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► To cite this version:

Elodie Quer, Manon Helluy, Virginie Baldy, Annie Desrochers. Does natural root grafting make trees better competitors?. *Oikos*, 2022, 2022 (12), pp.e09666. <10.1111/oik.09666>. <hal-04043031>

HAL Id: hal-04043031

<https://amu.hal.science/hal-04043031v1>

Submitted on 4 Apr 2023

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

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20

Abstract

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

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

Introduction

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

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

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

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

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

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

Material and methods

Study sites

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

Tree radial growth analyses by tree ring width series measurement

Field work was performed in summer 2017. At each site, all trees were felled with a chainsaw and cross-sectional disks were collected at ground level (0 m). Cross-sectional disks were air dried and sanded (80-400 grit) to reveal growth rings. Tree ring widths series were measured on cross-sectional disks from the stem base using a Velmex “TA Unislide” measurement system with ACU-Rite linear encoder and QC10V digital readout device (Velmex, Inc., Bloomfield, New York) interfaced with Measure J2X (Version 5.0x) ring-reading software (Project J2X, Voortech Consulting, Holderness, NH). Ring-width series were measured with 0.001 mm precision along two rays per wood disk when possible (i.e. when the rings were clearly visible) and visually cross-dated. To obtain a single series per tree, chronologies were averaged for each tree when two of them were available. A total of 110 tree ring width series were obtained. Tree age and stem size increasing over time promotes a decline of tree ring width along cross-sectional radius. To avoid this biological trend, we converted tree ring width series into basal area increment (BAI) to calculate annual tree growth (Biondi and Qeadan 2008) following equation (1) :

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

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

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

Intraspecific competition measurements by using competition indices

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

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

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

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

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

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

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

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

Results

Does root grafting improve tree growth?

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

Tree grafting status (i.e. Status), intraspecific competition (i.e. HEG) and tree size (i.e. BA) significantly affected annual radial growth of trees (i.e. BAI, LMER, $P < 0.001$, Table 3 and Fig. 1). Grafted trees (i.e. G) exhibited 0.40 mm² lower BAI than the average BAI of future grafted trees (i.e. BG, Table 3 and Fig. 1c). HEG had a negative effect on BAI (Table 3 and Fig. 1a), where a 1% increase in HEG induced a 0.65% reduction in BAI. Tree growth (i.e. BAI) increased with tree size (i.e. BA, Table 3). From 0 to 400 cm², tree growth (i.e. BAI)

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

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

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

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

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

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

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

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

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

Discussion

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

Future grafted trees had better growth rate than trees that would never form root grafts, 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

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

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

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

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

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

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

Speculations

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

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

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

References

- Adonsou, K. E., I. Drobyshev, A. DesRochers, and F. Tremblay. 2016. Root connections affect radial growth of balsam poplar trees. *Trees* 30:1775–1783. <https://doi.org/10.1007/s00468-016-1409-2>.
- Agriculture Canada Expert Committee on Soil Survey. 1987. The Canadian system of soil classification, 1646, 164. Research Branch, Agriculture Canada, Ottawa, Ontario.
- Armson, K. A. and Van Den Driessche, R. 1959. Natural root grafts in red pine (*Pinus resinosa* Ait.). *For. Chron.* 35:232–241. <https://doi.org/10.5558/tfc35232-3>.
- Bader, M. K.-F., and S. Leuzinger. 2019. Hydraulic coupling of a leafless kauri tree remnant to conspecific hosts. *iScience* 19:1238–1247. <https://doi.org/10.1016/j.isci.2019.05.009>.
- Baker, F. S. 1949. A revised tolerance table. *J. For.* 47:179–178. <https://doi.org/10.1093/jof/47.3.179>.
- Baric, S., C. Kerschbamer, J. Vigl, and J. Dalla Via. 2008. Translocation of apple proliferation phytoplasma via natural root grafts – a case study. *Eur. J. Plant. Pathol.* 121:207–211. <https://doi.org/10.1007/s10658-007-9256-z>.
- Barton, K. 2020. MuMIn: Multi-Model Inference. <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Basnet, K., F. N. Scatena, G. E. Likens, and A. E. Lugo. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo experimental forest, Puerto Rico. *Biotropica* 25:28. <https://doi.org/10.2307/2388976>.
- Bates, D., M. Maechler, B. Bolker, and S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, J. Fox, A. Bauer, and P. N. K. Krivisky. 2020. lme4: Linear Mixed-Effects Models using 'Eigen' and S4. <https://cran.r-project.org/web/packages/lme4/index.html>.

