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Growth and survival of lodgepole pine and Scots pine after 25 years in a reciprocal transplant experiment in Canada and Sweden

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ABSTRACT

Lodgepole pine is native to western North America, but it is also planted as a fast-growing alternative to Scots pine in Sweden. The production of these two species, when grown as native and as exotic species, was compared in a transcontinental two-species provenance experiment. The tests were planted in 1986 on five sites in northwestern Canada and two sites in Sweden, and included full-sib families, half-sib families, seed orchard collections and natural stand seed collections of both species. After 25 years, lodgepole pine produced 48% more volume (m^3ha^{-1}) and had 27% higher survival than Scots pine at one Swedish site, and had similar volume production and survival at a second. In the five Canadian sites, Scots pine produced on average 22% more volume than lodgepole pine. The variation between sites was, however, large. This higher volume of Scots pine in Canada could be due to higher survival (+28%) and less frequent damage; but higher top height for lodgepole pine in Canada indicated higher potential productivity. The results indicate that an exotic species may produce more than the native species, possibly thanks to higher survival, but it is also possible to increase production with successful population selection of the native species.

KEYWORDS: Species interaction; exotic species; productivity; provenance transfer; competition; genetic correlation; stem damage

Introduction

Introduced species have long been used in forestry to enhance productivity (Tigerstedt 1993), but few studies have adequately tested the actual effects of the introduction relative to native species. The realized niche of a species is strongly affected by its evolved tolerance to climate and pests, but when grown as an exotic species, it may flourish in the new environment, thanks to less pressure from pests and pathogens (Tigerstedt 1993). There are many examples of planned introductions of tree species that grow and perform well as exotics (Wang et al. 2006a; Cubbage et al. 2014; Verhaegen et al. 2014). One example where, in addition, the productivity is much lower in the natural range is the introduction of Monterey pine (*Pinus radiata* D. Don) to large areas in Australia, New Zealand, Chile and Africa, where it makes a very strong contribution to the forest industry (Piirto & Valkonen 2005).

Another example of an introduction of a tree species for use in forestry is the planting of the interior variety of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), native to western North America, in northern and central Sweden. Observations from small plantations of lodgepole pine in Sweden and Finland from between 1910 and 1930 indicated that this exotic species could be more productive than the native Scots pine (*Pinus sylvestris* L.) (Elfving et al. 2001). In the 1960s, several provenance tests were established in Sweden to determine the most productive and well-adapted provenances from North America (Karlman 1986; Lindgren et al. 1988; Rosvall et al. 1998). Since 1970, more than 600 000 ha in northern and central Sweden have been planted with lodgepole pine (Skogsstyrelsen 2013). Around 130 field experiments that have been running for between 15 and 64 years indicate that it is on average ca. 36% more productive than Scots pine (Elfving & Norgren 1993; Elfving et al. 2001), probably because it has larger needle biomass at a given stem volume (Elfving et al., unpublished data) and larger needle area at a given stem volume (Norgren 1996). The risks associated with introducing the species to Sweden have been thoroughly reviewed by Karlman (1981, 2001).

As far as we know, there are no published, systematic cross-validations of main tree species, comparing the development in the home range with that under exotic conditions. To address this, we made use of a transcontinental reciprocal transplant experiment which was established to compare the productivity, survival rates and damage by pests and pathogens of Scots pine and lodgepole pine at five sites in western Canada and two sites in Sweden (A Joint Swedish – Canadian 1987; Lindgren & Lindgren 1990). The experiment was established in 1986 and included full-sib and half-sib families from the two species, together with seed-lots from collections in natural stands for reforestation (operational seed-lots). Test sites were chosen to represent a range of biotic and abiotic environments in western Canada and Sweden. The experiment was intended to quantify the benefits of using introduced lodgepole pine in Sweden and Scots pine in Canada, and to assess the potential spread of pests, pathogens and insects between the species. Early results from the Canadian test sites of this experiment have been published by Lindgren and Lindgren (1990), Van der Kamp et al. (1995) and Karlman et al. (1997) and further discussed by Karlman (2001). The average survival rates seven years after planting were 94% for lodgepole pine and 95% for Scots pine, with mean heights of about 1.70 and 1.45 m, respectively (Karlman et al. 1997).

