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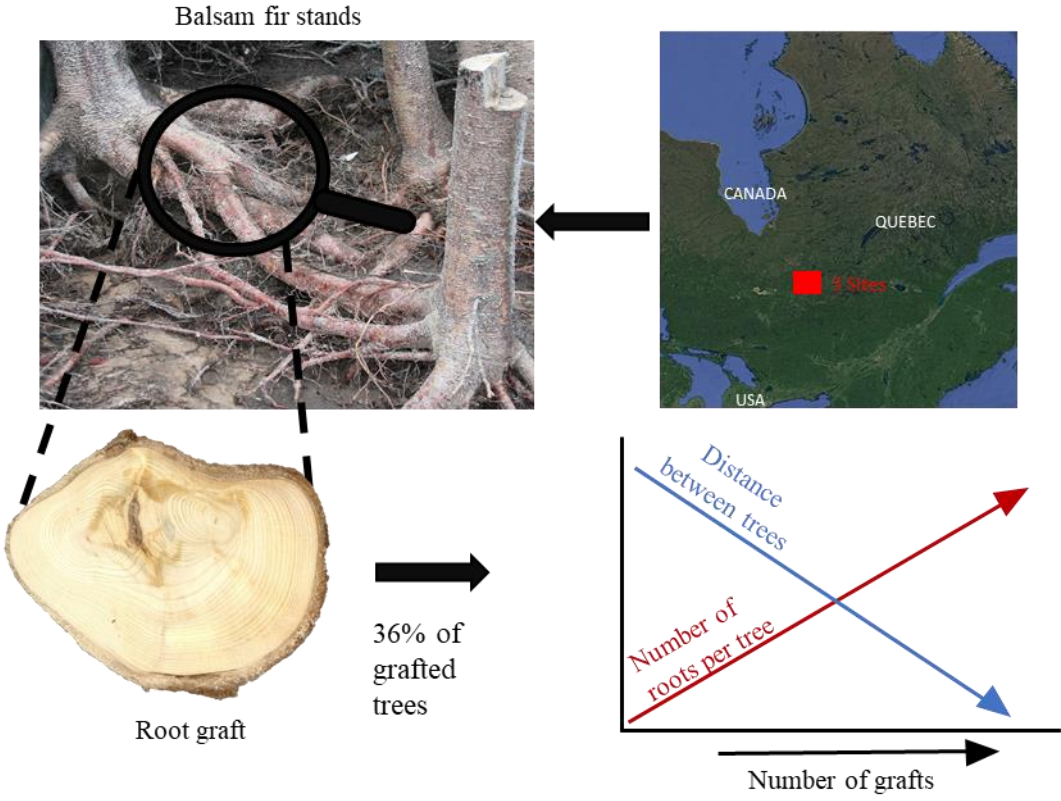


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Highlights

- Root systems of 3 balsam fir stands were excavated in the boreal forest of Quebec.
- Frequency and conditions conducive to natural root grafting were characterized.
- 36% of trees were grafted with another tree, corresponding to 1.3 grafts per tree.
- Tree proximity and number of roots per tree increased root grafting frequency.
- Grafts formed between trees from 12 to 106 years old.

Graphical abstract :



Ecological drivers of root grafting in balsam fir natural stands

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Abstract

Natural root grafts (anastomoses) result from the fusion of the vascular systems of two roots and allow trees to share water, nutrients and photosynthesis products, affecting tree growth and physiology. The aim of this study was to investigate the frequency of root grafting in balsam fir (*Abies balsamea* (L.) Mill) of the boreal forest of Quebec (Canada), and to identify ecological drivers such as tree proximity or size of stems and roots. One 50 m² area was hydraulically excavated in each of three natural balsam fir stands of various ages, tree diameters and densities. For each area, we measured the number of roots and grafts per tree, and the diameter and age of all stems, roots and grafts using dendrochronology techniques. Percentages of grafted trees and number of grafts per tree were similar between stands, corresponding to 36% (± 2.86 SE) and 1.30 (± 0.03 SE), respectively. Root grafting occurred at a wide range of tree ages from 12 to 106 years old. Mean distance between grafted trees was 47.91 cm (± 5.10 SE) and we did not observe any graft beyond a 2 m distance between trees. The number of grafts per tree increased with number of roots per tree and decreased with distance between trees. Root grafting also occurred at a wide range of root ages, from 5 to 64 years old. However, roots were relatively small at graft initiation, with an average root diameter of 3.94 cm (± 0.33 SE). These results demonstrate that balsam fir stands are highly connected through root grafting, occurring early in stand development and continuing throughout the life of the stands. The number of roots per tree and distance between trees were the best predictors for root grafting.

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

1. Introduction

Although competition for resources is commonly considered as the main tree interaction in forest ecosystems, it is increasingly understood that trees may interact in more complex ways via “root connections” (Klein et al., 2016; Lortie et al., 2004; McIntire and Fajardo, 2011). Mycorrhizal and suckering networks interconnecting indirectly root systems through fungal hyphae or directly through parental roots have been highlighted to alter forest stand dynamics by allowing exchanges of resources between trees (Adonsou et al., 2016a; Baret and DesRochers, 2011; Leake et al., 2004; Simard and Durall, 2004). However, root grafting, i.e. the fusion of the vascular system of two or more roots generally from the same species but also rarely between different species, constitutes another underestimated pathway for resource exchanges (Graham and Bormann, 1966; Lev-Yadun, 2011; Mudge et al., 2009). This phenomenon has been reported in nearly 200 perennial woody species in diverse habitats worldwide (Graham and Bormann, 1966; La Rue, 1952). Grafted trees, through an extended common root system, have reinforced mechanical support and are able to exchange water, nutrients, photosynthates but also pathogens (Bader and Leuzinger, 2019; Fraser et al., 2006; O’Neal and Davis, 2015). Grafted trees are thus not only in competition for resources but also in cooperation or facilitation (Eis, 1972; Keeley, 1988; Loehle and Jones, 1990; McIntire and Fajardo, 2011). It has been shown that the redistribution of resources between trees by a common root system can lead to increased tree growth and to delayed tree mortality (Adonsou et al., 2016b; Tarroux and DesRochers, 2011). Root grafting could thus be considered as an adaptive strategy to cope with environmental heterogeneity and disturbances, or as an adaptation to intense tree competition leading to a complex community structure and competitive ability (Adonsou et al., 2016b; Baret and DesRochers, 2011; Jelinkova et al., 2012; Salomón et al., 2016). In order to better understand the mechanisms determining root grafting and its influence on forest stands dynamics, several studies have tried to describe tree and stand

characteristics leading to root grafting (Fraser et al., 2005; Külla and Lõhmus, 1999; Tarroux and DesRochers, 2010). Proximity and high density of trees and roots have been shown to increase the probability of root contacts leading to root graft formation (Fraser et al., 2005; Gaspard and DesRochers, 2020; Tarroux and DesRochers, 2010). Moreover, soil properties that determine root system architecture can also increase root density in particular soil areas leading to root grafting. For instance in shallow or stoney soils, roots are constrained to a thin layer of soil promoting root encounter (Bormann and Graham, 1959; Eis, 1972; Tarroux and DesRochers, 2010). Finally, mechanical abrasion of root bark by trees swaying in the wind, greater in sandy soils, promotes the fusion of roots' vascular tissues and then graft formation (Basnet et al., 1993; Eis, 1972; Tarroux and DesRochers, 2010).

