Frequency of root grafting in naturally and artificially regenerated stands of *Pinus banksiana*: influence of site characteristics

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Abstract: We investigated the frequency of root grafting in naturally and artificially regenerated stands of jack pine (*Pinus banksiana* Lamb.) in the western boreal forest of Quebec, Canada. Twelve 30–60 m^2 plots were hydraulically excavated to determine effects of site characteristics on frequency and timing of root grafting. Naturally regenerated stands had grafted tree percentages similar to artificially regenerated stands (21%–71% across plots) but greater numbers of root grafts per tree (naturally regenerated, 0.73 graft·tree^{-1}; artificially regenerated, 0.52 graft·tree^{-1}). Mean percentages of grafted trees, number of grafts per tree, and the speed of graft formation were greater in sandy soils (61%, 0.71 graft·tree^{-1} and 2.43 years, respectively) compared with clay soils (44%, 0.54 graft·tree^{-1} and 2.97 years, respectively). Proximity of trees was a better predictor of root grafting than stand density, despite many root grafts being found with distant trees (>2 m) in artificially regenerated stands. Our results suggested that root grafts form early in stand development. Even if trees are initially separate entities, this relatively high level of root grafting produces stands where trees are extensively interconnected.

Résumé : Nous avons étudié la fréquence des greffes racinaires dans des peuplements de pin gris (*Pinus banksiana* Lamb.) d'origines naturelle et artificielle dans la forêt boréale de l'ouest du Québec, au Canada. Douze parcelles de 30 à 60 m^2 ont été excavées à l'aide d'un jet d'eau pour déterminer les effets des caractéristiques de la station sur la fréquence et la période de formation des greffes racinaires. Les peuplements régénérés naturellement avaient des pourcentages d'arbres greffés semblables à ceux des peuplements régénérés artificiellement (de 21 % à 71 % dans l'ensemble des placettes), mais avaient un plus grand nombre de greffes par arbre (régénérés naturellement : 0,73 greffe·arbre^{-1}; régénérés artificiellement : 0,52 greffe·arbre^{-1}). Le pourcentage moyen d'arbres greffés, le nombre de greffes par arbre et la vitesse de formation des greffes étaient plus élevés dans les sols sableux (respectivement 61 %, 0,71 greffe·arbre^{-1} et 2,43 années) que dans les sols argileux (respectivement 44 %, 0,54 greffe·arbre^{-1} et 2,97 années). La proximité des arbres était une meilleure variable prédictive des greffes racinaires que la densité des peuplements, même si plusieurs greffes racinaires ont été observées entre des arbres distants de plus de 2 m dans les peuplements régénérés artificiellement. Nos résultats indiquent que les greffes racinaires se forment tôt au cours du développement d'un peuplement. Même si les arbres sont des entités initialement séparées, le nombre relativement élevé de greffes racinaires produit des peuplements dans lesquels les arbres sont abondamment interconnectés.

[Traduit par la Rédaction]

Introduction

Trees are traditionally considered as distinct entities that compete with one another for resources within forest stands. However, morphological connections that link the vascular systems of individuals can form between trees via branch or root grafts. Root grafts have been frequently observed within rather than between species of woody perennials, with reports on more than 150 angiosperm and gymnosperm species worldwide (Bormann 1966; Graham and Bormann 1966). Both intratree (self- or autografts) and intertree root grafts are especially common in temperate zone species of pines such as *Pinus resinosa* Ait., *Pinus strobus* L., and *Pinus radiata* D. Don (Armson and van den Driessche 1959; Bormann 1966; Horton 1969; Wood and Bachelard 1970; Stone and Stone 1975; Dosen and Iyer 1979), but intraspecific grafts are less commonly encountered in *Pinus taeda* L., *Pinus elliotti* Engelm., and *Pinus contorta* Dougl. ex Loud. (Miller and Woods 1965; Schultz and Woods 1967; Parsons 1992; Fraser et al. 2005, 2006). Since trees can share resources such as water, nutrients, or photosynthates through root grafts (Bormann 1966; Stone and Stone 1975; Fraser et al. 2006), the presence of these connections implies that trees are not independent of one another and that root grafting could likely play a significant role in stand dynamics. For example, survival of suppressed trees could be enhanced through carbohydrate transfers from vigorous neighbours (Fraser et al. 2006). Moreover, the interweaving and grafting of root systems can give individual trees better stability and wind firmness (Coutts 1983; Keeley 1988; Bas-

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net et al. 1993) but can also constitute pathways for the spread of infections to healthy trees (Gordon and Roth 1976; Epstein 1978*a*, 1978*b*; Reynolds and Bloomberg 1982). Consequently, the adaptive significance of this trait is still in dispute (Loehle and Jones 1998).