The so-called enemy release hypothesis (Keane & Crawley 2002; Mitchell & Power2003) implies that a species can be more successful when used as an exotic species compared to being a native species, since in the new environment it does not meet the threats (pests and pathogens) that have evolved during its existence in its native environment. One effect of this could be higher production (Keane & Crawley 2002). The opposite may also occur. A new pathogen or insect may seriously attack the exotic species so it produces considerably less in its new environment (Garbelotto & Pautasso 2012). Another explanation for better success is that the biota in the new environment suits the introduced species better than where it is native. For lodgepole pine, for instance, Gundale et al. (2014) showed that the Swedish soil provides better biota than the Canadian soil, and McIntosh et al. (2012) found that the nitrogen availability was better in the Swedish soil than in the Canadian since the latter had higher net nitrogen immobilization. With this study we want to compare the production of lodgepole pine and Scots pine when growing as native species and as exotic species. The results are discussed in the light of the "enemy release hypothesis" and possible differences in soil conditions between Sweden and Canada. The occurrence of diseases and insects in this material will be reported in a concurrent article, and the objectives of this work were (1) to compare the productivity after 25 years in the field between Scots pine and lodgepole pine when grown as native and exotic species in Canada and Sweden, (2) to provide possible reasons for the growth differences on the two continents, (3) to evaluate differences between provenances of both species and (4) to evaluate the phenotypic stability over environmental gradients of the species.

Materials and methods

Plant material

Full-sib families, half-sib families, seed orchard seed-lots and operational seed-lots of lodgepole pine and Scots pine were used (Table 1(a,b)). Due to the young age of the lodgepole pine and Scots pine seed orchards resulting in reduced flower production, it was not possible to create full-sib families for all parents and populations. Consequently, also half-sib and polycross families had to be included, together with operational seed-lots. The lodgepole pine full-sib families were created in four seed orchards in Sweden (Norrberge, Sör Nedansjö, Lögdö and Galtström) belonging to SCA (Svenska Cellulosa Aktiebolaget). The orchards were composed of phenotypically selected but untested parent trees originating from British Columbia and Yukon, and a total of 42 parents were used to create 32 full-sib families. Seed for lodgepole pine half-sib families was collected from selected parent trees in close proximity to the test sites. Seven operational lodgepole pine wild-stand seed collections were also included. The Scots pine full-sib families were created in several Swedish seed orchards by crossing among phenotypically selected but untested parent trees. Several half-sib Scots pine families were created by applying a pollen mix to parent trees in two seed orchards in Sweden (Skogsgård and Klocke, in which three and 20 pollen donors were used, respectively). Half-sib and full-sib families were grouped into provenances based on the location of origin of the parent trees (Figure 1).

