. As distance-
340 dependent indices include spatial arrangement of trees, they are often more efficient for
341 describing the effects of competition on tree growth in natural and heterogenous stands
342 (Prevosto 2005, Contreras 2011). However, several studies, including ours, showed that
343 distance-independent indices performed universally better for tree growth modelling (Biging
344 and Dobbertin 1995, Stadt et al. 2007, Helluy et al. 2020).

345 The significant interaction between BAL competition index and root grafting status indicates
346 that effect of root grafting on growth was related to intraspecific competition. However, the
347 interaction between BAL and root grafting status showed that at low to moderate intraspecific
348 competition, growth of grafted trees was greater than growth of non-grafted trees while it was
349 the reverse at high levels of intraspecific competition (Table 5 and Fig. 2b). Above the value of
350 5000 BAL, corresponding approximatively to a stand density of 12500 stems ha⁻¹, growth of
351 grafted tree was lower than growth of non-grafted trees (Tables 5, Fig. 2b).

352 Slower growth indicates a reduced vigor and a greater sensitivity to disturbances in grafted trees
353 under high intraspecific competition. We showed that our trees were differentially affected by
354 root grafting and intraspecific competition depending on their size within the union (Fig. 3b).
355 Within two grafted trees, the one with the larger crown and higher evapotranspiration rate

356 probably has a greater ability to divert resources from the communal root system; hence under
357 intraspecific competition, the translocation of resources to smaller trees might be very limited
358 or null (Bormann and Graham 1959, Eis 1972, Loehle and Jones 1990). Sharing a common root
359 system may thus be a constraint to tree growth under highly stressful conditions, especially for
360 the smaller members of a union (Eis 1972). Within grafted trees, when intraspecific competition
361 is low, the smallest trees may benefit from resources through root grafting, but when
362 competition intensifies, these resources are no longer redistributed and this affects growth of
363 the smallest trees. At early stages of balsam fir stand development, tree size and growth are
364 constrained, and they release later when canopy gaps arise (Morin and Laprise 1997, Ruel et al.
365 2003). As intraspecific competition among balsam fir stands was mainly driven by tree size,
366 greater competition pressure might occur later when trees are larger. Thus, under moderate
367 intraspecific competition, delayed root grafting might partially explain the delayed self-thinning
368 of balsam fir stands under high-density of trees. Since root grafts allow the translocation of
369 substances through the phloem (Graham 1960), phytohormones implicated in apical dominance
370 may be translocated between interconnected trees (Schier 1972). Larger trees may thus send
371 signals to smaller trees, reducing growth and stimulating the self-thinning of stands as the
372 proportion of root-grafted trees increases with stand development. This hypothesis is supported
373 by the fact that when the trees were independent (i.e. BG), their growth was greater but once
374 they were grafted the negative effect of competition on growth was rapid and marked (Fig. 2b).
375 A parallel can be drawn with suckering trembling aspen (*Populus tremuloides*) stands, that are
376 initially very dense with stems that are closely interconnected through parental roots
377 (DesRochers and Lieffers 2001, Jelinkova et al. 2009); These stands usually undergo a very
378 rapid and heavy self-thinning (Brown and DeByle 1989). At graft initiation, balsam fir trees
379 were 38 years old on average (Quer et al. 2020), which might explain why the effect of

380 competition occurred later in stand development compared to aspen stands where trees are
381 interconnected right from stand initiation (Schier 1972).

382 In conclusion, this study is the first to demonstrate that root grafting decreased tree growth with
383 increasing intraspecific competition. These results support the idea that root grafting allows
384 trees to respond (and compete) as a group rather than as individual stems and forces us to
385 reconsider traditional forest stand dynamics concepts such as competition, dominance and
386 succession. This is important not only for the fundamental science aspect of it, but also because
387 these findings influence the way that the forest should be managed. As intraspecific competition
388 was mainly driven by tree size and root grafting that occurred tardily in balsam fir stand
389 development, we suggest that apical dominance may be implicated in this effect and that it
390 could explain the delayed self-thinning of balsam fir stands. Further studies on phytohormone
391 translocation between grafted trees could help us better understand the ecological significance
392 of root grafting in forest stands dynamics.