Due to the relative complexity of studying natural root grafting in trees, little is known on the factors affecting its frequency. The degree to which the woody roots of neighbouring trees intermingle and ultimately form vascular linkages between individuals will likely depend on a variety of factors. First, the spacing of individual boles (Külla and Lõhmus 1999; Fraser et al. 2005) and overall stand density of trees (Kozlowski and Cooley 1961; Basnet et al. 1993) are thought to enhance the incidence of root grafting by locally increasing root density (Reynolds and Bloomberg 1982). Since trees in naturally regenerated stands usually have more aggregated spatial distributions and higher initial densities than artificially regenerated stands (plantations), natural stands would be expected to contain more root grafts than plantations (Schultz 1972; Külla and Lõhmus 1999). Second, soil texture and slope position can influence root system form and architecture by constraining vertical rooting depth, horizontal root system spread, intermingling, and contact. Consequently, the propensity to form grafts is not only likely influenced by biologically determined properties of root form (Wagg 1967), including genetic relatedness (Reinartz and Popp 1987; Keeley 1988; Loehle and Jones 1998) but also controlled by extrinsic factors such as soil mechanical resistance, shear strength, moisture status, drainage class, temperature, and aeration (Gregory 1987). Third, friction between abutting roots caused by wind swaying of stems possibly enhances root grafting by wearing the root bark and facilitating contact between cambial tissues of the adjacent roots, thereby allowing grafts to be formed (Kozlowski and Cooley 1961; Loehle and Jones 1998). As stones and sand are more abrasive than clay, it is generally thought that graft formation is facilitated in coarse-textured soils, increasing root grafting frequency (Cook and Welch 1957; Bormann and Graham 1959). However, the processes involved in vascular fusion are very sensitive to disturbance, since grafting is related to wound healing and plant immune responses; instead of leading to root union, abrasion between roots that is exacerbated by wind swaying could also disrupt the delicate processes involved in the establishment of vascular continuity between individuals (Kozlowski and Cooley 1961; Graham and Bormann 1966; Loehle and Jones 1998). Nevertheless, root grafts have been found in all soil types, and no previous study has specifically tested the effects of soil texture on root grafting frequency and processes (Eis 1972; Stone 1974; Dosen and Iyer 1979). Finally, Eis (1972) suggested that root size (as a proxy for age) had an effect on the time needed for a root graft to be formed and that smaller roots with thinner bark would form grafts more quickly than larger (older) ones with well-developed bark. Fraser et al. (2005) effectively found an increase in root grafting frequency with tree age in *P. contorta* stands ranging from 2 to 46 years old, but the majority of grafts had formed by the time the roots were 20 years old.

Until now, most estimates of root grafting frequency were based on observations of stump calluses (Schultz 1972), translocation of dyes, poisons, or radioactive tracers (Bormann and Graham 1959; Graham 1959; DeByle 1964), and partial excavations (Stone 1974; Gordon and Roth 1976; Fraser et al. 2005). However, using similar trees from the same site, Bormann and Graham (1959) showed that translocation techniques significantly underestimated root grafting frequency compared with complete excavation of root systems. At the same time, studies based on partial excavations of living stumps or pairs of contiguous trees tend to overestimate root grafting frequency, since individuals are not randomly chosen within a stand. Accurate estimates of natural root grafting frequency are necessary to determine which factors affect root graft formation and their possible influence on stand dynamics. Jack pine (*Pinus banksiana* Lamb.) is the most abundant and harvested pine species in eastern Canada, but there currently is no evidence of root grafting for this species. The main objective of this study was thus to determine root grafting frequency in naturally and artificially regenerated stands of jack pine. Using complete excavation of root systems, we compared root grafting frequency for stands growing on coarse- and fine-textured soils and examined the effects of stand density, distance between trees, and tree and root size. Timing of root grafting, i.e., when grafts occurred during the tree's life history and how long it took for two individual roots to graft, was also analysed using dendrochronology techniques.

Methods and materials

Study sites

The study sites were located in the western balsam fir – paper birch (*Abies balsamea* (L.) Mill. – *Betula papyrifera* Marsh.) bioclimatic domain of the Quebec boreal forest (Grondin 1996). For the last three decades (1971–2000), annual precipitation for the region has averaged 918 mm (rainfall 670 mm, snowfall 248 mm) with an average daily temperature of 1.2 °C and an average 2344 degree-days above 0 °C (Environment Canada 2004). Root systems of jack pine were excavated in six artificially regenerated and six naturally regenerated stands, which were located between 47°58′N and 48°44′N and between 77°24′W and 79°25′W. Naturally regenerated stands were of postfire origin, while artificially regenerated stands were planted after clearcutting. Stand age ranged from 35 to 90 years with stand densities of 3000–6200 stems·ha^{-1} (Table 1). For each stand type (naturally versus artificially regenerated), half were growing on sandy soils, while the other half were on clay soils (Table 1). The regional surficial geology is characterized by thick glacial, glaciofluvial, and glaciolacustrine deposits. These deposits represent the retreat of the Laurentide ice sheet (10 100–8000 years BP) during the last glacial cycle and the submergence of the region by proglacial Lake Barlow-Ojibway (Veillette 1994). In this project, sites located on sandy sediments were associated with glaciofluvial deposits (eskers) and sites located on fine-grained sediments in the clay plain were associated with glaciolacustrine deposits. In terms of selection criteria, stands had to contain >90% jack pine stems, have a minimum density of 3000 stems·ha^{-1}, and be mature (>30 years old). Although artificially regenerated stands were younger than naturally regenerated stands, trees in both stand types were of similar size (basal area, P = 0.751; height, P = 0.154) (Table 1). All

Table 1. Characteristics of the 12 excavated plots.

Plot	Size of excavated area (m^2)	Stand type	Soil type	Stand age (years)	Density ($stems \cdot ha^{-1}$)	Mean basal area (cm^2)	Mean height (m)	No. of excavated trees	No. of grafts	No. of grafted trees	Mean no. of grafts per tree	Grafted tree (%)
N1	40	N	S	55	4400	233	15	17	15	12	0.88	70.6
N2	40	N	S	55	4000	136	16	16	11	9	0.69	56.2
N3	50	N	S	90	4600	264	14	23	19	14	0.83	60.9
N4	60	N	C	45	6200	111	12	35	22	20	0.63	57.1
N5	40	N	C	45	6200	163	13	23	20	14	0.87	60.9
N6	45	N	C	75	3100	363	20	14	7	3	0.50	21.4
P1	40	P	S	35	3800	335	16	15	10	9	0.67	60.0
P2	40	P	S	35	4000	265	14	16	10	9	0.63	56.2
P3	40	P	S	35	5000	92	9	20	12	12	0.60	60.0
P4	30	P	C	35	4000	274	12	12	6	5	0.50	41.7
P5	40	P	C	35	3000	123	12	14	4	4	0.29	28.6
P6	30	P	C	35	4000	307	12	11	5	6	0.45	54.5
Mean	41.3			48	4358	222	14	18	12	9.8	0.63	52.3

Note: N corresponds to naturally established stands P corresponds to artificially regenerated stands, S corresponds to sandy soils, and C corresponds to clayey soils.

sites were located near a water source (pond, lake, or river) to allow hydraulic excavation. To include a minimum of 10 trees within an excavation plot, the area sampled ranged in size from 30 to 60 m^2. Initial tree spacing in the artificially regenerated stands varied from 1.7 m × 3 m (on sand) to 2 m × 2 m (on clay).