443 Biging, G. S., and M. Dobbertin. 1995. Evaluation of competition indices in individual tree
 444 growth models. *For. Sci.* 41:360–377. <https://doi.org/10.1093/forestscience/41.2.360>.
 445 Biondi, F., and F. Qeadan. 2008. A theory-driven approach to tree-ring standardization:
 446 defining the biological trend from expected Basal Area Increment. *Tree-Ring Res.*
 447 64:81–96. <https://doi.org/10.3959/2008-6.1>.
 448 Bormann, F. H. and Graham, B. F. 1959. The occurrence of natural root grafting in eastern
 449 white pine, *Pinus Strobus* L., and its ecological implications. *Ecology* 40:677–691.
 450 <https://doi.org/10.2307/1929820>.
 451 Bormann, F. H. 1966. The structure, function, and ecological significance of root grafts in *Pinus*
 452 *strobus* L. *Ecol. Monogr.* 36:1–26. <https://doi.org/10.2307/1948486>.
 453 Bouchard, M., D. Kneeshaw, and Y. Bergeron. 2006. Forest dynamics after successive spruce
 454 budworm outbreaks in mixedwood forests. *Ecology* 87:2319–2329.
 455 [https://doi.org/10.1890/0012-9658\(2006\)87\[2319:FDASSB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2319:FDASSB]2.0.CO;2).
 456 Brooker, R. W. 2006. Plant-plant interactions and environmental change. *New Phytol.*
 457 171:271–284. <https://doi.org/10.1111/j.1469-8137.2006.01752.x>.
 458 Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P.
 459 Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket,
 460 S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K.
 461 Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant
 462 communities: the past, the present, and the future. *J. Ecol.* 96:18–34.
 463 <https://doi.org/10.1111/j.1365-2745.2007.01295.x>.
 464 Brown, J.K., and N. V. DeByle. 1989. Effects of prescribed fire on biomass and plant
 465 succession in western aspen. Research Paper INT-412. US Department of Agriculture,
 466 Forest Service, Intermountain Forest and Range Experiment Station.

- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America. Volume 1. Conifers.* Agriculture Handbook, Washington, USA.
- Connolly, J., and P. Wayne. 1996. Asymmetric competition between plant species. *Oecologia* 108:311–320. <https://doi.org/10.1007/BF00334656>.
- Contreras, M. A. 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *For. Ecol. Manage.* 11:1939–1949. <https://doi.org/10.1016/j.foreco.2011.08.031>.
- DesRochers, A., and V. J. Lieffers. 2001. The coarse-root system of mature *Populus tremuloides* in declining stands in Alberta, Canada. *J. Veg. Sci.* 12:355–360. <https://doi.org/10.1139/cjfr-31-6-1012>.
- Dosen, R. C., and J. G. Iyer. 1979. Effect of grafted roots of stumps on the growth of a thinned red pine plantation. *Tree Plant. Notes* 30:1–3.
- Duchesneau, R., I. Lesage, C. Messier, and H. Morin. 2001. Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *For. Ecol. Manage.* 140:215–225. [https://doi.org/10.1016/S0378-1127\(00\)00281-4](https://doi.org/10.1016/S0378-1127(00)00281-4).
- Eis, S. 1972. Root grafts and their silvicultural implications. *Can. J. For. Res.* 2:111–120. <https://doi.org/10.1139/x72-022>.
- Environment and Natural Resources Canada. 2019. Canadian climate normal 1981–2010 station data. https://climat.meteo.gc.ca/climate_normals/results_1981_2010_f.html?searchType=stnName&txtStationName=amos&searchMethod=contains&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=6019&dispBack=1. Accessed 17 Oct 2019.

491 Epstein, A. H. 1978. Root graft transmission of tree pathogens. *Annu. Rev. Phytopathol.*
 492 16:181–192. <https://doi.org/10.1146/annurev.py.16.090178.001145>.

493 Fox, J., S. Weisberg, B. Price, M. Friendly, J. Hong, R. Andersen, D. Firth, S. Taylor, and R
 494 Core Team. 2020. effects: effect displays for linear, generalized linear, and other
 495 models. <https://cran.r-project.org/web/packages/effects/index.html>.

496 Fraser, E. C., V. J. Lieffers, and S. M. Landhäusser. 2005. Age, stand density, and tree size as
 497 factors in root and basal grafting of lodgepole pine. *Can. J. Bot.* 83:983–988.
 498 <https://doi.org/10.1139/b05-048>.

499 Fraser, E. C., V. J. Lieffers, and S. M. Landhäusser. 2006. Carbohydrate transfer through root
 500 grafts to support shaded trees. *Tree physiol.* 26:1019–1023.
 501 <https://doi.org/10.1093/treephys/26.8.1019>.

502 Freckleton, R. P., and A. R. Watkinson. 2001. Asymmetric competition between plant species.
 503 *Funct. Ecol.* 15:615–623. <https://doi.org/10.1046/j.0269-8463.2001.00558.x>.

504 Gaspard, D. T., and A. DesRochers. 2020. Natural root grafting in hybrid poplar clones.
 505 *Trees*:1–10. <https://doi.org/10.1007/s00468-020-01966-z>.