Balsam fir (*Abies balsamea* (L.) Mill) is a common tree species of the boreal forest in Quebec that can grow for prolonged periods of time in dense understory environments (Burns and Honkala, 1990; Ruel et al., 2003). It has shallow rooting and maintains an abundant seedling bank on the ground leading to the formation of very dense stands after disturbances remove canopy trees (Morin and Laprise, 1997). These conditions seem conducive of root grafting and could explain how balsam fir can survive for such prolonged periods in the understory. However, there is no recent work on root grafting in balsam fir and only anecdotal observations of possible root grafts have been made when studying butt-rotting fungi (Redmond, 1957). In order to better understand the ecological significance of root grafting in balsam fir it is necessary to investigate the occurrence of root grafts, their frequency and the timing of their initiation. We make the hypothesis that root grafts formation is common in balsam fir and that their frequency depends on age and size of trees and roots and on the distance between trees. Aims of this study were: (i) to estimate the frequency of root grafting in balsam fir stands of the boreal forest in Quebec, (ii) to describe age and size distributions of roots and trees at graft initiation,

(iii) to investigate the effect of the tree proximity, the size of stems, the number and the size of roots on the number of grafts per tree.

2. Material and method

2.1. Study sites and stands characterization

Study sites were located in Abitibi-Témiscamingue in the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain of Quebec boreal forest (Grondin et al., 1998). Annual total precipitation for the region averaged 929 mm (253 mm of snow and 675 mm of rain) with a daily temperature of 1.5 °C and an average of 2366 degree-days above 0 °C (Climate normal 1981-2010, Environment Canada 2018). The three sites were located on the Ontario-Quebec clay belt characterized by post-Wisconsinian lacustrine deposits forming heavy clay soils (at least 60% clay), offering a large physiographic unit with very similar soil conditions over the landscape (Canada Soil Survey Committee, 1987, Vincent and Hardy, 1977). 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). We selected monospecific, healthy, naturally regenerated and mature stands (> 30 years old) based on their proximity to a water source and a gentle slope in order to be able to carry out the hydraulic excavation of the root systems. Excavated areas were approximately 50 m² and included a minimum of 15 living trees per area, corresponding to stands with a minimum density of 3000 stems ha⁻¹ (Table 1). Before excavation, distance between trees and DBH of each tree were measured. Trees were then cut down with a chainsaw and cross-sectional disks were collected at ground level (0 m). Disks of stems were air dried and sanded (80-400 grit) to reveal growth rings. As balsam fir is known to often present missing growth rings at the trunk base, the age of trees was estimated by counting

growth rings and visually cross-dating chronologies of all trees using pointer years such as narrow or wide rings (Parent et al., 2002, Schweingruber, 1988). A total of 125 stem disks were analyzed. Excavated area stand density ranged 6000 stems ha⁻¹ to 14200 stems ha⁻¹. Age and diameter at breast height (DBH, 1.30 m) of trees differed among sites (ANOVA, $F_{\text{age}} = 52.28$, $F_{\text{DBH}} = 18.16$, $P < 0.001$) and ranged 39-74 years old and 7.9-16.5 cm, respectively. Mean age was lowest in S1 and highest in S3 while DBH decreased with increasing density (S1 < S3 < S2) (Table 1).

2.2. Root systems excavation and root measurements

The root system of each tree was hydraulically excavated using a firefighter's lance coupled to a high-pressure water pump (Mark III, Wajax, Lachine, Quebec), following Tarroux and DesRochers (2010) (Supplementary material, Figure S1). To uncover all the roots, the excavation depth was between 30 to 60 cm. Complete excavation of root systems took about three weeks per site. Excavation revealed buried rotted stumps that were not included in the analyses. Standing dead or moribund trees and their associated root systems and grafts were analyzed if their state of decomposition allowed a clear visualization of growth rings. For each site, we counted number of grafts and roots (diameter > 1.5 cm) per tree. Grafts and cross-sectional disks of each root (> 1.5 cm) were collected for dendrochronological analyses in the laboratory. The age of roots and root grafts were determined by counting and cross-dating the root disks with those of their corresponding stem after they were air-dried and sanded (80-400 grit) (Tarroux and DesRochers, 2010). Root disks were collected nearest to the stump in order to facilitate growth rings analysis and to avoid missing rings that are more common as we move away from the tree stump (Krause and Morin, 1999). The age of roots determined near the stump corresponds to the time when the root was produced by the tree. The grafts then form later in the life of the root, that is why the age of root grafts needs to be determined directly on

the graft itself to identify the year when the two roots start producing a single and common wood layer. Root grafts are thus always “younger” than the root itself.

To determine if grafts formed a complete morphological union, they were cut into cross-sectional disks throughout their length to confirm if grafted roots shared common growth rings (Supplementary material, Figure S2) (Graham and Bormann, 1966). Few very intertwined roots were rejected in the lab as they were not grafted and did not share a common wood layer after being cut. Age of grafts was determined by counting the number of common growth rings between the two grafted roots. Age of trees at graft initiation was determined by calculating the difference between the age of tree and the age of the associated graft. Due to the eccentric root growth, root diameter was calculated by averaging perpendicular measurements of the longest and the shortest diameters of the root (Adonsou et al., 2016a). Root diameter at graft initiation was calculated by using the same method but measurements were realized on graft sections, before the first common growth ring between two roots (Supplementary material, Figure S2). A total of 698 root disks and 58 grafts were analyzed.

2.3. Statistical analyses

Statistical analyses were done using R software version 3.5.1 (R core team, 2019). Differences in mean DBH, age of trees and root diameter between the three sites (S1, S2 and S3) were tested by one-factor ANOVAs, followed by post-hoc Tukey tests. Because of violation of ANOVA assumptions, differences in mean distances, number of roots and graft age were analyzed using Kruskal Wallis test followed by post hoc Wilcoxon tests. The effect of sites on percentage of grafted trees was tested by using Pearson’s Chi-squared test. Number of grafted roots and trees according to their diameter, age at graft initiation and distance between trees were also tested using Pearson’s Chi-squared test. We developed a generalized linear model with a negative binomial function (GLM.NB.) to identify which predictors between tree age

(years), DBH (cm), number of roots, mean root diameter (cm) and distance (m) were the best predictors to explain the number of grafts per tree.