Field sampling

Sampling was conducted between June 2002 and October 2007. Trees were felled with a chainsaw and cross-sectional disks were collected at both ground level (0 m) and breast height (1.30 m) for age determination. Height and diameter at breast height of all trees within a plot were measured to determine the importance of tree size on root grafting. The plots were then excavated with a high-pressure water spray using a forestry water pump (Mark III; Wajax, Lachine, Quebec) to expose the root systems and root grafts. All trees, roots, and grafts were mapped by hand and distance between trees in each plot was recorded. The presence of stumps from dead trees (trees with dead crowns) was also recorded as they were uncovered during excavation. Root diameter was recorded for each root >2 cm and a cross-sectional disk was taken as close as possible to the stem base, where it is larger, to ensure that roots had enough growth rings to allow cross-dating (Krause and Morin 1999, 2005). Roots commonly have many missing growth rings, but ring series tend to be more complete close to the stump compared with more distal locations along a given root (Krause and Eckstein 1993). All putative grafts were checked in the field by removing bark followed by partial dissection to confirm a common wood layer between the two roots. Root diameter was also measured near the grafting point; all grafts were collected and taken to the laboratory for dissection and examination under a binocular microscope.

Laboratory work

After air-drying, all stem and root disks were progressively sanded (80–500 grit). Graft and root samples required particular attention because of eccentric growth and the presence of discontinuous growth rings (Krause and Eckstein 1993). Highly problematic sections (with very narrow or incomplete growth rings) were cut with razorblades and ring-to-ring contrast improved with white chalk. The age of trees and roots was determined by counting growth rings and visually cross-dating using pointer years, such as frost marks, light rings, compression wood, and narrow and wide rings (Schweingruber 1988). To estimate how long it took for a root to reach the location where it grafted with a root from another tree, root age was determined near the stem base and at the graft location. Stem disks at ground level were cross-dated with the breast height sections to alleviate the occurrence of missing rings at ground level (Fortin 2004). The time (year) at which root grafting began and ended was determined; since it was difficult to determine when the bark between two roots in a graft was broken because of callus tissue, the beginning year (t_0) of graft formation was recorded as the year following the last complete growth ring on each root. The last year (t_f) was recorded as the year when a common growth ring was complete between the grafted roots. Time for graft formation was thus defined as the difference between t_f and t_0, which corresponds to the number of growth rings needed for the initiation (bark deformation and rupture) and completion of a graft.

Statistical analyses

Relationships between the number of root grafts per tree (NUMBER), the percentage of grafted trees per site (PERCENT), and mean stand density, soil type (sandy or clay), and stand type (naturally or artificially regenerated) were analysed with mixed linear models in R (version 2.7.2) (R Development Core Team 2008) (Table 2) using the function lme in the nlme library (linear and nonlinear mixed effects models; Pinheiro et al. 2008) The linear mixed model is a parametric model for longitudinal, clustered, or repeated-measures data that incorporates random effects while quantifying the linear relationship between a continuous dependent variable and various predictor variables (West et al. 2007). Site effects were incorporated as the random effects in the models, making the results more widely applicable to the boreal forest of eastern Canada. Two linear mixed models (lme) were also used to examine relationships between the distance separating grafted trees and stand type, soil type, and stand density together with stand age and tree basal area (Table 2). In the first model (DISTGRA), we took the distance between the grafted trees for each graft. Since trees can bear more than one graft, a second model (DISTPAIR) was developed where we considered only grafted pairs of trees without considering each graft separately. As DISTGRA and DISPAIR results were similar, only DISTGRA results are presented.

In parallel analyses, logistic regression was used to examine the relationship between the presence of a root graft and the distance between trees. To avoid "sacrificial pseudoreplication" error that is incurred when data from different experimental units are treated as independent replicates and pooled in the same analysis (Hurlbert 1984), a single logistic regression was used for each site. Goodness-of-fit of the model was assessed using the test devised by Le Cessie and van Houwelingen (1991), while omission of important or inclusion of extraneous variables was checked using Cook's distances and hat values (Everitt and Hothorn 2006). Independence of variables and randomness of residuals were also verified (Everitt and Hothorn 2006). Logistic regressions were not appropriate for sites P2 and P3, given their highly significant goodness-of-fit values, and therefore, these results are not presented.

Two other lme examined which site factors affected the ages of trees (AGETREE) and roots (AGEROOT) at the beginning of graft formation, while the time required to complete grafts ($t_f - t_0$) was examined in the model LENGTH (Table 2). For the latter model, the Fligner–Killeen test of homogeneity of variances was nearly significant (P = 0.056), and therefore, the data were transformed with a tangent function, which greatly improved homoscedasticity (P = 0.856). The influence of site characteristics on the age difference of roots between the cross section near the base of the stem and the graft location (DIFFAGER; i.e., the time it took for a root to reach the position of the graft) was tested with a mixed linear model (Table 2). Finally, the influence of soil/stand types and stand density on the number of dead stumps was also examined using a linear mixed model (DEAD model, Table 2).

