

**EFFECT OF NATURAL ROOT GRAFTING ON GROWTH RESPONSE OF
 JACK PINE (*PINUS BANKSIANA*; PINACEAE)¹**

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- *Premise of study:* Trees are traditionally considered as distinct entities even though they can share a communal root system through root grafts, which are morphological unions between two or more roots. Little is known regarding the ecological significance of natural root grafting, but because grafted trees can share resources and secondary compounds, growth of linked trees can be affected directly by the presence of root grafts. Traditional forest ecology concepts may have to be revised to include direct interactions between connected trees.
- *Methods:* We hydraulically excavated six 30–50-m² plots (three natural stands and three plantations). We measured yearly radial growth and determined the influence of root grafting on radial growth of grafted trees.
- *Key results:* During periods of root graft formation, root grafting tended to reduce radial growth of jack pine trees, after which growth generally increased. The influence of root grafting on growth was more significant in natural stands, where root grafting was more frequent than in plantations.
- *Conclusions:* These results suggest that root grafting initially is an energetically costly process but that it is afterward nonprejudicial and maybe beneficial to tree growth. The use of a communal root system allows for a maximum use of resources by redistributing them among trees, leading to increased tree growth.

Key words: dendrochronology; Pinaceae; *Pinus banksiana*; radial growth; root grafting.

An increasing number of studies suggest that in some environments (stressed or resource-limited), positive interactions or facilitation play a more important role than competition (Bertness and Callaway, 1994; Bruno et al., 2003; Fajardo and McIntire, 2010). However, trees are still considered as distinct entities competing with each other for resources. It is nonetheless accepted that trees can indirectly act on their neighbors by modifying their common environment through root exudates, mycorrhizae, or altered soil conditions through shedding of plant parts (Woods and Brock, 1964; Brownlee et al., 1983; Pallardy, 2008). Moreover, since many tree species can share a communal root system (Graham and Bormann, 1966), it is likely that they can also directly affect growth of adjacent trees. Some species such as poplars (*Populus* spp.) regenerate by root suckering, thereby producing stands where most trees are interconnected through their parental roots (De Byle, 1964; DesRochers and Lieffers, 2001). Other species where trees are originally distinct (i.e., seedlings) can later form root grafts, which are morphological unions between two or more roots (Eis, 1972; Tarroux and DesRochers, 2010). Although natural root grafts are often viewed as natural curiosities or rare events

(Graham and Bormann, 1966), they are common and have been observed in more than 150 species (Bormann, 1966), particularly in pine species (*Pinus* spp.) around the world (LaRue, 1934; Armson and Van den Driessche, 1959; Bormann, 1966; Graham and Bormann, 1966; Horton, 1969; Wood and Bachelard, 1970; Eis, 1972; Stone and Stone, 1975; Fraser et al., 2005, 2006; Tarroux and DesRochers, 2010).

Little is known regarding the ecological significance of natural root grafting, although many agree that it could confer evolutionary advantages to forests stands and that root grafting is a real adaptive trait rather than an accidental consequence of roots crossing one another (Loehle and Jones, 1990; Basnet et al., 1993; Tarroux and DesRochers, 2010). For example, joined root systems can give trees better wind stability (Graham and Bormann, 1966; Coutts, 1983; Kumar et al., 1985; Keeley, 1988; Basnet et al., 1993), preventing weaker trees from blowing down and opening up stands, which could then make stands more susceptible to windthrow (Franklin and Forman, 1987). In this case, root grafting could be seen as an example of cooperative behavior (Kozłowski et al., 1991). Interconnected trees can also share resources like water, photosynthates, or nutrients (Bormann, 1966; Stone and Stone, 1975; Fraser et al., 2006), which could enhance survival of suppressed trees through support by their connected neighbors (Bormann, 1966; Graham and Bormann, 1966; Fraser et al., 2006). The theory that root grafting can increase the absorptive capacity or the area of coverage for nutrition by roots and, thus, lead to maximal exploitation of resources has already been mentioned (Bormann, 1966; Loehle and Jones, 1990; Basnet et al., 1993). According to Basnet et al. (1993), maximal exploitation of resources for grafted trees could even result in faster growth rates. Root grafting also enhances survival of roots, snags, and stumps of dead or cut trees (Fraser et al., 2006, 2007; Tarroux and DesRochers, 2010; Tarroux et al., 2010), which could in this case constitute a drain on resources for residual living trees (Tarroux et al., 2010).

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This relationship could be seen as a form of parasitism if assimilates acquired through root grafts prolong survival of suppressed trees at the expense of dominant trees that appear to be disadvantaged by the union (Stone, 1974; Stone and Stone, 1975; Loehle and Jones, 1990). It could also be seen as an example of cooperation, to ensure that soil resources remain within individuals of a species and prevent roots or seedlings of another species from invading the space. A better understanding of root grafting may constitute a “grand challenge” in plant functional ecology (Koerner, 2011).