506 Graham, B. F. 1960. Transfer of dye through natural root grafts of *Pinus strobus* L. *Ecology*
 507 41:56–64. <https://doi.org/10.2307/1931939>.

508 Graham, B. F., and F. H. Bormann. 1966. Natural root grafts. *Bot. Rev.* 32:255–292.

509 Grondin, P., C. Anseau, L. Bélanger, J. Bergeron, Y. Bergeron, A. Bouchard, J. Brisson, L.
 510 De Grandpré, G. Gagnon, and C. Lavoie. 1996. Cadre bioclimatique de référence des
 511 régions écologiques du Québec. *Manuel de Foresterie*. Québec, Canada: Les Presses de
 512 l'Université Laval:134–279.

513 Hegyi, F. 1974. A simulation model for managing jack-pine stands. Pages 74–90 *Growth*
 514 *Models for Tree and Stand Simulation*. J. Fries. Royal College of Forestry, Stockholm.

515 Helluy, M., B. Prévosto, M. Cailleret, C. Fernandez, and P. Balandier. 2020. Competition and
 516 water stress indices as predictors of *Pinus halepensis* Mill. radial growth under drought.
 517 For. Ecol. Manage. 460:117877. <https://doi.org/10.1016/j.foreco.2020.117877>.
 518 Jelinkova, H., F. Tremblay, and A. DesRochers. 2009. Molecular and dendrochronological
 519 analysis of natural root grafting in *Populus tremuloides* (Salicaceae). Am. J. Bot.
 520 96:1500–1505. <https://doi.org/10.3732/ajb.0800177>.
 521 Keeley, J. E. 1988. Population variation in root grafting and a hypothesis. Oikos 52:364.
 522 <https://doi.org/10.2307/3565212>.
 523 Klein, T., R. T. W. Siegwolf, and C. Korner. 2016. Belowground carbon trade among tall trees
 524 in a temperate forest. Science 352:342–344. <https://doi.org/10.1126/science.aad6188>.
 525 Kunstler, G., D. Falster, D. A. Coomes, F. Hui, R. M. Kooyman, D. C. Laughlin, L. Poorter,
 526 M. Vanderwel, G. Vieilledent, S. J. Wright, M. Aiba, C. Baraloto, J. Caspersen, J. H. C.
 527 Cornelissen, S. Gourlet-Fleury, M. Hanewinkel, B. Herault, J. Kattge, H. Kurokawa, Y.
 528 Onoda, J. Peñuelas, H. Poorter, M. Uriarte, S. Richardson, P. Ruiz-Benito, I.-F. Sun, G.
 529 Ståhl, N. G. Swenson, J. Thompson, B. Westerlund, C. Wirth, M. A. Zavala, H. Zeng,
 530 J. K. Zimmerman, N. E. Zimmermann, and M. Westoby. 2016. Plant functional traits
 531 have globally consistent effects on competition. Nature 529:204–207.
 532 <https://doi.org/10.1111/j.1461-0248.2012.01803.x>.
 533 Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen and S. P. Jensen. 2020. lmerTest:
 534 Tests in linear mixed effects models. [https://cran.r-](https://cran.r-project.org/web/packages/lmerTest/index.html)
 535 [project.org/web/packages/lmerTest/index.html](https://cran.r-project.org/web/packages/lmerTest/index.html).
 536 La Rue, C. D. 1952. Root-grafting in tropical trees. Science 115:296–296.
 537 <https://doi.org/10.1126/science.115.2985.296>.
 538 Lev-Yadun, S. 2011. Why should trees have natural root grafts? Tree Physiol. 31:575–578.
 539 <https://doi.org/10.1093/treephys/tpr061>.