Two model selection techniques were used to determine the most suitable models for NUMBER and PERCENT. First, all plausible models were compared based on the Akaike information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2004). Differences in AICc values (ΔAICc) were calculated for the respective models relative to the "best" model, i.e., the model with the lowest AICc. Models with ΔAICc < 2.0 and high Akaike weights (ω_i, interpreted as probabilities) were deemed to have the greatest statistical support (Table 3) (Burnham and Anderson 2004). Second, traditional backward model selection techniques were used to corroborate the model selected by the Akaike weights (Burnham and Anderson 2004). Since there were too many parameters to test for the other models (DISTGRA, AGETREE, AGEROOT, DIFFEAGER, LENGTH, and DEAD), simple backward elimination was performed (Table 4). Multiple comparisons of means (Tukey's tests) were used when the soil × stand interaction was significant (Table 5). Predicted values for the number of grafts and the percentage of grafted trees per site were also compared with the observed data using a simple linear regression to determine the predictive power of the selected models NUMBER and PERCENT. A significance level of P = 0.05 was used for all response variables.

Results

Root grafts were found in all 12 study sites for a total of 141 (Table 1). The number of root grafts per site varied from 4 to 22 (Table 1). Mean number of root grafts per tree was significantly greater in naturally regenerated stands ($0.73 \cdot \text{tree}^{-1}$) compared with artificially regenerated stands ($0.52 \cdot \text{tree}^{-1}$) ($P$ = 0.031) (Tables 1 and 4). Trees growing in sandy soils had more root grafts on average ($0.71 \cdot \text{tree}^{-1}$) than trees growing in clay soils ($0.54 \cdot \text{tree}^{-1}$) ($P$ = 0.008) (Tables 1 and 4). The number of root grafts per tree increased with stand density (P = 0.029) (Table 4). The following equation (R^2 = 0.997, P < 0.001) predicted the number of root grafts per tree in relation to stand type, soil type, and stand density (Fig. 1*a*):

$$[1] \quad \text{Grafts per tree} = 0.27258613 + (-0.14970216 \times \text{A}) + (0.18390226 \times \text{B}) + (0.00007743 \times \text{stand density})$$

where A = 0 in naturally regenerated stands and A = 1 in artificially regenerated stands and B = 0 in clay soils and B = 1 in sandy soils. Overall, 54% (range 21%–71% across the various plots) of the study trees developed at least one root graft within the excavated areas (Table 1). Mean percentages of grafted trees were higher in sandy soils (61%) than in clayey soils (44%) (P = 0.003) (Tables 1 and 4) and increased with stand density (P = 0.002) (Table 4). However, the percentage of grafted trees per site was similar (P = 0.502) in naturally regenerated stands (55%) and in artificially regenerated stands (50%) (Tables 1 and 4). The following equation (R^2 = 0.762, P < 0.001) predicted the percentage of grafted trees according to soil type and stand density (Fig. 1*b*):

Table 2. Mixed linear models containing all explanatory variables tested with the lme function.

Global model	
NUMBER	stand + soil + density + soil × stand
PERCENT	stand + soil + density + soil × stand
DISTGRA	stand + soil + density + surface1 + surface2 + stand age + soil × stand
DISTPAIR	stand + soil + density + surface1 + surface2 + stand age + soil × stand
AGETREE	stand + soil + density + tree surface + stand age + distance + soil × stand
AGEROOT	stand + soil + density + tree surface + root surface + stand age + distance + soil × stand
DIFFAGER	stand + soil+ density + stand age + soil × stand
LENGHT	stand + soil + density + root surface1 + root surface2 + sum of root surface + stand age + distance + soil × stand
DEAD	stand + soil + density + soil × stand

Note: Stand is the stand type (naturally versus artificially regenerated), soil is the soil texture (clay versus sand), soil × stand is the interaction between soil type and stand type, density is the number of stems·ha^{-1}, stand age is the average age of the trees within a site, distance is the distance between grafted trees, surface1 and surface2 correspond to the cross-sectional surface area of the smaller and the larger tree of the grafted pair, respectively, root surface1 and root surface2 correspond to the surface of the smaller and the larger root of the grafted pair recorded near the stump base, respectively, sum of root surface is the sum of root surface1 and root surface2, tree surface is the basal area of the grafted tree recorded at 0 m, and root surface is the surface of the grafted root.

Table 3. Models selected according to results of the small sample adjusted Akaike information criterion (AICc).

Model	Factors tested	ΔAICc	ω_i
NUMBER	stand + soil + density	0.00	0.47
	stand + soil	1.03	0.28
	soil + density	2.68	0.12
	stand	4.06	0.06
	stand + density	6.15	0.02
	soil	6.35	0.02
	stand + soil + soil × stand	6.62	0.02
	stand + soil + density + soil × stand	8.77	0.01
PERCENT	soil + density	0.00	0.92
	stand + soil + density	5.57	0.06
	soil	8.29	0.01
	stand + soil + density + soil × stand	9.59	0.01
	stand + soil	12.53	0.00
	stand + density	12.58	0.00
	stand	13.38	0.00
	stand + soil + soil × stand	18.80	0.00

Note: ΔAICc correspond to the differences in AICc values from the best model, with values <2 having greatest support. Akaike weights (ω_i) determine the probability of a model being the best explanatory model, considering the data and the suite of candidate models.

$$[2] \quad \text{Percentage of grafted trees} = 3.505125 + (17.692874 \times \text{B}) + (0.009177 \times \text{stand density})$$

where B = 0 in clay soils and B = 1 in sandy soils.