In previous work, we found a high level of root grafting in natural stands and plantations of jack pines (Tarroux and DesRochers, 2010). We also found that growth response of trees to commercial thinning was affected by the presence of root grafts, because roots of trees that had died and rotted away were maintained alive by standing residual trees (Tarroux et al., 2010). The effect of root grafting on growth of trees, however, was never evaluated.

The main objective of this study was thus to determine the influence of root grafting on radial growth of jack pine (*Pinus banksiana*, L.). Since trees linked by root grafts are able to share resources (Fraser et al., 2006), we hypothesized that radial growth of grafted trees would be enhanced by the presence of root grafts (Graham, 1959; Bormann, 1966; Graham and Bormann, 1966; Loehle and Jones, 1990).

MATERIALS AND METHODS

Study sites—Three plantations and three natural jack pine stands were excavated between June 2002 and October 2007. Stands were located in the western balsam fir–paper birch (*Abies balsamea*–*Betula papyrifera*) bioclimatic domain (Gronzin, 1996) between 48°26'N and 48°43'N and between 77°38'W and 77°54'W. Natural stands were of postfire origin, growing on sandy soils (regenerated by seed; sites 1, 2, and 3 of Tarroux et al. [2010]), while plantations were growing on clayey soils (sites P4, P5, and P6 of Tarroux and DesRochers [2010]). Natural regeneration of jack pine is often deficient on clayey soils after harvesting, resulting in more plantations being established on these sites, compared to sandy sites where natural regeneration is usually abundant, especially after fire (Sims et al., 1990). Sandy sediments of the region are associated with glacioluvial deposits (eskers), while fine-grained sediments in the clay plain are associated with glaciolacustrine deposits. These deposits arose from the last glacial cycle and the submergence of the region by proglacial Lake Barlow-Ojibway and represent the retreat of the Laurentide ice sheet (10 100–8000 yr before present (Veillette, 1994)). The average climate for the last three decades showed that mean yearly precipitation was 918 mm (rainfall, 670 mm; snowfall, 248 mm) and mean daily temperature was 1.2°C, with an mean 2334 degree-days above 0°C (Environment Canada, 2010). Table 1 summarizes the characteristics of the six excavated plots. The three natural stands were commercially thinned in 1998, so we only considered growth of trees until this date,

while for the three plantations, radial growth was studied until the excavation date (2004–2005).

Field and laboratory work—Height and diameter at breast height (DBH) were measured on each tree to determine the status of trees at the time of excavation (dominant, codominant, or suppressed). Trees were felled with a chainsaw, and root systems were hydraulically excavated using a high pressure water spray from a Wajax water pump (Mark III, Wajax, Lachine, QC). Cross-sectional disks were taken at ground level (0 m), at breast height (1.30 m) and from each root with a diameter >2 cm. All suspected root grafts were checked in the field by removing bark and by partial dissecting the suspected graft to confirm a common wood layer between the two roots. In the laboratory, the age of trees, roots, and grafts was determined by counting and cross-dating growth rings (Tarroux and DesRochers, 2010; Tarroux et al., 2010). Radial growth was measured on cross sections taken from the stem base (0 m) using a Velmex (Bloomfield, New York, USA) bench interfaced with a computer (Tarroux et al., 2010). The ring-width series from the pith to the outermost ring of each wood disk was measured on four rays when possible (Tarroux et al., 2010). Curves of radial growth were then crossdated and validated using the computer programs COFECHA (Grissino-Mayer, 2001) and TSAPWin (RINNTech, Engineering and Distribution, Heidelberg, Germany). To decrease the influence of size differences between trees of different ages and sizes in the ring-width chronologies, we standardized the series using the program ARSTAN (Grissino-Mayer, 2001). The time (year) at which root grafting began and ended was determined to calculate the time period for complete graft formation.

Statistical analyses—Statistical analyses were done in the program R version 2.7.2 (R Development Core Team, 2008), and a significance level of $P = 0.05$ was used for all response variables. To examine how root grafting affected yearly growth of trees, we analyzed yearly radial growth (from stand initiation up to 1998 for natural stands and up to 2004–2005 for plantations) of grafted and nongrafted trees with a hierarchical mixed linear model (lme function; GROWTH model). Contrary to a traditional analysis of variance, linear mixed models include both fixed-effect parameters and random effects for repeated-measures data to estimate the relationship between a continuous dependent variable and the various predictors (West et al., 2007). Years and root grafting status (NG for nongrafted, G for grafted) were fixed as categorical factors, and each ray measurement was nested within its corresponding tree. Because yearly growth values are not independent from one another (growth of year t is strongly affected by the value of year $t - 1$), a first-order autoregressive correlation structure was used to reflect the strong correlation existing between successive observations (repeated measures), but that correlation decreases with spacing of the observations in time (Grissino-Mayer, 2001; Pinheiro et al., 2008). Because root grafts did not form at the same time among the six sites, a different model was used for each site. Root graft formation could take place over several years; consequently, for each graft, we considered the entire period of root graft formation and showed how radial growth was affected during and after this period.