393

394 **Speculations**

395 Since root grafting is of common occurrence in balsam fir stands, there are likely other
396 benefits to being grafted to a neighbor, that may not be directly reflected in individual tree
397 growth. These benefits are probably the evolutionary agents that lead to the selection for the
398 enhanced formation of root grafts (Keeley 1988). We assumed that the ecological significance
399 of root grafting was based on resource translocation between trees but it could also be based on
400 its structural role by improving mechanical support for trees and their root systems (Dosen and
401 Iyer 1979, Stokes et al. 1995). Balsam fir is the main host of spruce budworm (*Choristoneura*
402 *fumiferana* Clem.; Morin et al. 1993), and outbreaks promote higher rates of wind-related
403 mortality by increasing wind penetration in the stand (Taylor and MacLean 2009). Thus, in post

404 outbreak stands root grafting may increase tree stability and constitute a benefit to being grafted
405 to a neighbor.

406 Root grafting could also help trees indirectly “control” their environment by maintaining
407 neighboring trees through root grafts; when suppressed trees die, canopy gaps occur and other
408 opportunistic species could take the available space such as following severe and repeated
409 spruce budworm outbreaks where the canopy becomes sparse. A change in the direction of
410 succession may occur and lead to the dominance of other tree species if they successfully
411 establish in the open spaces left by dead balsam fir trees (Bouchard et al. 2006, Sainte-Marie et
412 al. 2014). However, when dominant trees are grafted to suppressed neighbors or to live stumps,
413 their root systems continue to occupy the soil leaving no space for invasion (Loehle and Jones
414 1990). Root grafting may thus reduce inter-specific competition for water, minerals or light if
415 other trees species are not able to establish (Lev-Yadun 2011). This could be seen as a
416 cooperative relationship to ensure that soil resources of a site remain within the species (Tarroux
417 and DesRochers 2010).