In five naturally regenerated stands (N1, N2, N3, N4, and N5) and two artificially regenerated stands (P1 and P6), graft presence was negatively correlated with the distance between trees. Logistic regressions were not significant for sites N6, P4, and P5. Distance between grafted trees decreased with stand age (P = 0.045) but increased with basal area of the smallest tree within a grafted pair (P < 0.001) (Table 4). Average distance between grafted trees was greater in clayey compared with sandy soils in the artificially regenerated stands and with either sand or clay in naturally regenerated stands (P = 0.006) (Tables 4 and 5; Figs. 2*a* and 2*b*). Stand density did not affect distance between grafted trees (P = 0.573) (Table 4).

Age of trees at the time of graft formation ranged from 1 to 90 years across all sites (Figs. 2*c* and 2*d*). Stand type, stand age, tree size, distance between trees, and the soil × stand interaction were all significant predictors of tree age at the time of graft formation (Table 4). Root grafts established when trees were older in naturally regenerated (Fig. 2*c*; Table 4) compared with artificially regenerated stands (Fig. 2*d*; Table 4) (P < 0.001). In the oldest naturally regenerated stands (N3 and N6), 92% of root grafts formed when trees were 44 to 90 years old, while in the youngest naturally regenerated stands (N1, N2, N4, and N5), 95% of root grafts formed before the trees were 45 years old. Older (P < 0.001) and larger (P = 0.005) trees formed root grafts later than did younger and smaller trees (Table 4). Root

Table 4. Models chosen using backwards elimination with significance values for each linear mixed-effects model retained.

Model	Selected factors	Estimated value	SE	df	*P*
PERCENT	soil (sand)	17.693	4.285	9	**0.003**
	density	0.009	0.002	9	**0.002**
NUMBER	stand (plantation)	–0.150	0.057	8	**0.031**
	soil (sand)	0.184	0.053	8	**0.008**
	density	0.001	0.000	8	**0.029**
DISTGRA	stand (plantation)	0.587	0.256	7	0.056
	soil (sand)	0.159	0.223	7	0.498
	stand age	–0.016	0.007	7	**0.045**
	surface1	0.001	0.000	128	**0.001**
	soil (sand) × stand (plantation)	–1.221	0.319	7	**0.006**
AGETREE	stand (plantation)	–12.453	2.462	9	**0.001**
	soil (sand)	2.469	2.095	297	0.240
	stand age	0.743	0.064	297	**<0.001**
	tree surface	0.009	0.003	297	**0.005**
	distance	8.164	1.150	297	**<0.001**
	soil (sand) × stand (plantation)	10.261	3.362	9	**0.014**
AGEROOT	soil (sand)	6.857	1.884	8	**0.007**
	density	0.003	0.001	8	**0.009**
	stand age	0.723	0.048	8	**<0.001**
	tree surface	0.839	0.409	254	**0.041**
	distance	3.897	1.129	254	**0.001**
DIFFAGER	*P* > 0.1 for all explanatory variables; therefore, no model was selected				
LENGTH	distance	–0.597	0.271	120	0.029
	soil (sand)	–1.011	0.298	10	0.007
DEAD	stand (plantation)	–382.568	149.1226	9	**0.0304**
	density	0.166	0.076	9	0.0567

Note: Statistically significant values ($P < 0.05$) are given in bold. The stand type or soil type given in parentheses corresponds to the type considered by the model. For example, in PERCENT, soil (sand) with an estimated value of 17.693 means that in sandy soils, the percentage increased by 17.693%.

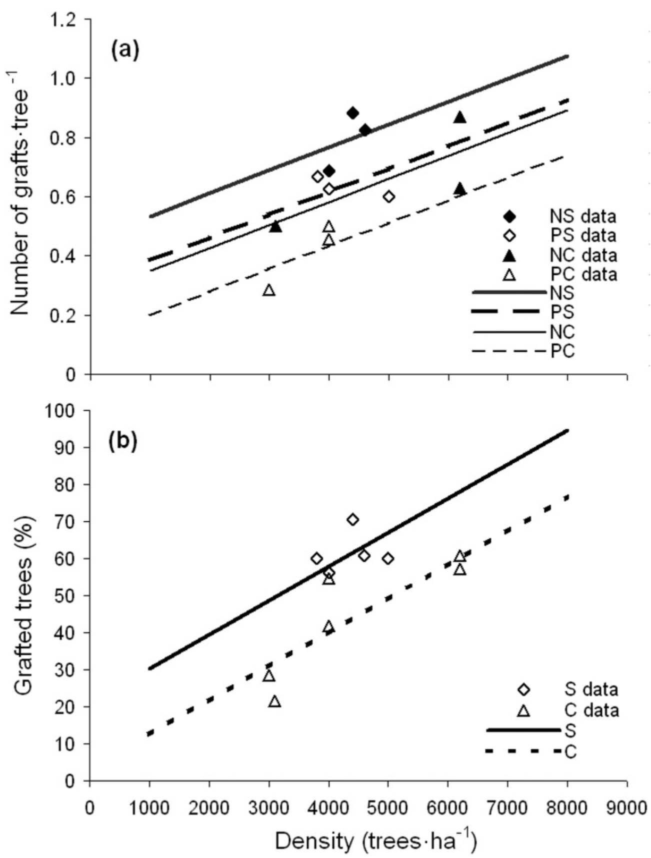
Table 5. Tukey multiple comparisons of means for each model where the soil × stand interaction was significant.