We included mean distance between trees and distance to the nearest tree as predictors; however, after preliminary analysis we only used distance to the nearest tree as it performed better. Full data set were used for this model independently of site because the response variable variance (number of grafts per tree) was similar across sites. Only distance to the nearest tree was considered to calculate the model. The full model (including all the predictors) was simplified in order to determine the most parsimonious model using the function StepAIC (package "MASS", Venables and Ripley, 2002). StepAIC performs stepwise variable selection that adds or removes predictors to produce a model that minimizes Akaike's Information Criterion (AIC). Predictions of the most parsimonious model were represented graphically using "visreg" function (package "visreg", Breheny and Burchett, 2017). We used conditional inference tree (function "Ctree" in package "partykit") to help interpret the results. It estimates a regression relationship by binary recursive partitioning in a conditional inference framework that is based on maximally selected rank statistics (Hothorn et al., 2006). Conditional inference tree was realized by using the variables of the best model fitted using GLM.NB.

3. Results

Root grafting was observed in the three excavated stands for a total of 58 grafts per 45 grafted trees corresponding to 1.3 grafts per grafted tree on average (Table 2). In total, 698 roots were excavated and 87 of them were grafted to roots of another tree. Percentage of grafted trees was similar between sites, corresponding to 36% on average (Pearson's χ^2 test, $\chi^2 = 0.94$, $P > 0.05$) even if tree and root diameters, mean distance between trees, tree and graft ages were different (ANOVAs, $F_{\text{Root_diameter}} = 7.09$, Kruskal Wallis test, $\chi^2_{\text{min_distance}} = 13.73$, $\chi^2_{\text{Graft_age}} = 8.31$, $P < 0.05$; Table 1 and 2). Mean graft age was 13.57 years (± 0.98 SE), with the youngest

graft being 2 years old and the oldest graft 39 years old. Root grafting occurred mainly between healthy trees of the same diameter class (Supplementary material, Table S4). The difference in diameter between two grafted trees generally did not exceed 10 cm. Only 7 grafts were between two dead trees or between a healthy and a dead/moribund tree. Most of grafts were formed near the stumps (< 30 cm). During root graft formation, a callus formed around the fusion point of the vascular tissues deforming the roots making it difficult to estimate one dominant root over the other (Supplementary material, Figure S2). However, most of grafts were constituted by similarly-sized roots (Supplementary material, Table S4). Grafts between two roots occurred from every angle but most of the grafts were formed when two main lateral roots encountered (Supplementary material, Figure S3a). Other dominant types of grafts were formed when a root touched the stump of a neighboring tree, generally involving a dominant and a smaller tree (Supplementary material, Figure S3b). Age of grafted trees at graft initiation ranged 12-106 years old across the sites and averaged 38 years old (± 3.0 SE). Relative distribution of grafted trees did not vary significantly among age classes at graft initiation but 71% of trees were grafted before 45 years old (Figure 1). Mean DBH of grafted trees was 14.1 cm (± 1.8 SE) across sites and it ranged 1.30-77 cm. Proportion of grafted trees was similar across tree DBH classes (Pearson's χ^2 test, $\chi^2 = 2.36$, $P > 0.05$, results not shown).

Root grafting occurred in roots as young as 5 years old and as old as 64 years old. Sixty-five percent of roots were grafted before 30 years old and mean root age at graft initiation was 26.48 years (± 1.35 SE) (Figure 2A). Mean root diameter at graft initiation was 3.94 cm (± 0.33 SE) and 63% of roots were grafted at a diameter less than 4 cm (Figure 2B). We found no graft from roots smaller than 0.40 cm in diameter or larger than 14.94 cm.

Mean distance between grafted trees was 47.91 cm (± 5.10 SE) and we did not observe any graft beyond a 181 cm distance. Percentages of root grafts did not significantly differ between our 25 cm distance classes but tended to decrease with increasing distance (Figure 3). We

showed that 84% of all root grafts occurred between trees < 75 cm apart and that the majority (62%) of grafts formed between trees distant 4-50 cm (Figure 3).

Age of trees, DBH and mean root diameter were not significant predictors of the number of root grafts per tree (GLM.NB, $P > 0.05$) (Table 3). However, the number of grafts per tree increased with number of roots per tree (GLM.NB, $P < 0.05$) and decreased with distance between trees (GLM.NB, $P < 0.001$) (Table 3, Figure 4). The following equation (1) predicted the number of root grafts per tree according to the number of roots and the distance between trees (Figure 4): (1) $\text{Log (Number of grafts per tree)} = 0.61 + (0.11 \times \text{number of roots}) - 2.33 \text{ minimal distance between trees.}$

The conditional inference tree model showed the same significant predictors as the MPM selected and both models had similar R^2 (33% and 44% respectively). When distance between trees was less than 0.13 m, predicted number of root grafts was the highest, around 5 grafts. When distance between trees was above 0.77 m, trees were generally not grafted. If distance was between 0.13 and 0.77 m and if trees had 10 or less than 10 roots, number of root grafts predicted was around 1. However, for similar distances, trees that had more than 10 roots had predicted numbers of root grafts around 4 grafts (Figure 5).

4. Discussion

We confirmed here for the first time the occurrence of root grafting in balsam fir. Root grafting has been reported in several fir species such as silver fir (*Abies alba* Mill.; Elwes and Henry, 1909), white fir (*Abies concolor* (Gordon and Glend.) Lindl. ex Hildebr.; Jepson, 1909) and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.; Graham and Bormann, 1966), suggesting that most species of this genus could form root grafts. Excavated stands were highly interconnected with on average 36% of grafted trees indicating that root grafting is a common occurrence in balsam fir (Table 2). This percentage is lower than in pine stands, usually

recognized to have strong root grafting propensity (up to 90% in *Pinus resinosa* Sol. ex Aiton or to 50% in *Pinus strobus* L.)(Bormann, 1966). Root grafting occurrence in balsam fir was however similar to other natural stands of boreal forest species such as Norway spruce (33%) (Küllä and Löhmnus, 1999) and balsam poplar (48%) (Adonsou et al., 2016a).