540 Loehle, C., and R. H. Jones. 1990. Adaptive significance of root grafting in trees. *Funct. Ecol.*
 541 4:268–271. <https://www.jstor.org/stable/2389347>.
 542 Lorimer, C. G. 1983. Tests of age-independent competition indices for individual trees in
 543 natural hardwood stands. *For. Ecol. Manage.* 6:343–360. [https://doi.org/10.1016/0378-](https://doi.org/10.1016/0378-1127(83)90042-7)
 544 1127(83)90042-7.
 545 Lortie, C. J., R. W. Brooker, P. Choler, Z. Kikvidze, R. Michalet, F. I. Pugnaire, and R. M.
 546 Callaway. 2004. Rethinking plant community theory. *Oikos* 107:433–438.
 547 <https://doi.org/10.1111/j.0030-1299.2004.13250.x>.
 548 MacFarlane, D. W., and R. K. Kobe. 2006. Selecting models for capturing tree-size effects on
 549 growth–resource relationships. *Can. J. For. Res.* 36:1695–1704.
 550 <https://doi.org/10.1139/x06-054>.
 551 Mazerolle, M. J. 2020. AICcmodavg: Model selection and multimodel inference based on
 552 (Q)AIC(c). <https://cran.r-project.org/web/packages/AICcmodavg/index.html>.
 553 McIntire, E. J. B., and A. Fajardo. 2011. Facilitation within species: a possible origin of group-
 554 selected superorganisms. *Am. Nat.* 178:88–97. <https://doi.org/10.1086/660286>.
 555 McIntire, E. J. B., and A. Fajardo. 2014. Facilitation as a ubiquitous driver of biodiversity. *New*
 556 *Phytol.* 201:403–416. <https://doi.org/10.1111/nph.12478>.
 557 Morin, H., and D. Laprise. 1997. Seedling bank dynamics in boreal balsam fir forests. *Can. J.*
 558 *For. Res.* 27:1442–1451. <https://doi.org/10.1139/x97-113>.
 559 Morin, H., D. Laprise, and Y. Bergeron. 1993. Chronology of spruce budworm outbreaks near
 560 Lake Duparquet, Abitibi region, Québec. *Can. J. For. Res.* 23:1497–1506.
 561 <https://doi.org/10.1139/x93-189>.
 562 Mudge, K., J. Janick, S. Scofield, and E. E. Goldschmidt. 2009. A history of grafting. Pages
 563 437–493 in J. Janick, editor. *Horticultural Reviews*. John Wiley & Sons, Inc., Hoboken,
 564 NJ, USA. <https://doi.org/10.1002/9780470593776.ch9>.

565 O'Neal, E. S., and D. D. Davis. 2015. Intraspecific root grafts and clonal growth within
 566 *Ailanthus altissima* stands influence *Verticillium nonalfalfae* transmission. *Plant Dis.*
 567 99:1070–1077. <https://doi.org/10.1094/PDIS-07-14-0722-RE>.
 568 Pretzsch, H., and P. Biber. 2010. Size-symmetric versus size-asymmetric competition and
 569 growth partitioning among trees in forest stands along an ecological gradient in central
 570 Europe. *Can. J. For. Res.* 40:370–384. <https://doi.org/10.1139/X09-195>.
 571 Prevosto, B. 2005. Les indices de compétition en foresterie : exemples d'utilisation, intérêts et
 572 limites. *Rev. For. Française*:413–430. <https://doi.org/10.4267/2042/5062>.
 573 Quer, E., V. Baldy, and A. DesRochers. 2020. Ecological drivers of root grafting in balsam fir
 574 natural stands. *For. Ecol. Manage.* 475:118388.
 575 <https://doi.org/10.1016/j.foreco.2020.118388>.
 576 R Core Team. 2019. R: A language and environment for statistical computing. R Foundation
 577 for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
 578 Reynolds, K. M., and W.J. Bloomberg. 1982. Estimating probability of intertree root contact in
 579 second-growth Douglas-fir. *Can. J. For. Res.* 12: 493–498. <https://doi.org/10.1139/x82->
 580 077.
 581 Rigg, G. B., and E. S. Harrar. 1931. The root systems of trees growing in sphagnum. *Am. J.*
 582 *Bot.* 18:391–397. <https://doi.org/10.1002/j.1537-2197.1931.tb09598.x>.
 583 Ruel, J.-C., C. Larouche, and A. Achim. 2003. Changes in root morphology after
 584 precommercial thinning in balsam fir stands. *Can. J. For. Res.* 33:2452–2459.
 585 <https://doi.org/10.1139/x03-178>.
 586 Sainte-Marie, G., D. Kneeshaw, D. MacLean, and C. Hennigar. 2014. Estimating forest
 587 vulnerability to the next spruce budworm outbreak: Will past silvicultural efforts pay
 588 dividends? *Can. J. For. Res.* 45:314–324. <https://doi.org/10.1139/cjfr-2014-0344>.

589 Salomón, R. L., E. Tarroux, and A. DesRochers. 2016. Natural root grafting in *Picea mariana*
 590 to cope with spruce budworm outbreaks. *Can. J. For. Res.* 46:1059–1066.
 591 <https://doi.org/10.1139/cjfr-2016-0121>.

592 Schier, G. A. 1972. Apical dominance in multishoot cultures from aspen roots. *Forest Science*
 593 18:147–149.

594 Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry
 595 in competition among plants. *Oecologia* 113:447–455.
 596 <https://doi.org/10.1007/s004420050397>.

597 Signorell, A., K. Aho, A. Alfons, N. Anderegg, T. Aragon, and A. Arppe. 2020. DescTools:
 598 Tools for descriptive statistics. [https://cran.r-](https://cran.r-project.org/web/packages/DescTools/index.html)
 599 [project.org/web/packages/DescTools/index.html](https://cran.r-project.org/web/packages/DescTools/index.html).