Model	Interaction	Difference	Lower limit	Upper limit	*P*
DISTGRA	PC–NC	0.933	0.512	1.353	**<0.001**
	NS–NC	–0.128	–0.422	0.166	0.668
	PS–NC	–0.185	–0.508	0.139	0.450
	NS–PC	–1.061	–1.486	–0.636	**<0.001**
	PS–PC	–1.117	–1.563	–0.672	**<0.001**
	PS–NS	–0.056	–0.386	0.273	0.971
AGETREE	PC–NC	–11.417	–17.744	–5.089	**<0.001**
	NS–NC	20.882	16.590	25.174	**<0.001**
	PS–NC	–8.700	–12.527	–4.873	**<0.001**
	NS–PC	32.299	25.575	39.023	**<0.001**
	PS–PC	2.717	–3.720	9.153	0.696
	PS–NS	–29.582	–34.033	–25.131	**<0.001**

Note: Statistically significant values ($P < 0.05$) are given in bold. Interaction codes: N corresponds to naturally regenerated stands and P to artificially regenerated stands, S to sandy soils, and C to clayey soils.

grafts between trees that were located farther apart also formed later (in relation to tree age) than root grafts between trees close to one another ($P < 0.001$) (Table 4). Grafts formed at the same time in sandy or clayey artificially regenerated stands ($P = 0.696$) (Fig. 2*d*), while they formed 20 years earlier on average in clayey soils compared with sandy soils for naturally regenerated stands ($P < 0.001$) (Table 5; Fig. 2*c*). Root grafts also formed 29 years earlier in sandy artificially regenerated compared with sandy naturally regenerated stands ($P < 0.001$) (Figs. 2*c* and 2*d*), while the difference between naturally and artificially established stands (11 years) was much smaller in clayey soils ($P < 0.001$) (Table 5; Figs. 2*c* and 2*d*). Stand density did not affect tree age at the time of graft formation ($P = 0.463$), but

Fig. 1. Prediction of the (*a*) number of grafts per tree (eq. 1) in relation to stand type (naturally (N) versus artificially (P) regenerated), soil type (sand (S) versus clay (C)), and stand density and (*b*) percentage of grafted trees (eq. 2) in relation to soil type and stand density.



root grafts formed between older roots in denser stands (P = 0.009) and sandy soils (P = 0.007) (Table 4). There was no difference between the ages of grafted roots in artificially and naturally regenerated stands (Table 4). Similar to tree age at graft initiation, age of grafted roots was also affected by the age of trees ($P < 0.001$), by tree size (P = 0.004), and by the distance between trees ($P < 0.001$); roots of older, larger, and more widely spaced trees formed root grafts later than roots from younger, smaller, and closer trees (Table 4). The difference between the age of roots near the stem base and at the graft location varied from 0 to 24 years (mean ± SD = 3.10 ± 0.85 years) and was not significantly affected by any site characteristic (Table 4).

Root grafts required between 1 and 8 years to complete (mean = 2.7 years) (Fig. 3). Ninety percent of grafts took less than 4 years to complete (time where a complete and common growth ring was visible between the two roots). Grafts between closely spaced trees needed more time to complete formation than grafts between trees that were farther apart (P = 0.029). Root grafts formed faster in sandy soils (2.43 years) compared with clayey soil (2.97 years) (P = 0.007), while stand density, stand age, stand type, root surface, and the soil × stand interaction did not affect the time required to form a root graft ($P > 0.05$ for all explanatory variables) (Table 4).

Between 250 and 1429 dead trees (snags or stumps of dead trees) per hectare (one to eight dead trees per site) were found during excavation (Table 6). The number of dead trees was highest in denser (P = 0.057) and naturally regenerated stands (985 dead trees·ha^{-1}) compared with artificially regenerated stands (472 dead trees·ha^{-1}) (P = 0.03) (Tables 4 and 6). The number of dead trees was similar for sandy and clayey sites (P = 0.52) (Tables 4 and 6). In nine of the 12 sites, we found some dead trees grafted with living trees and all of their grafted root systems (100%) were entirely or partially alive at the time of the excavation (Table 6).

Discussion

A high level of intraspecific root grafting was found for jack pine, both in postfire naturally regenerated and in artificially regenerated stands. Root grafts were found in all excavated sites (Table 1), suggesting that root grafts likely exist in most jack pine stands. Pine species are reputed for their capacity to form root grafts; percentages of grafted trees reached 30% in mature *P. contorta* (Fraser et al. 2005), 50% in *P. strobus* (Bormann 1966), and up to 90% in *P. resinosa* stands (Horton 1969). Various researchers have proposed that the proximity of trees is a more relevant indicator of root grafting frequency than is stand density (Gordon and Roth 1976; Reynolds and Bloomberg 1982; Külla and Lõhmus 1999; Fraser et al. 2005), since stands may present the same density but the spatial arrangement of trees could be different. Our results indeed suggest that proximity of trees is a better predictor of root grafting than stand density; although density increased root grafting frequency (models PERCENT and NUMBER), it did not affect distance between grafted trees (model DISTGRA) (Table 4). This indicates that stand density poorly reflected spatial distributions of individuals within stands. Distance between trees was also a better predictor than stand density in explaining the timing of root graft formation and the time required to complete graft formation (models AGETREE, AGEROOT, and LENGHT) (Table 4).

Sandy soils increased the occurrence of root grafting (number of grafts per tree, percentage of grafted trees), although many root grafts were also found in clay soils (Table 4; Fig. 1). More abrasive, coarse-textured soils may indeed be more efficient in breaking root bark away so that cambia contact to form root grafts (Cook and Welch 1957), thereby increasing root grafting frequency. Sandy soils also increased the speed of graft formation, while it took longer to complete grafts between trees that were close to one another (model LENGTH) (Table 4).

Carbohydrate transfers decrease with increasing distance between grafted trees and preferentially travel from large to small trees within a graft (Armson and van den Driessche 1959; Stone and Stone 1975; Fraser et al. 2006). Our results showed that distance between grafted trees was affected by basal area of the smaller tree (Table 4), suggesting that root grafts would be preferentially formed with a neighbouring tree if it were smaller. Perhaps dominant and suppressed trees produce secondary metabolites in different proportions, allowing roots to communicate in the same way that chemical inhibitors are produced to prevent root contact (Reinartz and Popp 1987). The fact that distance between grafted trees

Fig. 2. Mean percentages of root grafts (*a* and *b*) within each distance class between grafted trees and (*c* and *d*) age of trees at graft initiation time according to stand type (naturally (N) versus artificially (P) regenerated) and soil type (sand (S) versus clay (C)). Error bars are ±1SE.