Tree proximity was the most important driver for root grafting as the number of grafts per tree decreased with increasing distance between trees (Table 3, Figure 4). These results confirm the postulate that distance between trees is the main predictor of root grafting beyond stand density, age or size of trees and roots (Gaspard and DesRochers, 2020; Küllä and Löhmnus, 1999; Tarroux and DesRochers, 2010). This could be explained by (i) a shorter time for roots of close trees to meet and a greater probability to cross, (ii) the fact that tree proximity promotes mechanical abrasion and root friction caused by wind swaying and thus root grafting (Cook and Welch, 1957; Küllä and Löhmnus, 1999). Proximity is a better predictor of root grafting than stand density because the latter does not reflect spatial arrangement of trees (Tarroux and DesRochers, 2010). Our results confirmed this assumption, as tree density was three times higher in S1 than in S3 but percentages of grafted trees were similar (Tables 1 and 2). Distance between grafted trees averaged 50 cm, as was found for lodgepole pine and Norway spruce, suggesting that close proximity between trees is necessary for root grafting (Figure 3) (Fraser et al., 2005; Küllä and Löhmnus, 1999). In our three stands, 80% of grafted trees were linked to their closest neighbor and thus grafted trees were mostly observed between trees in clusters, which is not well reflected by stand density. Dense tree clusters are very common in balsam fir stands that can maintain an abundant seedling bank on the ground conducive to closely growing tree formations (Morin and Laprise, 1997; Ruel et al., 2003).

The number of grafts per tree increased with the number of roots per tree (Table 3, Figure 4). As it was reported in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and hybrid poplar (*Populus maximowiczii* × *Populus balsamifera*), positive correlation between root grafting and

number of roots per tree is probably due to the higher probability of intertree root contacts (Gaspard and DesRochers, 2020; Reynolds and Bloomberg, 1982). This effect was particularly important when distance between trees was between 0.13 and 0.77 m; At these distances, the predicted number of grafts for trees with less than 10 roots was around 1 and around 4 if trees had more than 10 roots (Figure 5). Since root density decreases with increasing distance from the stem, trees with a greater number of roots increased root grafting probability (Küllä and Lõhmnus, 1999). We found two trees that presented an above-average number of grafts (> 1.3 grafts per tree) even if they were distant of more than 50 cm to the closest tree (Figure 4). These two trees were larger than the average of grafted trees (DBH > 14.1 cm) and had lots of roots (> 9 roots per tree). The resulting greater probability of forming root grafts could thus be due to the larger area of soil they occupy. However, the percentage of observed trees with more than 10 roots was low (approx. 13%) so this modeling result has to be considered with care (Tables 1 and 2).

When trees increase in size and age, their roots become larger and have more ability to anchor firmly in the soil. During root grafting formation radial growth of the two roots is maintained at the point of contact, creating a pressure point, stronger for larger roots, can possibly facilitating the fusion of vascular tissues (Reynolds and Bloomberg, 1982). In this way, positive correlations are often found between number of grafts per tree, DBH, mean tree age, and mean root diameter (Bormann, 1966; Bormann and Graham, 1959; Fraser et al., 2005; Tarroux and DesRochers, 2010). However, these factors did not explain root grafting in balsam fir (Tables 2 and 3). Balsam fir growing in close-stems formations responds vigorously to release following disturbances and goes through a self-thinning stage caused by strong competition for light (Bégin et al., 2001). During self-thinning, stands undergo a shift in DBH frequency of live trees and diameter distribution becomes increasingly skewed (McCarthy and Weetman, 2007). These changes in tree size hierarchy could explain why DBH was not a good predictor of root grafting

for this species. Self-thinning in balsam fir forests of western Newfoundland begun once stands reached stem densities of approximately 31000 stems ha⁻¹ at around 60-65 years old (McCarthy and Weetman, 2007). Mean tree age was 74 years old in Site 3 with a density of 6000 stems ha⁻¹; Self-thinning stage could thus have been in progress at the time of excavation. Trees in sites 1 and 2 seemed too young for being in this self-thinning stage. However, the observations of dead trees and stumps during the excavation and the large distribution of tree DBH suggest that stands could undergo the preliminary stage of self-thinning at excavation time.

Moreover, results on balsam fir age determination have to be considered with care because the physiological age of a balsam fir can differ from its chronological age (Bégin et al., 2001; Morris, 1948). Indeed, trees can undergo intermittent radial and height growth interruptions during their understory development leading to absent growth rings at the stem base and consecutively in the root system (DesRochers and Gagnon, 1997; Morin and Laprise, 1997; Parent et al., 2000, 2002). Missing growth rings could be expected to be particularly numerous in the in closed-stems formations leading to underestimation of the true age of trees and their roots (Krause and Morin, 1995).

In our study, natural root grafts were found in a variety of tree ages and sizes, respectively from 12 to 106 years old and from 1.3 to 77 cm in DBH. Similarly, root grafting occurred from 1 to 90 years in jack pine stands (Tarroux and DesRochers, 2010) and from 2 to 46 years in lodgepole pine stands (Fraser et al., 2005). The oldest root graft that we found was 39 years old and belonged to a 77 and a 74 years old trees (in S3). The youngest tree that was grafted was 36 years old at time of excavation and its oldest graft was 24 years old (in S1). This study is limited to the excavation time and we cannot predict the evolution of the grafts or whether grafts will continue to form over time. Though these large variations in the timing of graft formation means that grafting was not restricted to a particular period but could continue throughout the life of stands and that grafts could persist throughout stand development.

According to our results, root grafts also appear to form in roots of any age: root age at graft initiation averaged 26.5 years but varied from 5 to 64 years. Root age at graft initiation averaged 20 years but ranged between 2-41 years in trembling aspen (*Populus tremuloides* Michx; Jelinkova et al., 2009) and begun between 10-20 years (46% of cases) but ranged between 7-35 years in Norway spruce (Küllä and Lõhmnus, 1999). However, root grafting initiated when roots were relatively small: 63% of roots were grafted at a diameter under 4 cm (Figure 2). This is probably because small roots have thinner bark, facilitating the fusion of vascular tissues during graft initiation (Eis, 1972).