418

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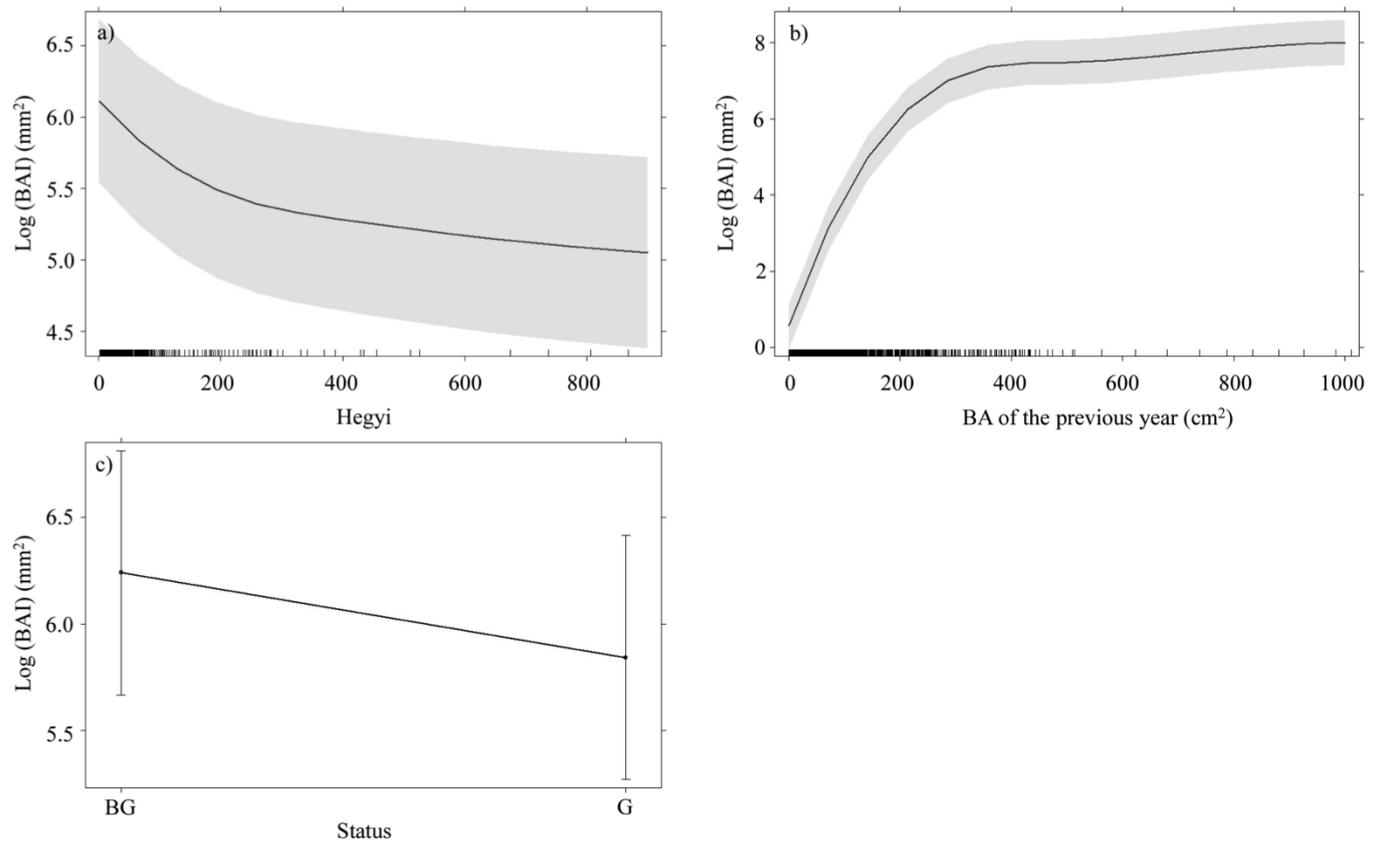
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