To determine whether root grafting affected the diameter of trees, we compared the basal diameter at the time of excavation (2004–2005 for plantations or in 1998 for natural stands) for grafted and nongrafted trees with a hierarchical mixed linear model (DIFFAFTER_N for natural stands, DIFFAFTER_P for plantations) using the lme function. Another model was created to verify whether the growth of grafted and nongrafted trees was similar *before* root grafting (DIFFBEFORE_N, DIFFBEFORE_P models). Sites were treated as random effects. Basal diameters were obtained using diameter values at ground level obtained with ring-width series.

Status of trees (dominant, D; codominant, C; or suppressed, S) *before* root grafting were determined by comparing basal diameter values. For the plantations, status of trees *after* root grafting was obtained using height and diameter at breast height recorded just before excavation. In natural stands (thinned in 1998), it was not possible to use height and diameter at breast height (some trees had been cut), so we determined status of trees *after* root graft formation using only diameter values at ground level obtained with ring-width series in 1998. The different size classes were determined by comparing size of each tree with the mean stand value using t tests; suppressed trees were significantly smaller, codominant trees were similar, and dominant trees were significantly larger than the mean value. An analysis of variance (ANOVA) was then used to confirm that mean size values of the three classes differed significantly from each other ($P > 0.05$). To verify whether root grafting affected the size distribution structure of stands, we compared the frequency of each size category according to graft presence (grafted, G; nongrafted, NG) using a glmer function in the lme4 library (linear mixed-effects models using S4 classes; Bates and Maechler, 2009). A generalized linear mixed-effects model allows

TABLE 1. Characteristics of the six excavated plots of either natural stands (nat.) or plantations (plant.) of *Pinus banksiana*.

Characteristic	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
Stand type	nat.	nat.	nat.	plant.	plant.	plant.
Size of excavated area (m ²)	40	50	50	30	40	30
Stand age (yr)	50	55	60	35	35	35
Density (trees·ha ⁻¹)	4200	3800	5000	4000	3000	4000
Mean DBH (cm)	12.27	15.61	12.80	18.67	12.53	19.78
Mean height (m)	14.38	18.40	12.65	12.36	12.21	12.34
No. excavated trees	13	18	25	12	14	11
No. grafts	12	12	18	6	4	5
No. grafted trees	9	8	15	5	4	6
Mean no. grafts per tree	0.92	0.67	0.72	0.50	0.29	0.45
Percentage of grafted trees	69	44	60	42	29	54

the application of a Poisson regression. A model was created with the frequency of each status obtained *before* root grafting (STATUBEF_P and STATUBEF_N models) and another with the frequency *after* root grafting (at the time of excavation for STATUAFTER_P model and in 1998 for STATUBEF_N model), which allowed us to follow variation in stand structure with time. Multiple comparisons of means (Tukey tests) were used when the interaction between tree status (D or C or S) and root grafting (G or NG) was significant.

RESULTS

Natural stands—Trees of site 1 were established at the beginning of the 1950s (Fig. 1A). Root grafting was initiated 20 years later (1970), and the last root graft was formed in 1992 (Fig. 1A). Eight grafts (67% of grafts) formed between 1970

and 1980 (period b) and four (33% of grafts) between 1986 and 1992 (period d; Fig. 1A). GROWTH models showed that before root grafting started (period a; Fig. 1A), trees that would later form grafts generally had better growth than the other trees (only significant in 1967 and 1968). When trees became grafted (period b), growth of grafted trees decreased and was less than growth of nongrafted trees (Fig. 1A). Between 1980 and 1986 (period c), growth of grafted trees slightly increased but remained significantly less than that of nongrafted trees until 1983 (Fig. 1A). After 1992 (period e), growth of grafted trees increased similarly as during period c, although differences in radial growth between grafted and nongrafted trees were not significant (Fig. 1A). Trees in site 2 were established at the end of 1940s, and the first and last root grafts were formed in 1961