Balsam fir is shade tolerant and competition for light is a key factor of tree interactions and community structure (Kunstler et al., 2012; Messier et al., 1999). As resources are redistributed among grafted trees, a shaded tree could receive photosynthates from a well-lit grafted neighbor (Fraser et al. 2006). Root grafting could thus explain this great shade tolerance in balsam fir, allowing it to survive in the understory for several decades before release. This notion supports the hypothesis that natural root grafting allows intraspecific cooperative relationships between trees and limits tree competition effects by maintaining tree growth through resources translocation instead of competing for them (Loehle and Jones, 1990; Lev-Yadun, 2011). Our study thus suggests that communal root systems established between grafted trees could sustain tree growth within tree clusters and reduce intraspecific competition for soil resources and light. It could also explain why competition indices are often inconclusive for this species. In their study, Duchesneau et al. (2001) found that growth of balsam fir saplings (height < 200 cm) receiving less than 25% of full sunlight was not affected by intraspecific competition. It suggests that root grafts could allow suppressed grafted trees to persist under conditions where un-grafted trees would be removed by competition (Fraser et al., 2006). Root grafting could thus delay self-thinning through greater survival rates of suppressed trees, resulting from carbohydrate and water transfers from vigorous and dominant neighboring trees (Adonsou et

al., 2016b; Fraser et al., 2006). During self-thinning stage, tree density decreases leading to an increase of distance between trees and likely to a decrease in the formation of new grafts.

Root grafting should be considered in forest management since it can influence forest dynamics, by modulating competition relationships between trees or constitute a way for diseases to spread. Considering that balsam fir frequently develops dense tree clusters, pre-commercial or commercial thinning is often prescribed to release growth and reduce competition for resources (Ruel et al., 2003). However, residual grafted trees may not benefit from reduced competition by thinning if roots and stumps of the removed trees keep on living and drain carbohydrates from residual trees, limiting growth of treated stands (Fraser et al., 2007; Tarroux et al., 2010). Vigorous residual grafted trees could benefit from the acquisition of new functional roots from a removed connected neighbor but if the imbalance between residual root biomass and leaf area is too large, growth of residual trees may suffer. In two naturally regenerated stands of *Pinus banksiana*, commercially thinned 5 years prior excavation (46% and 56% of trees removed), dendrochronological analyses showed that radial growth of residual trees grafted to removed trees was lower than that of non-grafted tree after 4 years (Tarroux et al., 2010). The amount of resources translocated between two grafted trees is proportional to the number of grafts per tree (O'Neal and Davis, 2015). Since the number of grafts per tree averaged 1.3 in *Abies balsamea* versus 0.79 in *Pinus banksiana*, a larger negative effect of thinning on fir growth can be expected. This effect should be particularly noticeable during the mortality phase or the self-thinning phase of natural balsam fir stands development, since this is the period when the number of grafted stumps and suppressed trees is likely to be the highest. Lighter thinning and from below is thus advised in such stands in order to reduce the imbalance between live root biomass and residual leaf area after thinning (Eis 1972; Tarroux et al., 2010). Thinning from below only removes the smallest trees, hence creating a smaller imbalance between residual leaf area and the “communal” root biomass of a stand. This smaller imbalance allows stands to

increase photosynthetic capacity and maintain growth rather than having to invest photosynthates into the support of too much root biomass when larger trees are removed (i.e. thinning from above) (DesRochers and Liefers, 2001).

In conclusion, although our stand characteristics differed, natural root grafting was found in the three excavated balsam fir stands. Root grafts were formed early or later in tree development (from 12 to 106 years old). Proximity of trees and the number of roots per tree increased the number of root grafts per tree, most likely because these factors are conducive to increased root contacts. These results suggest that studying the spatial arrangement (e.g. local tree and root density near grafted trees) might help to better predict probability of root grafting. Since balsam fir stands were highly connected through root grafts, trees can redistribute resources within the stand, which could explain how balsam fir can survive for such prolonged times in the understory. Root grafting could reduce intraspecific competition for soil resources and light and allow grafted trees to persist under conditions where un-grafted trees would be removed. Integrating root grafting knowledge into silvicultural practices could improve management of balsam fir stands. For instance, limiting the “waste” of photosynthates in the support roots and stumps of thinned grafted trees by using thinning from below could trigger an increase in photosynthetic capacity and growth resulting from the increase in available resources.

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Figures:

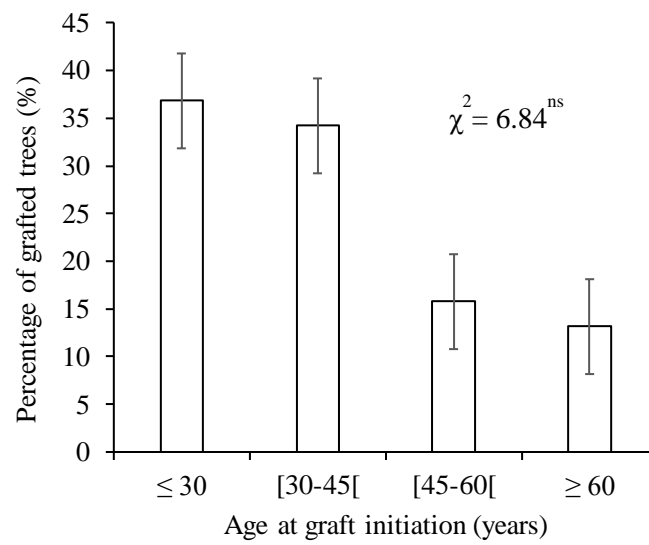


Figure 1: Percentage of grafted *Abies balsamea* trees observed in the 3 sites (\pm SE) in relation to tree age at graft initiation. Differences between classes were tested by using Pearson's χ^2 test (χ^2 value is represented, ns: non-significant, with $P = 0.07$ and $N = 38$).

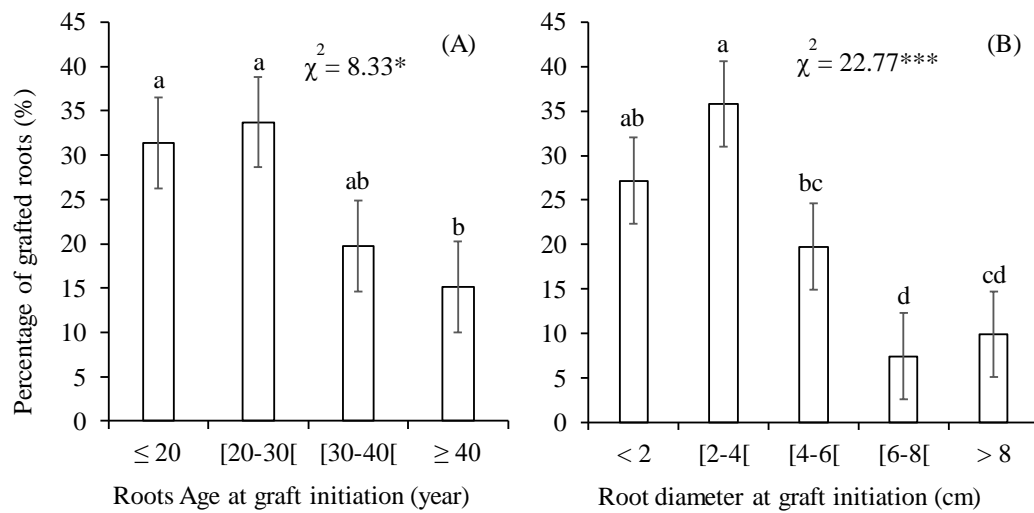


Figure 2: Percentage of grafted *Abies balsamea* roots observed in the 3 sites (\pm SE) in relation to root age (A) and root diameter (B) at graft initiation. Differences between classes were tested by using Pearson's χ^2 test (a > b > c > d, different letters indicate significant differences, χ^2 value are represented with *: $P < 0.05$ and N = 86, ***: $P < 0.001$ and N = 81).