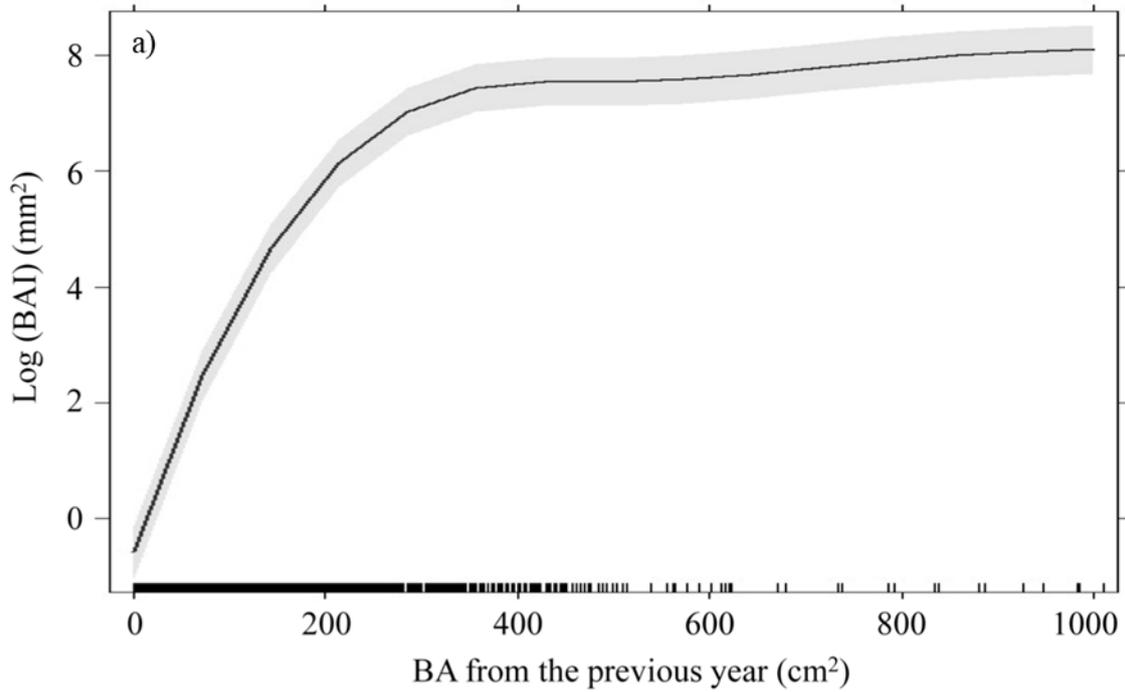
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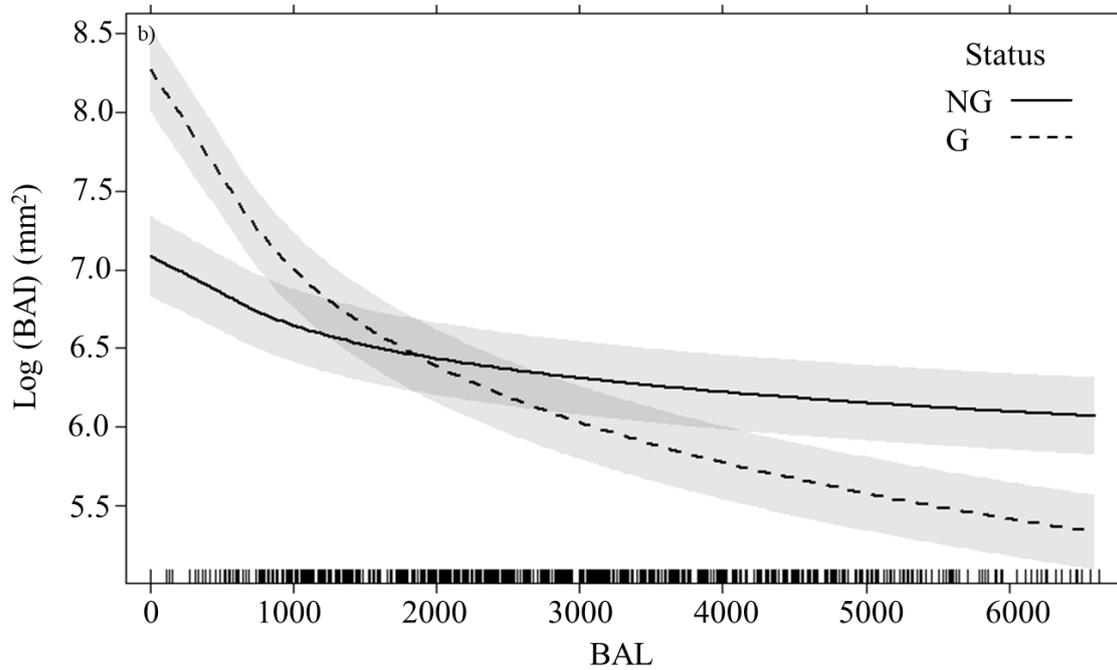