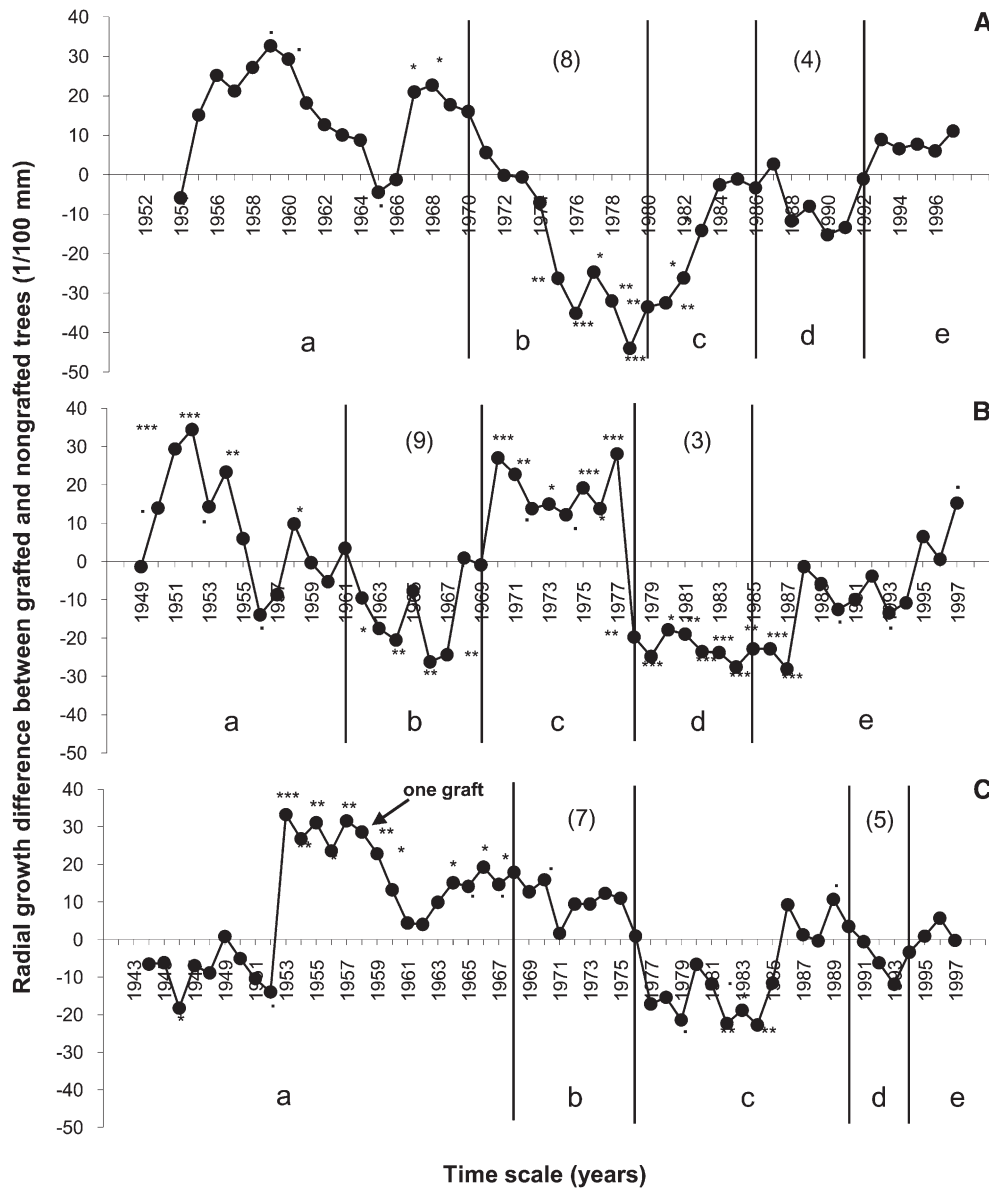


Fig. 1. Yearly radial growth differences (1/100 mm) between grafted and nongrafted trees of *Pinus banksiana* from natural stands (A) site 1, (B) site 2 and (C) site 3. Period “a” corresponds to the period before root grafting, “b” and “d” to periods of root grafting, “c” and “e” to periods without graft formation. Significance levels: *** <0.0001; ** <0.001; * <0.01; • <0.05. Number in parentheses is the number of root grafts formed within the corresponding time period.

and 1985, respectively (Fig. 1B). Nine grafts (75% of grafts) occurred between 1961 and 1969 (period b) and three grafts (25% of grafts) formed between 1978 and 1985 (period d; Fig. 1B). Before trees grafted (period a), trees that would later form grafts had greater radial growth than nongrafted trees from 1950 to 1955 and in 1960 (Fig. 1B). When trees began to form root grafts (period b), growth of grafted trees decreased and became less than radial growth of nongrafted trees (Fig. 1B). Between 1970 and 1977 (period c), radial growth of grafted trees was greater than that of nongrafted trees, while it decreased again during the second root grafting period (period d; Fig. 1B). After 1987 (period e), growth of grafted trees gradually increased and was similar to that of nongrafted trees (Fig. 1B). Trees were established at the beginning of the 1940s at site 3 (Fig. 1C). In this site, the first root graft occurred in 1958, which was followed by two periods of root grafting; seven grafts (55% of grafts) formed between 1968 and 1976 (period b), and three grafts (37% of grafts) formed between 1990 and 1994 (period d; Fig. 1C). Growth of grafted trees decreased after the first graft in 1958 and slowly increased over that of nongrafted trees until 1975 (during period b), when more root grafts were formed (Fig. 1C). Growth of grafted trees decreased rapidly after period b and slightly increased at the end of period c until the last root grafting period (period d), when it decreased again (Fig. 1C).

Before root grafting occurred, basal diameter of trees that would later form root grafts in natural stands was greater than that of nongrafted trees (DIFFBEFORE_N model; $P = 0.026$; Table 2). There was an interaction between root grafting and dominance status before root grafting (STATUBEF_N model; $P < 0.05$; Table 3, Fig. 2A), showing that few suppressed trees made root grafts compared to the number of dominant trees, because observed frequencies of G:S were significantly less than observed frequencies of G:D ($P = 0.045$). However, the proportion of codominant grafted trees was similar to the proportion of dominant and suppressed trees. For the nongrafted trees, observed frequencies of each status were equally distributed ($P > 0.05$; Table 4, Fig. 2A). For trees of the same dominance status, there was no difference between the proportion of grafted and nongrafted individuals (NG:S and G:S, NG:C and G:C, NG:D and G:D, $P > 0.05$; Table 4, Fig. 2A). After the periods of root grafting, stem basal diameters of grafted and nongrafted trees were similar (DIFFAFTER_N model; $P = 0.995$), and most trees were in the codominant category (STATUAFTER_N model; $P < 0.05$; Table 4, Fig. 2B). Frequency of codominant trees for grafted (G:C) and nongrafted (NG:C) trees was similar ($P = 0.997$) and was higher than frequency of suppressed and dominant trees (Table 4, Fig. 2B).