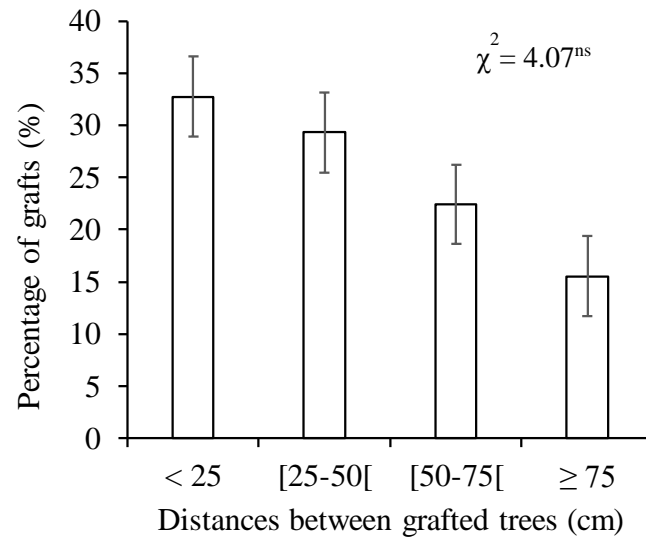


Figure 3: Percentage of root grafts observed in the 3 sites (\pm SE) in relation to distance between grafted trees. Differences between distance classes were tested by using Pearson's χ^2 test (χ^2 value is represented, ns: non-significant with $P = 0.25$ and $N = 58$).

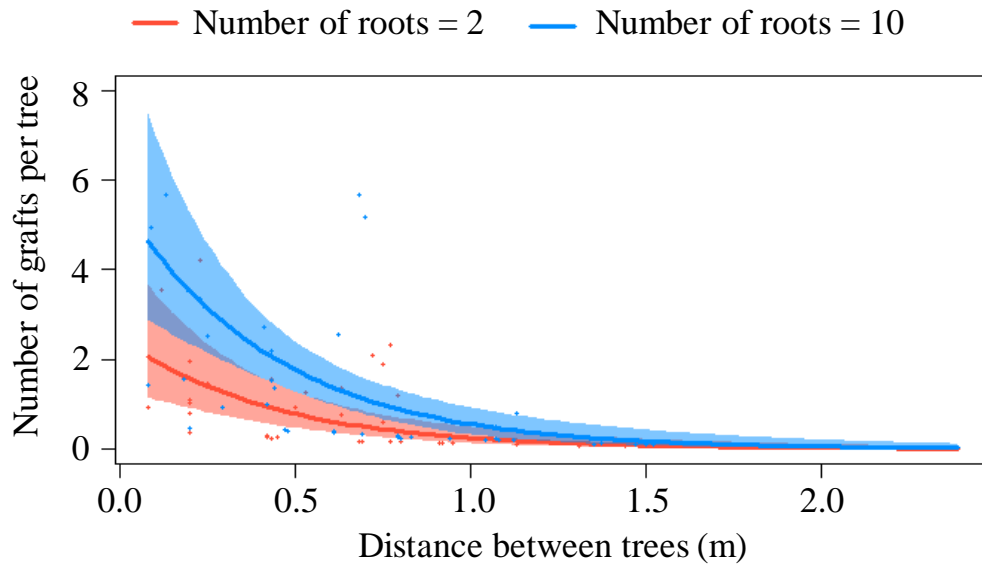


Figure 4: Model projections and partial residuals of number of grafts per *Abies balsamea* as a function of distance between trees and number of roots per tree. Number of roots = 2 and Number of roots = 10 correspond to the lower and upper percentiles (e.g. 10th and 90th). Point colors are determined by the closest value of the number of roots. (95% confidence intervals are highlighted, $R^2 = 33\%$, $N = 80$).

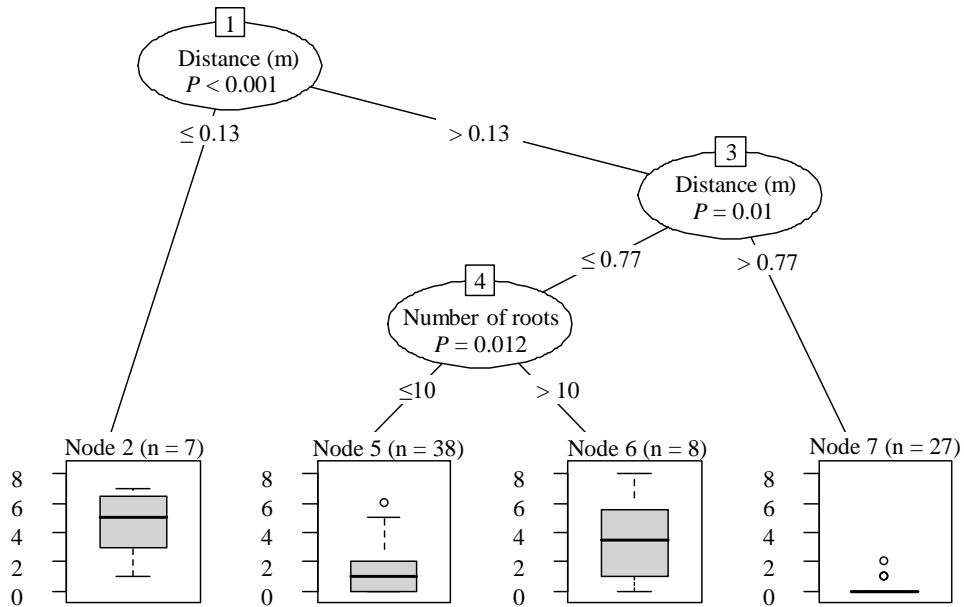


Figure 5: Conditional inference tree for number of grafts per tree in relation to number of roots and distance between grafted trees (m). The numbers inside the squares identify the nodes and the order of variable/partition entrances, starting with 1 in the root node. The predicted number of grafts per tree for each node is specified by boxplots in the lower part of the figure ($R^2 = 44\%$, $N = 80$).