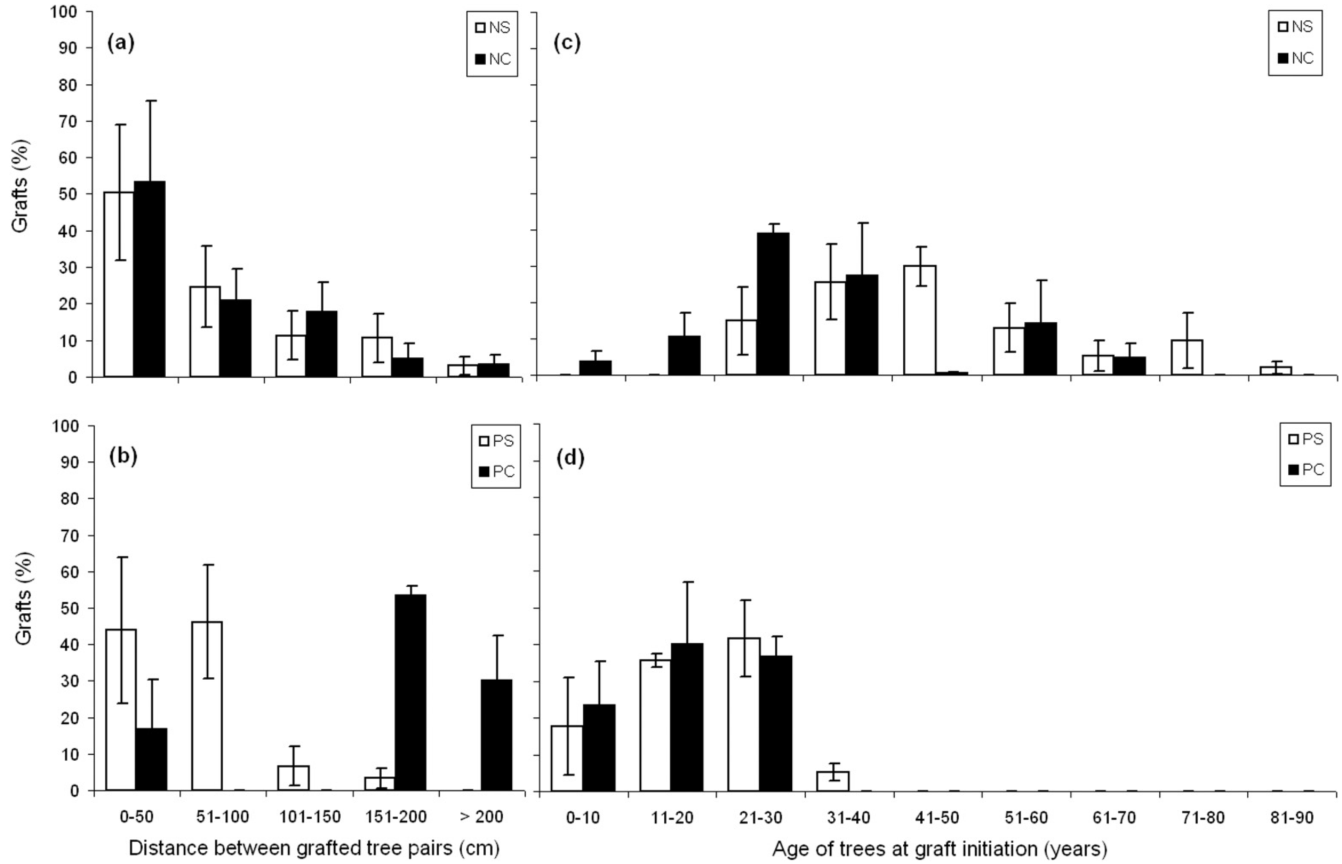
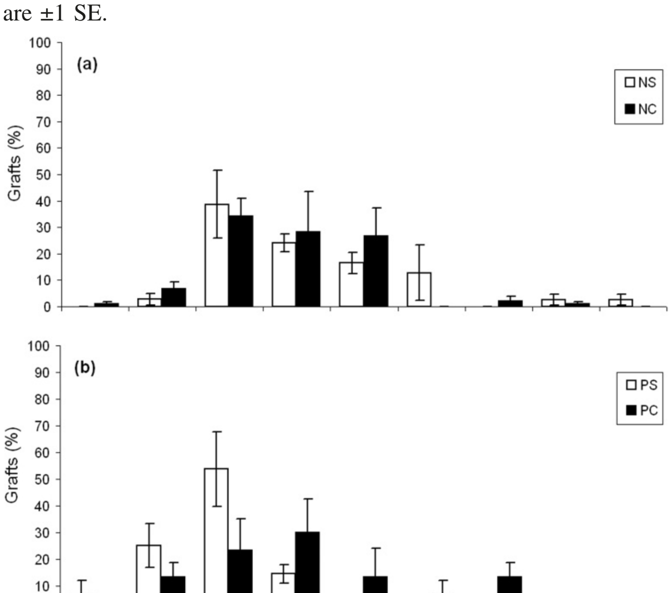


Fig. 3. Mean percentages of time required for complete graft formation for each stand type ((*a*) naturally (N) versus (*b*) artificially (P) regenerated) and soil type (sand (S) versus clay (C)). Error bars are ±1 SE.



was only affected by basal area of the smaller tree could also have been a result of root length, since small trees may not have sufficiently long roots to reach the roots of distant trees. Consequently, two small trees could not form root grafts unless they were very close to one another, although the roots of a small tree could be reached by those of a larger one. Factors other than root length are undoubtedly at play, since not all roots that came into contact formed root grafts. Indeed, we observed cases where roots of large trees passed through the root system of two or three close trees before forming a root graft with a more distant individual.