Plantations—Trees of all plantations were planted at the beginning of the 1970s (Fig. 3A). At site 4, root grafting began in

TABLE 3. Results of hierarchical mixed models (glmer function) testing the frequency of each tree status (dominant, D; codominant, C; suppressed, S) according to graft presence/absence (grafted, G; non-grafted, NG) before (STATUBEF) and after (STATUAFTER) grafting for natural stands (_N) and plantations (_P) of *Pinus banksiana*. The status (in parentheses) corresponds to the type considered by the model and statistically significant values ($P < 0.05$) are in boldface.

Model	Factors	Estimate	SE	P-value
STATUBEF_N	(Intercept)	3.664	0.092	<0.001
	typeNG	0.281	0.122	0.022
	statusD	0.338	0.121	0.005
	statusS	-1.766	0.242	<0.001
	typeNG:statusD	-0.999	0.183	<0.001
	typeNG:statusS	0.897	0.284	0.002
STATUBEF_P	(Intercept)	3.536	0.099	<0.001
	typeNG	0.000	0.120	<0.001
	statusD	-0.664	0.169	<0.001
	statusS	0.328	0.129	0.011
	typeNG:statusD	-1.374	0.263	<0.001
	typeNG:statusS	-1.656	0.197	<0.001
STATUAFTER_N	(Intercept)	4.374	0.065	<0.001
	typeNG	-0.102	0.094	0.280
	statusD	-2.253	0.210	<0.001
	statusS	-1.835	0.175	<0.001
	typeNG:statusD	0.620	0.270	0.021
	typeNG:statusS	0.225	0.242	0.351
STATUAFTER_P	(Intercept)	4.489	0.061	<0.001
	typeNG	-0.078	0.088	0.378
	statusD	-2.754	0.250	<0.001
	statusS	-2.754	0.250	<0.001
	typeNG:statusD	-17.959	2002.176	0.993
	typeNG:statusS	1.215	0.292	<0.001

1989 and ended in 2001 (period b). During root graft formation, growth of grafted trees was slightly better than growth of nongrafted trees, but yearly differences were not significant, except for 1994 when growth differences were marginally significant ($P = 0.056$; Fig. 3A). After this period of root graft formation (2001), growth of grafted trees decreased and became less than growth of nongrafted trees in 2002 (Fig. 3A). There were only two root grafts at site 5, where the first began to form in 1980 (period b) and the last in 1997 (period d, Fig. 3B). There was no significant difference between radial growth of grafted and nongrafted trees, except in 1979 where growth of trees that would later form root grafts was slightly greater than growth of nongrafted trees (Fig. 3B). Five root grafts were found at site 6, where there were three periods of root grafting formation; one graft began to form in 1982 and one in 1986 (period b), two grafts formed between 1992 and 1996 (period d), while the last graft formed between 1999 and 2002 (period f; Fig. 3C). In 1982 and 1986 (period b), while growth of grafted trees was greater than growth of nongrafted trees, formation of the first two grafts was followed by growth decreases (Fig. 3C). Radial growth was similar between grafted and nongrafted trees between 1986 and 2001 (periods c–f), and after the formation of the last root graft in 2000, growth of grafted trees was significantly less than that of nongrafted trees (Fig. 3C). Before root grafting occurred (DIFFBEFORE_P model), stem diameter was marginally influenced by root graft status ($P = 0.094$; Table 2), i.e., diameter of future grafted trees was slightly less than that of nongrafted trees. Most nongrafted trees were codominant individuals ($P < 0.05$), while size-class distribution of future grafted trees was distributed more evenly among the three classes ($P > 0.05$) with a trend for more trees in the suppressed

TABLE 2. Results of hierarchical mixed models (lme) testing diameter at stem base of grafted (G) and nongrafted trees (NG) before (DIFFBEFORE) and after (DIFFAFTER) root grafting for natural stands (_N) and plantations (_P) of *Pinus banksiana*. The grafting status (in parentheses) corresponds to the type considered by the model and statistically significant values ($P < 0.05$) are in boldface.