600 Stadt, K. J., C. Huston, K. D. Coates, Z. Feng, M. R. T. Dale, and V. J. Lieffers. 2007.
 601 Evaluation of competition and light estimation indices for predicting diameter growth
 602 in mature boreal mixed forests. *Ann. For. Sci.* 64:477–490.
 603 <https://doi.org/10.1051/forest:2007025>.

604 Stokes, A., A. H. Fitter, and M. P. Courts. 1995. Responses of young trees to wind and shading:
 605 effects on root architecture. *J. Exp. Bot.* 46:1139–1146.
 606 <https://doi.org/10.1093/jxb/46.9.1139>.

607 Tarroux, E., and A. DesRochers. 2010. Frequency of root grafting in naturally and artificially
 608 regenerated stands of *Pinus banksiana*: influence of site characteristics. *Can. J. For. Res.*
 609 40:861–871. <https://doi.org/10.1139/X10-038>.

610 Tarroux, E., and A. DesRochers. 2011. Effect of natural root grafting on growth response of
 611 jack pine (*Pinus banksiana*; *Pinaceae*). *Am. J. Bot.* 98:967–974.
 612 <https://doi.org/10.3732/ajb.1000261>.

- Tarroux, E., A. DesRochers, and C. Krause. 2010. Effect of natural root grafting on growth response of jack pine (*Pinus banksiana*) after commercial thinning. *For. Ecol. Manage.* 260:526–535. <https://doi.org/10.1016/j.foreco.2010.05.008>.
- Taylor, S. L., and D. A. MacLean. 2009. Legacy of insect defoliators: increased wind-related mortality two decades after a spruce budworm outbreak. *For. Sci.* 55:256–267. <http://doi.org/10.1093/forestscience/55.3.256>.
- Valladares, F., C. C. Bastias, O. Godoy, E. Granda, and A. Escudero. 2015. Species coexistence in a changing world. *Front. Plant Sci.* 6:866. <https://doi.org/10.3389/fpls.2015.00866>.
- Vincent, J.-S., and L. Hardy. 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. *Rev. Geogr. Montr.* 31:357–372. <https://doi.org/10.7202/1000283ar>.
- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends. Ecol. Evol.* 5:360–364. [https://doi.org/10.1016/0169-5347\(90\)90095-U](https://doi.org/10.1016/0169-5347(90)90095-U).
- Wimmler, M.-C., A. G. Vovides, R. Peters, M. Walther, N. Nadezhdina, and U. Berger. 2022. Root grafts matter for inter-tree water exchange – a quantification of water translocation between root grafted mangrove trees using field data and model-based indications. *Ann. Bot.* 20:1–14. <https://doi.org/10.1093/aob/mcac074>.
- Wykoff, W. R., N. L. Crookston, and A. R. Stage. 1982. User's Guide to the Stand Prognosis Model. General Technical Report INT-133. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