Table 1: Main characteristics of the three *Abies balsamea* excavated stands.

| Site | S1 | S2 | S3 | Total |
|--------------------------------------|---------------|---------------|---------------|--------------|
| Number of excavated trees | 71 | 24 | 30 | 125 |
| Number of excavated roots | 352 | 161 | 185 | 698 |
| | | | | Mean |
| Stand age (years) | 36 | 51 | 74 | 54 |
| Density (stems.ha ⁻¹) | 14 200 | 4800 | 6000 | 8 333 |
| Mean tree age (years) ± SE | 39 ± 15 a | 49 ± 10 b | 74 ± 14 c | 49 ± 1.84 |
| Mean DBH (cm) ± SE | 7.9 ± 0.7 a | 16.5 ± 1.6 b | 11.9 ± 0.8 b | 10.5 ± 0.6 |
| Mean distance between trees (m) ± SE | 0.46 ± 0.06 a | 0.81 ± 0.12 b | 0.77 ± 0.06 b | 0.65 ± 0.05 |

Note: Totals and means were calculated including all sites ± Standard Error. DBH: Diameter at Breast High. When $P < 0.05$, different letters indicate significant differences between sites, a < b < c.

Table 2: Root systems and grafts characteristics of the three *Abies balsamea* excavated stands.

| Site | S1 | S2 | S3 | Total |
|--|--------------------|--------------------|--------------------|------------------|
| Number of grafts | 30 | 12 | 16 | 58 |
| Number of grafted trees | 23 | 10 | 12 | 45 |
| Number of grafted roots | 47 | 18 | 22 | 87 |
| | | | | Mean |
| Percentage of grafted trees (%) \pm SE | 32.4 a | 41.7 a | 40.0 a | 36.0 \pm 2.86 |
| Mean number of grafts per grafted tree | 1.3 | 1.2 | 1.3 | 1.3 \pm 0.03 |
| Mean graft age (years) \pm SE | 11.66 \pm 1.06 a | 11.54 \pm 1.32 a | 19.43 \pm 2.51 b | 13.57 \pm 0.98 |
| Mean diameter of roots (cm) \pm SE | 6.93 \pm 0.27 a | 8.27 \pm 0.42 a | 10.28 \pm 0.46 b | 8.12 \pm 0.21 |
| Mean number of roots per tree \pm SE | 5.97 \pm 0.26 a | 6.71 \pm 0.30 a | 6.61 \pm 0.21 a | 6.29 \pm 0.16 |

Note: Totals and means were calculated including all sites \pm Standard Error. When $P < 0.05$, different letters indicate significant differences between sites, $a < b < c$.

Table 3: Output of negative binomial generalized linear model (GLM.NB) testing the effects of tree age, DBH, number of roots per tree, mean root diameter and distance between trees on the number of root grafts per tree.

| | Number of grafts per tree | | |
|--------------------------|---------------------------|---------------|------------|
| | d.f. | Z value | P value |
| (Intercept) | 1 | 0.413 | ns |
| Age (year) | 1 | 0.492 | ns |
| DBH (cm) | 1 | 0.207 | ns |
| Number of roots | 1 | 2.582 | * |
| Mean root diameter (cm) | 1 | 0.597 | ns |
| Distance (m) | 1 | -5.411 | *** |
| All R ² (AIC) | | 0.16 (232.95) | |
| MPM R ² (AIC) | | 0.33 (230.4) | |

Note: Values of R² and AIC of the general model including all factors (All) and of the most parsimonious model (MPM) are shown. Variables retained in the most parsimonious models are reported in bold (d.f.= degree of freedom, P values = ns: non-significant with $P > 0.05$, *: $P < 0.05$, ***: $P < 0.001$, N = 80).

Supplementary material



Figure S1: Photograph of the excavated root systems of *Abies balsamea* in Site 1.



Figure S2: Photograph of a cross-section of an *Abies balsamea* root graft. Note the joining of xylem and phloem layers, and the central area with callus formation. Black arrow refers to a “bark pocket” pointing more or less complete fusion of the tissues. The white arrow shows first common growth ring between the two grafted roots.

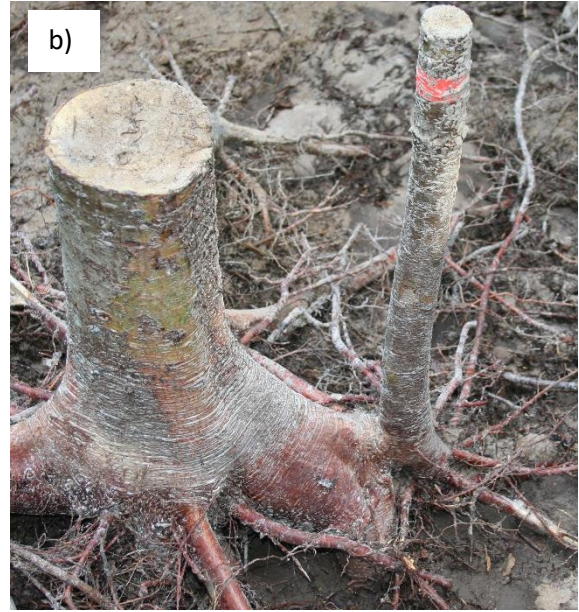
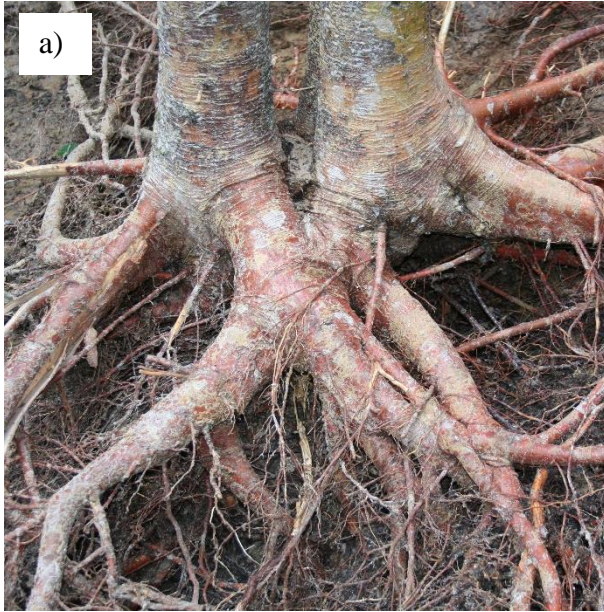


Figure S3: Photographs of root grafts between several *Abies balsamea*. a) A graft formed when main lateral of roots encountered. B) A graft formed when the root encountered the stump of the neighbor tree.