Model	Factors	Estimate	Standard error	P-value
DIFFBEFORE_N	graft (NG)	-335.111	145.651	0.026
DIFFBEFORE_P	graft (NG)	110.980	64.468	0.0945
DIFFAFTER_N	graft (NG)	-7.394	1263.326	0.995
DIFFAFTER_P	graft (NG)	-116.736	252.234	0.647

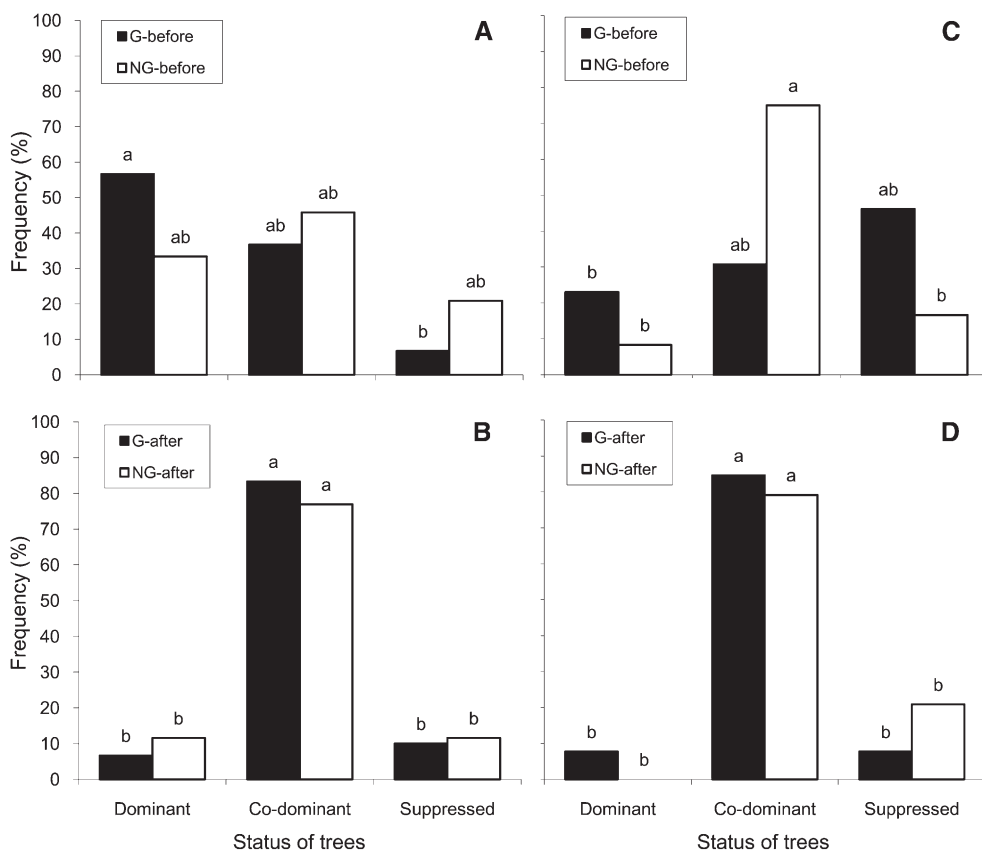


Fig. 2. Percentages of grafted and nongrafted trees of *Pinus banksiana* from natural stands (A) before and (B) after root graft formation and from plantations (C) before and (D) after root graft formation, according to their dominance status.

class (Table 2; Fig. 2C). At the time of excavation (2004–2005; DIFFAFTER_P model), there was no difference between stem basal diameter of grafted and nongrafted trees in plantations ($P = 0.647$; Table 2). Observed frequencies of each status (D, C, S) after root grafting (STATUAFTER_P) showed that most individuals became codominants (Tables 3, 4; Fig. 2D). Frequency of codominant trees was similar for grafted (G:C) and nongrafted (NG:C) trees ($P = 0.989$; Table 4) and was higher than frequencies of sup-

pressed ($P < 0.05$; G:S and NG:S; Table 4) and dominant (G:D and NG:D; Table 4) trees, regardless of root grafting status (Fig. 2D).

DISCUSSION

There are costs and benefits associated with natural root grafting. This study suggests that grafting is an energetically

TABLE 4. Tukey multiple comparisons of means for each model where the interaction “dominance status (dominant, D; co-dominant, C; suppressed, S) × grafting status (grafted, G; non-grafted, NG)” for *Pinus banksiana* was significant. Statistically significant values ($P < 0.05$) are in boldface.

Interaction	STATUBEF_N		STATUBEF_P		STATUAFTER_N		STATUAFTER_P	
	diff	P-value	diff	P-value	diff	P-value	diff	P-value
NG:C × G:C	12.667	0.938	37.333	0.216	-7.667	0.997	-6.667	0.989
G:D × G:C	15.667	0.865	-16.667	0.876	-71.000	0.013	-83.333	0.000
NG:D × G:C	-12.333	0.944	-25.000	0.593	-65.333	0.023	-89.000	0.000
G:S × G:C	-32.333	0.263	13.333	0.946	-66.667	0.020	-83.333	0.000
NG:S × G:C	-17.333	0.812	-15.333	0.908	-65.000	0.024	-71.333	0.000
G:D × NG:C	3.000	0.999	-54.000	0.037	-63.333	0.028	-76.667	0.000
NG:D × NG:C	-25.000	0.509	-62.333	0.015	-57.667	0.049	-82.333	0.000
G:S-NG × C	-45.000	0.064	-24.000	0.630	-59.000	0.043	-76.667	0.000
NG:S × NG:C	-30.000	0.330	-52.667	0.043	-57.333	0.050	-64.667	0.001
NG:D × G:D	-28.000	0.397	-8.333	0.993	5.667	0.999	-5.667	0.995
G:S × G:D	-48.000	0.045	30.000	0.414	4.333	1.000	0.000	1.000
NG:S × G:D	-33.000	0.246	1.333	1.000	6.000	0.999	12.000	0.880
G:S × NG:D	-20.000	0.712	38.333	0.196	-1.333	1.000	5.667	0.995
NG:S × NG:D	-5.000	0.999	9.667	0.986	0.333	1.000	17.667	0.618
NG:S × G:S	15.000	0.884	-28.667	0.459	1.667	1.000	12.000	0.880