634

635 **Fig. 1.** Predicted effects of: a) Hegyi competition index, b) Basal Area (BA) and c) graft status
 636 (Status) on *Abies balsamea* annual Basal Area Increment (BAI). BG: Before Grafting tree, G:
 637 Grafted. 95% confidence intervals are highlighted in grey. Black straight lines are data and N
 638 = 39.

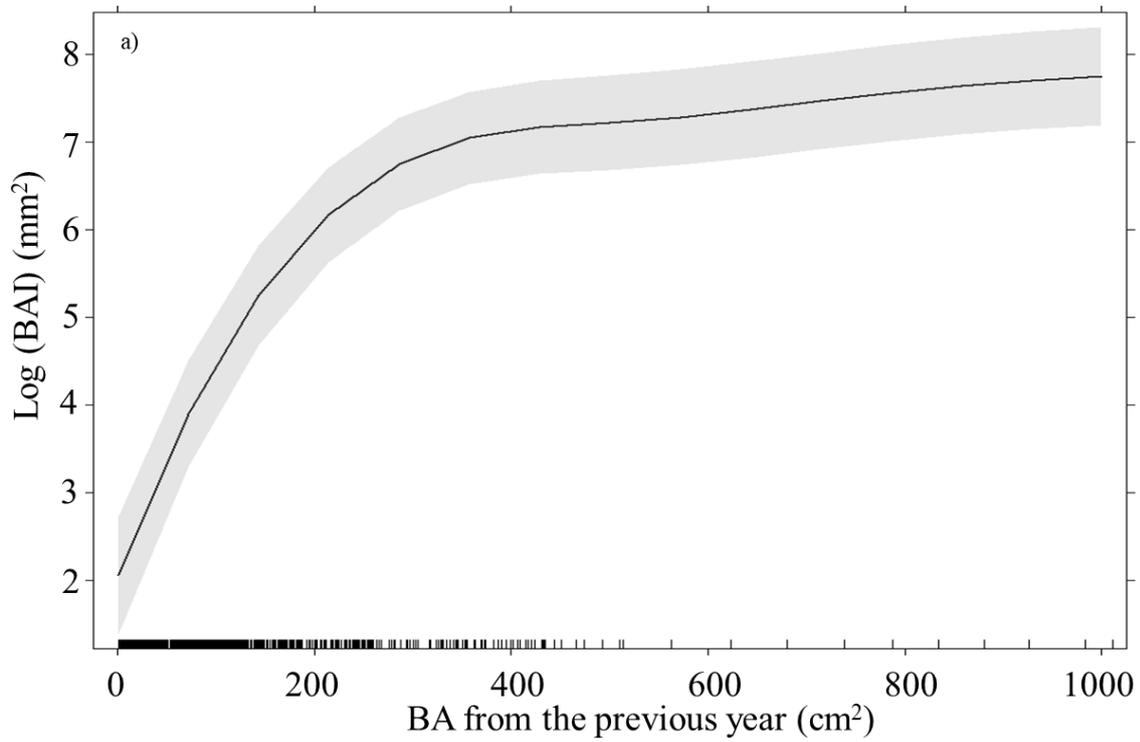


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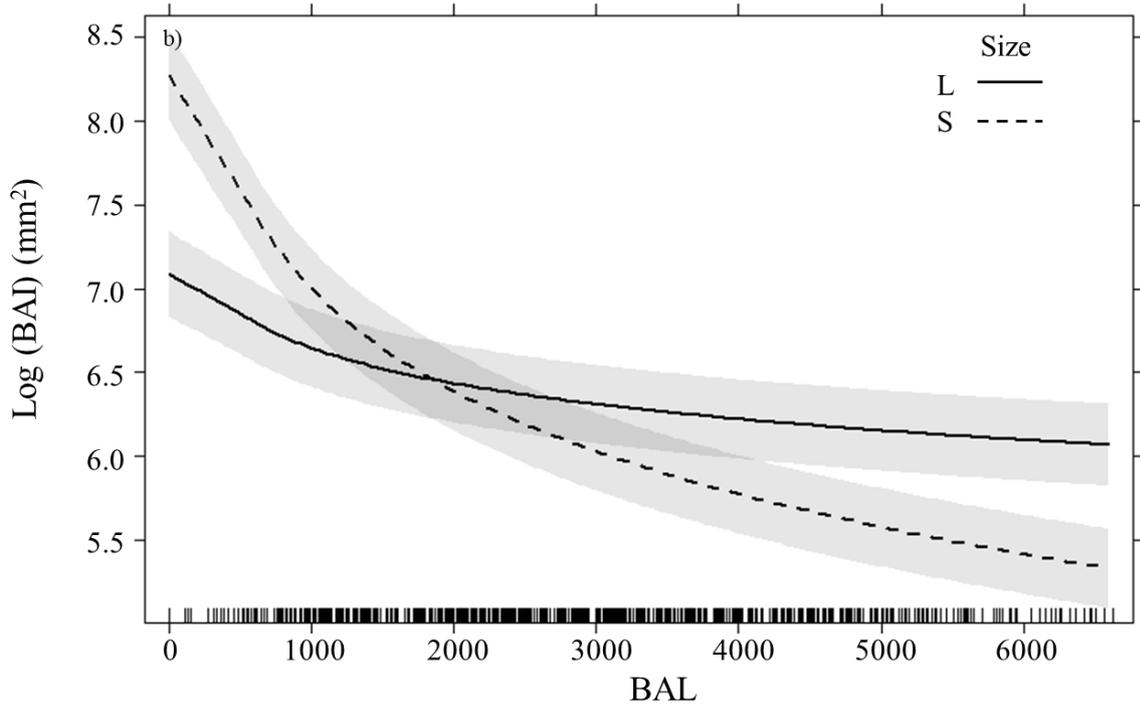


640

641 **Fig. 2.** Predicted effects of: a) Basal Area (BA), b) the interaction between Basal area of the
 642 larger tree (BAL) and graft status (Status) on *Abies balsamea* annual Basal Area Increment
 643 (BAI). G: Grafted, NG: Non-grafted. 95% confidence intervals are highlighted in grey. Black
 644 straight lines are data and N = 110.