Since trees in artificially regenerated stands are generally distributed more evenly and relatively far apart than individuals in naturally regenerated stands, roots have to travel greater distances to encounter roots extending from other trees. This probably explains why the number of root grafts per tree was smaller in artificially compared with naturally regenerated stands (Tables 1 and 4; Fig. 1*a*). The fact that the percentage of grafted trees per site was similar in plantations and natural stands (Tables 1 and 4) was unexpected, however. Interestingly, distance between trees was not as good a predictor of root grafting in artificially regenerated stands (logistic regression results), where many root grafts were found between trees located far from one another (Fig. 2*b*). This result suggests that root grafting constitutes a real adaptative trait for this species, i.e., that root grafts are integral to stand dynamics in jack pine. The fact that

Table 6. Number of stumps from dead trees found during excavation and percent survival of grafted roots and of total roots from dead trees.

Plot	No. of stumps·ha^{-1}	No. of stumps·plot^{-1}	No. of stumps grafted to live trees	% of grafted roots alive	% of total roots alive
N1	513	2	1	100	67
N2	1250	5	1	100	100
N3	1000	5	1	100	100
N4	1429	8	3	100	100
N5	1053	4	0	0	0
N6	667	3	2	100	80
P1	667	2	2	100	20
P2	500	2	2	100	23
P3	667	2	2	100	100
P4	250	1	0	0	0
P5	250	1	0	0	0
P6	500	2	1	100	20

Note: N corresponds to naturally regenerated stands and P to artificially regenerated stands.

average distance between grafted trees was significantly greater for clayey versus sandy artificially regenerated stands is probably due to the greater initial spacing of trees in clayey plantations. It could be argued that the greater number of root grafts per tree found in naturally regenerated stands is due to our artificially regenerated stands being younger than the naturally regenerated stands (Fraser et al. 2006). Yet, our results suggest that grafts formed early in stand development and that they disappeared with natural self-thinning and were replaced by younger root grafts in naturally regenerated stands. When comparing only naturally regenerated stands, we indeed found that root grafts in younger stands formed earlier than in older stands (Table 4). For example, no root grafts had formed before 45 years for the 90-year-old stand, while 95% of root grafts found in stands <60 years old were formed before 45 years. It is well known that post fire naturally regenerated jack pine stands usually have very high initial seedling densities (as high as 25 000 seedlings·ha^{-1}: Van Damme and McKee 1990; Gauthier et al. 1993; Lavoie and Sirois 1998) and that heavy natural self-thinning occurs between 15 and 30 years immediately following crown closure (Smith 1986). It is thus likely that the first root grafts formed in naturally regenerated stands had disappeared with the death of trees during this self-thinning phase. Conversely, initial densities in artificially regenerated stands were much lower, and intertree competition and mortality were also probably low. Consequently, we found more dead stumps in naturally regenerated compared with artificially regenerated stands (Table 4); some showed grafts (grafts with other dead trees) that were not tallied because their degree of decay prevented accurate dating. Moreover, postfire seedling regeneration of jack pine in sandy soils is usually better than in clayey soils (Bell 1991), which suggests that self-thinning rates were higher in sandy, naturally regenerated stands (Morris 2003). It would explain why we found that root grafts formed a little later in sandy compared with clayey, naturally regenerated stands (Fig. 2*c*). It is also plausible that root connections accelerate self-thinning in natural stands (Krasny and Johnson 1992). Due to their larger crown, larger members of a communal root system may be able to establish gradients that cause water to move preferentially towards them, at the expense of less vigorous trees, thereby hastening their death (Graham and Bormann 1966). Vegetatively regenerating species such as *Populus tremuloides* Michx., where most trees are interconnected through their parental roots (DesRochers and Lieffers 2001*a*, 2001*b*), are indeed reputed for their rapid natural self-thinning (Bella and Yang 1991; Krasny and Johnson 1992). Forces other than transpiration, however, are involved in the transport of water through a root complex, since dye was also observed to move from living trees to stumps (Greenidge 1955).

Complete excavation of root systems allowed us to uncover many stumps of trees that had died and rotted away (Table 6). Most of their roots, however, remained alive when they were grafted with standing trees. This could be seen as an example of cooperative relationship within a species to assure that soil resources on a site remain within the species and prevent roots or seedlings of another species from capturing the space, even after trees previously occupying that space have died. However, some interspecific root grafts have been found, albeit very rarely, and thus were never studied in much detail (Graham and Bormann 1966). Root grafting could also be considered as a case of parasitism, if the biomass of dead or suppressed trees constitutes an excessively large photosynthate sink relative to benefits accrued from having a larger absorbing surface and stronger anchorage (Loehle and Jones 1998).

In conclusion, although site conditions affected root grafting frequency and timing, root grafts were found in all excavated sites. Root grafting frequency and the speed of graft formation were greater in sandy soils, probably caused by greater abrasiveness of sand-sized compared with clay-sized mineral particles. Proximity of trees increased root grafting frequency, although grafts between distant trees were also found, especially in artificially regenerated stands. Our results suggest that root grafts are formed early in stand development. Thus, even if jack pine trees initially begin life as individual seedlings in naturally and artificially regenerated stands, this relatively high level of root grafting produces stands where adult trees are extensively interconnected with one another. Stands may thus behave more as a functional unit than as a group of individual trees. Since root grafts allow trees to potentially share resources (photosynthates and water) and pathogens, they likely influence tree mortality, stand structure, and forest dynamics. It thus seems important to consider root grafting frequency to anticipate management consequences on tree and stand development.

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