costly process but that once completed, the grafts seemed to enhance radial growth of trees. Root grafting tended to reduce radial growth of jack pine trees during root graft formation, especially in natural stands that contained higher numbers of root

grafts compared with plantations (Fig. 1). It is not completely unambiguous that root grafting caused growth increases in trees, because growth of trees that would later form grafts was generally better than growth of nongrafted trees in natural

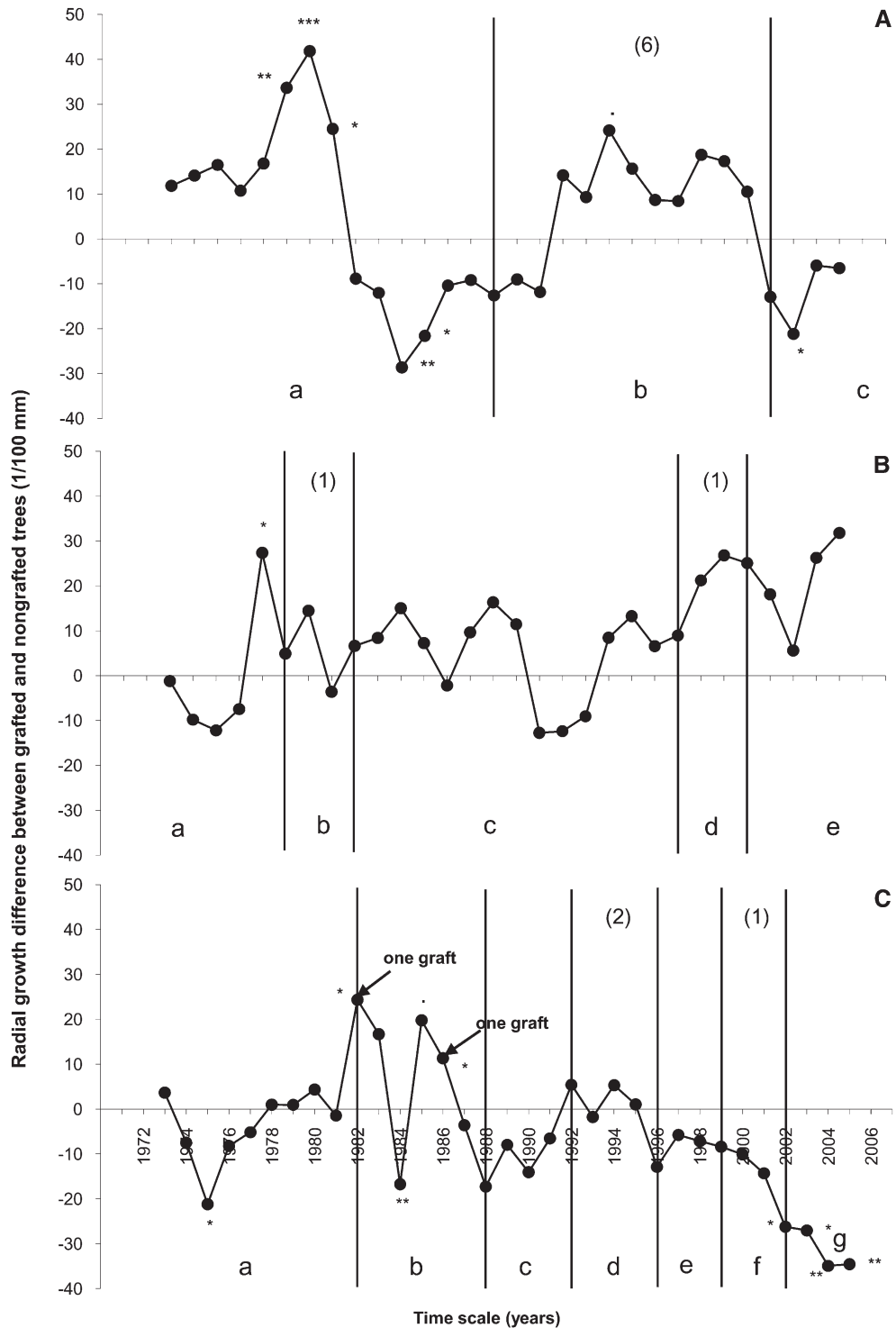


Fig. 3. Yearly radial growth differences (1/100mm) between grafted and nongrafted trees from plantations of *Pinus banksiana*: site 4 (A), site 5 (B) and site 6 (C). Period “a” corresponds to the period before root grafting, “b”, “d”, and “f” to periods of root grafting, “c”, “e”, and “g” to periods without graft formation. Significance levels: *** <0.0001; ** <0.001; * <0.01; • <0.05. Number in parentheses is the number of root grafts formed within the corresponding time period.