645



646

647 **Fig. 3.** Predicted effects of: a) Basal Area (BA), b) the interaction between Basal area of the
 648 larger tree (BAL) and the size of grafted tree within the unions (Size) on *Abies balsamea* annual
 649 Basal Area Increment (BAI). L: Larger tree, S: Smallest tree. 95% confidence intervals are
 650 highlighted in grey. Black straight lines are data and N = 37.

651 **Table 1:** Root grafting occurrence and site characteristics of the three *Abies balsamea*
 652 excavated stands (according to Quer et al. 2020).

Site	S1	S2	S3	Mean	Total
Stand age (years)	36	51	74	54	–
Density (stems ha ⁻¹)	14 200	4800	6000	8 333	–
Number of excavated trees	71	24	30	–	125
Percentage of grafted trees (%) ± SE	32.4	41.7	40.0	36.0 ± 2.86	–
Mean number of grafts per grafted tree	1.3	1.2	1.3	1.3 ± 0.03	–
Mean graft age (years) ± SE	11.7 ± 1.1	11.5 ± 1.3	19.4 ± 2.5	13.6 ± 1.0	–
Mean Basal Area of the Larger trees index (BAL)	5691.7 ± 209.6	3258.7 ± 235.5	3649.5 ± 328.8	4659.9 ± 185.1	–

653

654 **Table 2:** Linear mixed-effects models tested to describe the annual Basal Area Increment (BAI)
 655 of future and grafted *Abies balsamea* according to the competition indexes (HEG and BAL),
 656 the Basal Area of the previous year (BA) and the graft presence (Status). Trees, sites and years
 657 were set as random effects.

Models tested	Marginal R ²	Conditional R ²	AICc
log(BAI) ~ Status	0.102	0.603	4737.42
log(BAI) ~ log(BAL)	0.177	0.723	4606.04
log(BAI) ~ log(HEG)	0.497	0.808	4234.51
Log(BAI)~log(BA)	0.686	0.917	3115.59
log(BAI) ~ log(BAL) + log(BA)	0.704	0.910	3093.26
log(BAI) ~ log(HEG) + log(BA)	0.726	0.914	3058.97
log(BAI) ~ Status + log(BA)	0.704	0.903	3053.69
log(BAI) ~ log(BAL) + log(BA) + Status	0.719	0.899	3033.33
log(BAI) ~ log(HEG) + log(BA) + Status	0.739	0.906	3004.26

Note: Best model selected is in bold. Values of marginal R² and conditional R² of the models tested are shown accounting for fixed and random effects. AICc : Second-order Akaike Information Criterion.

658

659 **Table 3:** Output of the linear mixed-effects model testing the effect of the Basal Area (BA), the
 660 competition index (HEG) and graft status (Status) on the annual Basal Area Increment (BAI)
 661 of grafted and future grafted *Abies balsamea*. Trees, sites and years were fixed as random
 662 effects.

Parameters	Basal area increment		
	Estimates	Std. Errors	P value
(Intercept)	3.887	0.310	***
Status (G)	-0.397	0.050	***
HEG	-0.652	0.088	***
BA	0.750	0.017	***

Note: Parameters, estimated coefficient, standard errors (Std. Errors) and P values of the model are shown. (P values = ***: P < 0.001).

663

664 **Table 4:** Linear mixed-effects models tested to describe the annual Basal Area Increment (BAI)
 665 of grafted and non-grafted *Abies balsamea* according to the competition indexes (HEG and
 666 BAL), the Basal Area of the previous year (BA) and the graft presence (Status). Trees, sites and
 667 years were set as random effects.