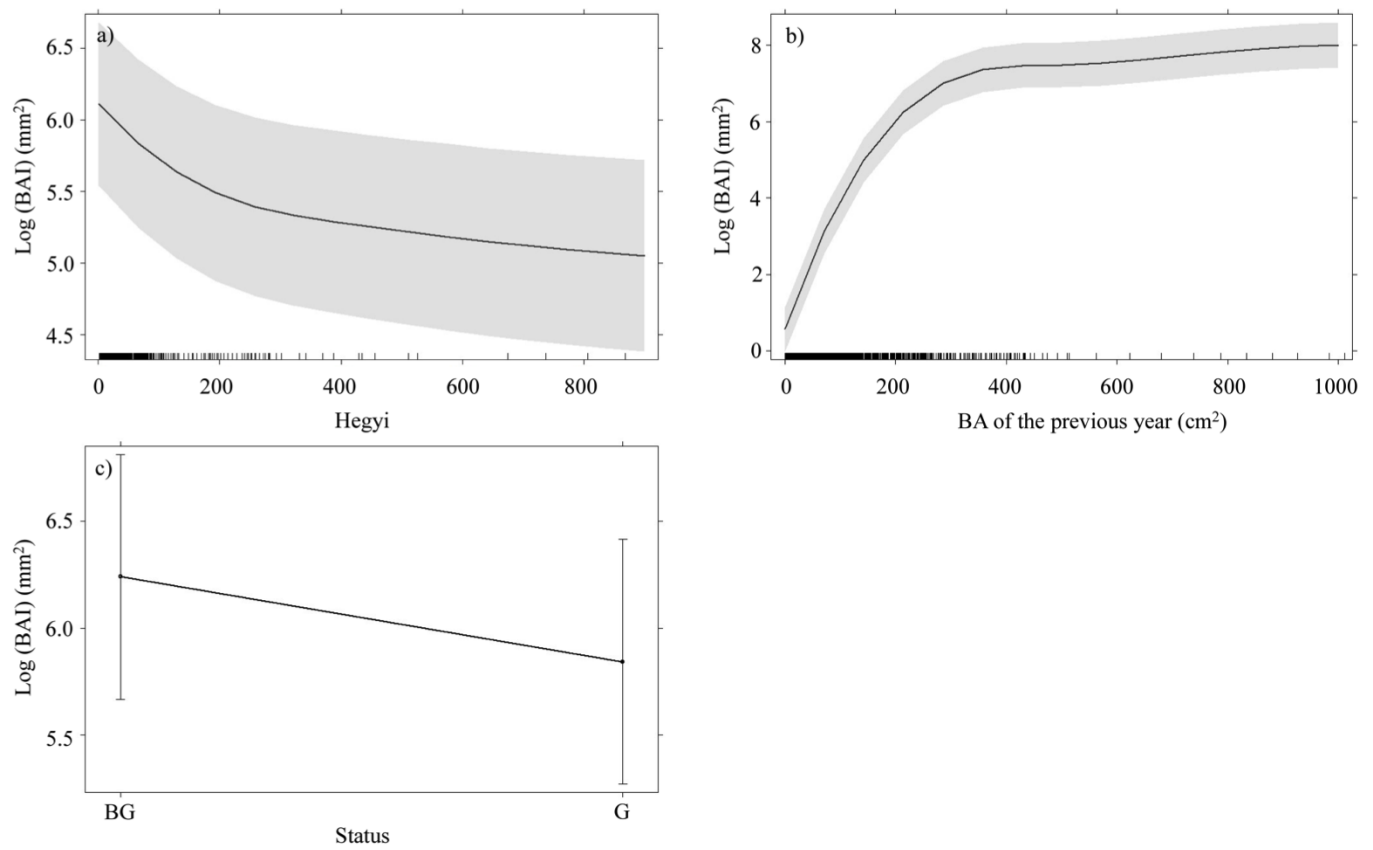


Fig. 1. Predicted effects of: a) Hegyi competition index, b) Basal Area (BA) and c) graft status (Status) on *Abies balsamea* annual Basal Area Increment (BAI). BG: Before Grafting tree, G: Grafted. 95% confidence intervals are highlighted in grey. Black straight lines are data and N = 39.