stands *before* root grafting, until a “grafting period” occurred and radial growth of grafted trees decreased (Fig. 1). As first suggested by Loehle and Jones (1990), root grafting is undoubtedly an energetically costly process, which could explain why in natural stands, root grafts preferentially formed between larger and dominant trees (Tables 2–4, Fig. 2A) and why radial growth decreased as root grafts were forming (Fig. 1). Callus tissue is normally produced around root grafts, and the structure of this wood is more complex than that of regular roots because tracheids are produced along two axes, allowing transfers between the two grafted roots (Bormann, 1966). Suppressed or weaker trees may lack energy to form root grafts, or perhaps their root systems do not extend far enough to reach roots of other trees. Because they receive less light, smaller suppressed trees in natural forests (initially more dense than plantations; Smith, 1997) have fewer carbohydrate reserves to allocate to root growth (and formation of root grafts) once maintenance respiration needs, i.e., the energy required to keep existing cells and tissues alive, have been satisfied (Kozłowski et al., 1991). Few root grafts formed before trees were 10 yr old (Figs. 1, 3), which could be a consequence of little contact between roots of small trees (Tarroux and DesRochers, 2010; Tarroux et al., 2010).

In plantations, the influence of root grafting during root graft formation was less apparent; in contrast to natural stands, growth of grafted trees did not significantly decrease compared to growth of nongrafted trees (Fig. 3). The impact of root grafts on radial growth could be less important in plantations because they contained fewer root grafts (Table 1) or because trees were evenly spaced within the stand, giving them access to more or less the same quantity of resources. Furthermore, trees in plantations were more vigorous than in natural stands, because they were younger but larger (Table 1). Trees originating from plantations often come from improved seed stocks, and soil resources in these clayey plantations may have been less limiting than in the sandy natural stands (Wilde et al., 1964; Bell, 1991). When growth is not limited by nutrients, water, or light availability, trees can increase their production of photosynthates (Salisbury and Ross, 1992). Carbohydrates formed within tree crowns (sources) travel downward to roots (sinks) according to the principle of source–sinks, and their production can be influenced by sink demand because photosynthetic reactions are facilitated when sinks are large (Salisbury and Ross, 1992). Faster growth rates of trees in plantations thus suggest that trees had enough resources to compensate for the cost of root graft formation without negatively affecting their diameter growth.

After each period of root graft formation, radial growth of grafted trees in natural stands usually resumed comparable or greater levels than nongrafted trees (Fig. 1). In plantations, growth did not seem to be enhanced by root grafting because stem basal diameter and yearly radial growth were similar between grafted and nongrafted trees at the time of excavation (Table 2, Fig. 3). Nevertheless, the fact that trees that formed grafts tended to be smaller before root grafting occurred (DIFFBEFORE_P; Table 2) and became similar in size to nongrafted trees at the time of excavation (DIFFAFTER_P; Table 2) suggests that root grafting in plantations was also beneficial to tree growth. Bormann (1966), Graham and Bormann (1966), Loehle and Jones (1990), and Basnet et al. (1993) suggested that root grafting should enhance radial growth and stand survival by facilitating acquisition of resources by those members of the communal root system that are located farther away from such resources (water, for example). If most trees are interconnected, resources of a site become somewhat accessible for all

interconnected trees, rather than just for trees with the largest root systems. The use of a communal root system could thus maximize use of resources by redistributing them among trees and consequently equalizing tree growth and sizes within a stand (Walters, 1963). However, in our study, most trees were in the codominant size category at the time of excavation, whether they were grafted or not (Fig. 2B, D). Nevertheless, prior to root grafting, size distribution of trees that would later form root grafts differed greatly from the size distribution pattern found after root grafting, compared to that of nongrafted trees, showing that grafted trees further homogenized their size compared to nongrafted trees (Fig. 2). In natural stands, most future grafted trees were dominant trees, and only a few were suppressed, while the distribution of nongrafted trees was more regular among status classes (Fig. 2A). In plantations, most of the nongrafted trees were already codominant (Fig. 2C) and had remained codominant by the end of the study (Fig. 2D).

The fact that root grafting allows the sharing of resources and of secondary compounds among trees challenges the classic competition concept in its strict sense (Begon et al., 2006). Root grafting could be interpreted as an intraspecific cooperative behavior that maintains stand integrity (Loehle and Jones, 1990; Jelínková et al., 2009). Root grafting could promote dominance of a species on a site, with bigger trees supplying carbohydrates to suppressed trees within a root complex (Basnet et al., 1993), and circumvent the death of trees, that would create gaps in the stand and available space for other species to invade.

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