Models tested	Marginal R ²	Conditional R ²	AICc
log(BAI) ~ Status	0.029	0.849	6387.10
log(BAI) ~ log(BAL)	0.063	0.853	6226.78
log(BAI) ~ log(HEG)	0.249	0.839	6060.71
Log(BAI) ~log(BA)	0.557	0.895	5731.52
log(BAI) ~ Status + log(BA)	0.677	0.919	4632.29
log(BAI) ~ log(HEG) + log(BA)	0.673	0.916	4631.92
log(BAI) ~ log(BAL) + log(BA)	0.679	0.916	4611.80
log(BAI) ~ log(HEG) + log(BA) + Status	0.681	0.918	4632.71
log(BAI) ~ log(BAL) + log(BA) + Status	0.687	0.919	4612.52
log(BAI) ~ log(HEG) × Status + log(BA)	0.693	0.918	4618.56
log(BAI) ~ log(BAL) × Status + log(BA)	0.699	0.921	4593.91

Note: Best model selected is in bold. Values of marginal R² and conditional R² of the models tested are shown accounting for fixed and random effects. AICc : Second-order Akaike Information Criterion.

668

669 **Table 5:** Output of the linear mixed-effects model testing the effect of the Basal Area (BA) and
 670 the interaction between competition index (BAL) and graft status (Status) on the annual Basal
 671 Area Increment (BAI) of grafted and ungrafted *Abies balsamea*. Trees, sites and years were
 672 fixed as random effects.

Parameters	Basal area increment		
	Estimates	Std. Errors	P value
(Intercept)	3.062	0.240	***
Status (G)	1.975	0.430	***
BAL	-0.175	0.042	***
BA	0.802	0.017	***
BAL × Status (G)	-0.529	0.116	***

Note: Parameters, estimated coefficient, standard errors (Std. Errors) and P values of the model are shown. (P values = ***: P < 0.001).

673

674

675 **Table 6:** Linear mixed-effects models tested to describe the annual Basal Area Increment (BAI)
676 of grafted *Abies balsamea* according to the competition indexes (HEG and BAL), the Basal
677 Area of the previous year (BA) and the size of trees within unions (Size). Trees, sites and years
678 were set as random effects.

Models tested	Marginal R ²	Conditional R ²	AICc
log(BAI) ~ log(HEG)	0.138	0.918	899.49
log(BAI) ~ Size	0.146	0.92	893.63
log(BAI) ~ BA	0.418	0.92	795.39
log(BAI) ~ Size + log(BA)	0.499	0.922	791.31
log(BAI) ~ log(HEG) + log(BA)	0.705	0.94	718.78
log(BAI) ~ log(BAL) + log(BA)	0.698	0.94	717.15
log(BAI) ~ log(BAL)	0.756	0.957	667.24
log(BAI) ~ log(HEG) + log(BA) + Size	0.746	0.957	662.18
log(BAI) ~ log(BAL) + log(BA) + Size	0.723	0.957	660.92
log(BAI) ~ log(HEG) × Size + log(BA)	0.751	0.957	660.82
log(BAI) ~ log(BAL) × Size + log(BA)	0.698	0.939	646.21

Note: Best model selected is in bold. Values of marginal R² and conditional R² of the models tested are shown accounting for fixed and random effects. AICc : Second-order Akaike Information Criterion.

679

680 **Table 7:** Output of the linear mixed-effects model testing the effect of the Basal Area (BA) and
 681 the interaction between competition index (BAL) and size of grafted tree (Size) on the annual
 682 Basal Area Increment (BAI) of grafted *Abies balsamea*. Trees, sites and years were fixed as
 683 random effects.

Parameters	Basal area increment		
	Estimates	Std. Errors	P value
(Intercept)	5.046	0.240	***
Size (S)	4.364	0.529	***
BAL	-0.709	0.155	**
BA	0.767	0.043	***
BAL × Size (S)	-1.336	0.150	***

Note: Parameters, estimated coefficient, standard errors (Std. Errors) and P values of the model are shown. (P values = ***: P < 0.001 ; **: P < 0.01).

684