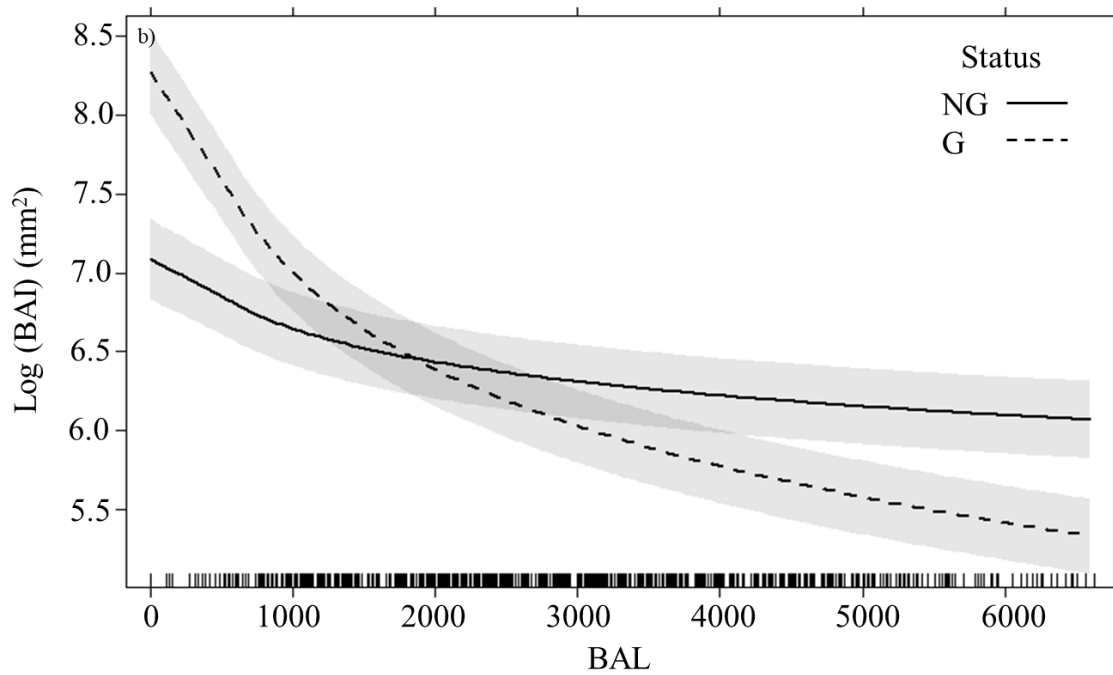
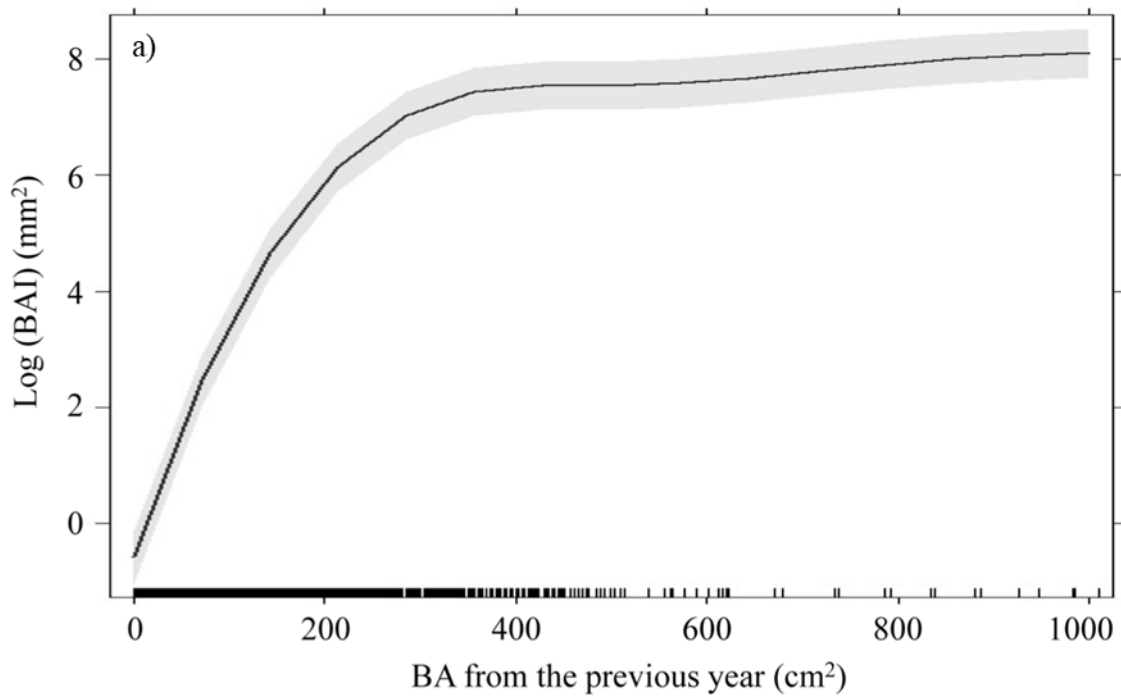


Fig. 2. Predicted effects of: a) Basal Area (BA), b) the interaction between Basal area of the larger tree (BAL) and graft status (Status) on *Abies balsamea* annual Basal Area Increment (BAI). G: Grafted, NG: Non-grafted. 95% confidence intervals are highlighted in grey. Black straight lines are data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