Table S4: Diameter (cm) and status (alive or dead) of trees and diameter (cm) at graft initiation of grafted roots in balsam fir stands according to grafts and sites. Tree No 1 is the biggest and Tree No 2 is the smallest tree of the pair of grafted trees. Root No 1 is the biggest and Root No 2 is the smallest grafted root. DBH: Diameter Breast Height. NA: Not Available.

| Grafts Labels | Sites | Statut, Tree No 1 | Statut,Tree No 2 | DBH, Tree No 1 (cm) | DBH, Tree No 2 (cm) | Diameter, Root No 1 (cm) | Diameter, Root No 2 (cm) |
|----------------------|--------------|--------------------------|-------------------------|----------------------------|----------------------------|---------------------------------|---------------------------------|
| G1 | 1 | Alive | Alive | 15.20 | 8.90 | 14.67 | 7.79 |
| G2 | 1 | Alive | Alive | 77.00 | 10.80 | 4.39 | 1.74 |
| G3 | 1 | Alive | Alive | 77.00 | 10.80 | 3.67 | 1.87 |
| G4 | 1 | Alive | Alive | 77.00 | 10.80 | 7.05 | 0.96 |
| G5 | 1 | Alive | Alive | 77.00 | 10.80 | 2.17 | 1.98 |
| G6 | 1 | Alive | Alive | 77.00 | 10.80 | 5.17 | 2.61 |
| G7 | 1 | Alive | Alive | 12.70 | 3.70 | 7.01 | 2.61 |
| G8 | 1 | Alive | Alive | 12.70 | 3.70 | 4.95 | NA |
| G9 | 1 | Alive | Alive | 12.90 | 12.30 | 2.36 | 2.34 |
| G10 | 1 | Alive | Alive | 12.70 | 3.70 | 2.12 | 1.40 |
| G11 | 1 | Alive | Alive | 12.70 | 3.70 | 1.14 | 1.02 |
| G12 | 1 | Alive | Alive | 7.10 | 3.10 | 3.26 | 3.01 |
| G13 | 1 | Alive | Alive | 11.30 | 7.10 | 2.50 | 1.86 |
| G14 | 1 | Alive | Alive | 20.90 | 16.10 | 4.39 | 4.02 |
| G15 | 1 | Alive | Alive | 12.90 | 12.30 | NA | NA |
| G16 | 1 | Alive | Alive | 12.70 | 3.70 | 1.89 | 1.02 |
| G17 | 1 | Alive | Alive | 15.80 | 8.70 | 1.95 | 1.35 |
| G18 | 1 | Alive | Alive | 15.80 | 8.70 | 3.57 | 2.06 |
| G19 | 1 | Alive | Alive | 15.80 | 8.70 | 4.72 | 2.06 |
| G20 | 1 | Alive | Alive | 15.80 | 8.70 | 3.77 | 3.25 |
| G21 | 1 | Alive | Alive | 11.30 | 8.70 | 8.76 | 4.27 |
| G22 | 1 | Alive | Alive | 15.80 | 11.30 | 2.58 | 2.44 |
| G23 | 1 | Alive | Alive | 19.50 | 18.10 | 4.68 | 4.30 |
| G24 | 1 | Alive | Alive | 10.80 | NA | NA | NA |
| G25 | 1 | Dead | Dead | 3.50 | 2.10 | 2.90 | 0.69 |
| G26 | 1 | Alive | Alive | 12.90 | 12.30 | 5.45 | 1.68 |
| G27 | 1 | Alive | Alive | 12.90 | 12.30 | 2.48 | 0.98 |
| G28 | 1 | Alive | Alive | 12.90 | 12.30 | 14.94 | 8.85 |
| G29 | 1 | Alive | Alive | 12.90 | 12.30 | 11.67 | 2.80 |
| G30 | 1 | Alive | Alive | 12.90 | 12.30 | 3.99 | 1.11 |
| G31 | 2 | Alive | Dead | 19.40 | 12.40 | 5.69 | NA |
| G32 | 2 | Alive | Alive | 30.30 | 15.00 | 6.31 | NA |
| G33 | 2 | Alive | Alive | 30.30 | 15.00 | 1.51 | NA |
| G34 | 2 | Alive | Alive | 30.30 | 15.00 | 1.36 | NA |
| G35 | 2 | Alive | Alive | 30.30 | 15.00 | 1.02 | 0.40 |
| G36 | 2 | Alive | Alive | 30.30 | 15.00 | 9.47 | 1.05 |
| G37 | 2 | Alive | Dead | 19.40 | 12.40 | 4.10 | 3.11 |
| G38 | 2 | Alive | Alive | 16.90 | 7.30 | 9.10 | 4.50 |
| G39 | 2 | Alive | Alive | 16.90 | 7.30 | 6.70 | 2.64 |

| | | | | | | | |
|-----|---|-------|-------|-------|-------|-------|------|
| G40 | 2 | Alive | Alive | 20.10 | 1.62 | 2.57 | 1.36 |
| G41 | 2 | Alive | Alive | 36.10 | 22.60 | 2.61 | 1.62 |
| G42 | 2 | Alive | Alive | 30.30 | 15.00 | 5.07 | 2.24 |
| G43 | 3 | Alive | Alive | 16.40 | 7.80 | 3.82 | 3.69 |
| G44 | 3 | Dead | Alive | 10.00 | 9.20 | 5.85 | 3.91 |
| G45 | 3 | Alive | Alive | 16.60 | 8.90 | NA | NA |
| G46 | 3 | Alive | Alive | 16.60 | 8.90 | 4.72 | 3.62 |
| G47 | 3 | Alive | Alive | 16.60 | 8.90 | NA | 4.01 |
| G48 | 3 | Alive | Alive | 16.40 | 13.80 | 11.83 | 6.41 |
| G49 | 3 | Alive | Alive | 16.60 | 10.30 | 1.60 | 1.54 |
| G50 | 3 | Alive | Dead | 16.60 | NA | NA | NA |
| G51 | 3 | Alive | Dead | 16.60 | NA | 2.88 | 2.82 |
| G52 | 3 | Alive | Alive | 19.70 | 12.40 | 4.47 | 4.04 |
| G53 | 3 | Alive | Alive | 16.60 | 10.30 | 4.80 | 3.37 |
| G54 | 3 | Alive | Alive | 16.60 | 10.30 | 6.41 | 3.10 |
| G55 | 3 | Alive | Alive | 19.70 | 12.40 | 7.42 | 6.01 |
| G56 | 3 | Alive | Alive | 16.40 | 13.80 | 6.56 | 4.81 |
| G57 | 3 | Dead | Alive | 9.40 | 4.80 | NA | NA |
| G58 | 3 | Alive | Alive | 16.40 | 7.80 | 4.73 | 1.60 |