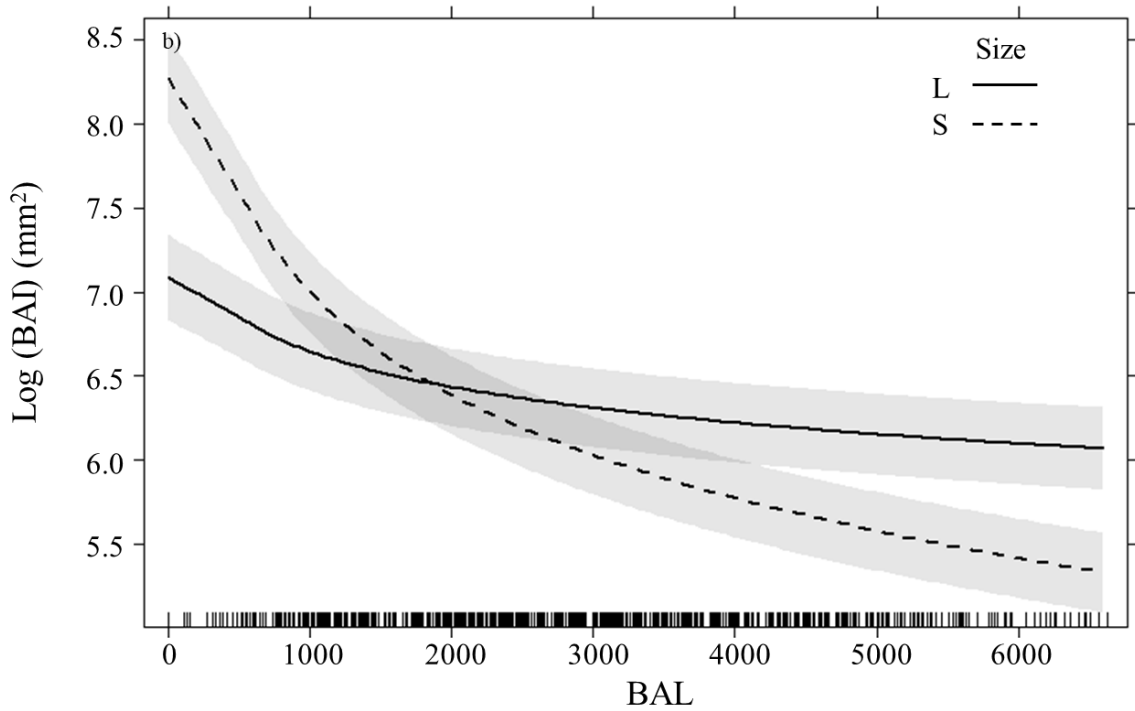
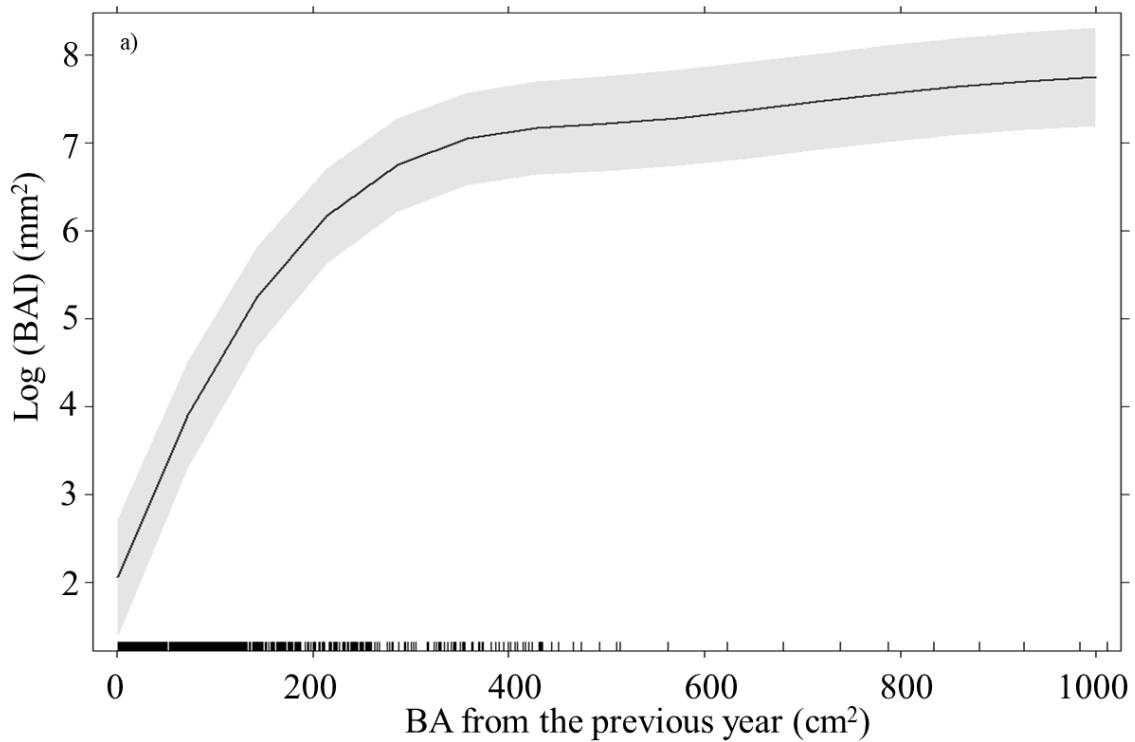


Fig. 3. Predicted effects of: a) Basal Area (BA), b) the interaction between Basal area of the larger tree (BAL) and the size of grafted tree within the unions (Size) on *Abies balsamea* annual Basal Area Increment (BAI). L: Larger tree, S: Smallest tree. 95% confidence intervals are highlighted in grey.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

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

Table 3: Output of the linear mixed-effects model testing the effect of the Basal Area (BA), the competition index (HEG) and graft status (Status) on the annual Basal Area Increment (BAI) of grafted and future grafted *Abies balsamea*. Trees, sites and years were fixed as random 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 = ***: $P < 0.001$).

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

Table 5: Output of the linear mixed-effects model testing the effect of the Basal Area (BA) and the interaction between competition index (BAL) and graft status (Status) on the annual Basal Area Increment (BAI) of grafted and ungrafted *Abies balsamea*. Trees, sites and years were 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 $\times$ Status (G)	-0.529	0.116	***

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

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.

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Table 7: Output of the linear mixed-effects model testing the effect of the Basal Area (BA) and the interaction between competition index (BAL) and size of grafted tree (Size) on the annual Basal Area Increment (BAI) of grafted *Abies balsamea*. Trees, sites and years were fixed as 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 $\times$ Size (S)	-1.336	0.150	***

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