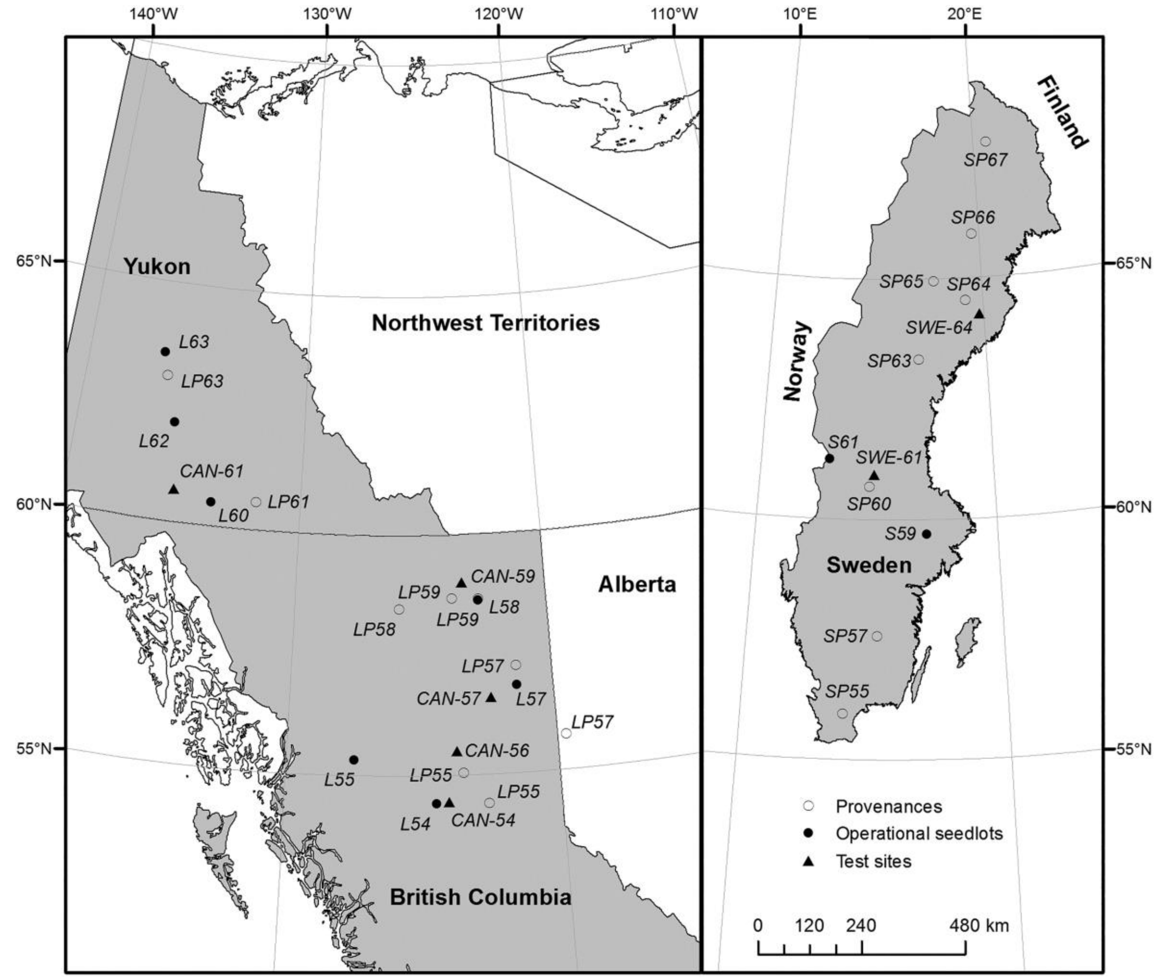

Figure 1. Locations of the test sites, and origins of provenances and operational control seed-lots in Canada and Sweden. The provenances and operational control seed-lots were collected from the area surrounding the point source located on the map. See Table 1 for definitions of the abbreviations.

Table 1. Origins of (a) lodgepole pine (LP or L) and (b) Scots pine (SP or S) seed used in the reciprocal transplant experiment.

(a)						
Origin	Provenance	Family structure	No. of families	Latitude (°N)	Longitude (Can: °W, Swe: °E)	Elevation (m)
Southern group	LP58	Full sibs	16	56.28–59.78	122.74–129.57	618–1020
Central group	LP61	Full sibs	8	60.75–60.89	129.52–134.80	579–926
Northern group	LP63	Full sibs	8	62.22–63.62	134.90–136.67	552–1091
Summit Lake	LP55	Half sibs	4	54.40	122.62	813
Philip Creek			4	55.05	123.50	1020
Saddle Hills	LP57	Half sibs	4	55.73	119.67	825
Beatton River			4	57.23	121.37	1010
Fort Nelson	LP59	Half sibs	2	58.65	122.70	495
Steamboat Mtn.			2	58.67	123.75	630
Fort St James	L54[a]		Unknown	54.42	124.50	805
Hazelton	L55[a]		Unknown	55.33	127.50	600
Beatton River	L57[a]		Unknown	56.83	121.37	800
Fort Nelson	L58[a]		Unknown	58.63	122.70	495
Squanga	L60[a]		Unknown	60.50	133.75	792
Carmacks	L62[a]		Unknown	62.07	135.70	569
Rusty Creek	L63[a]		Unknown	63.50	136.57	760

(b)						
Origin	Provenance	Family structure	No. of families	Latitude (°N)	Longitude (Can: °W, Swe: °E)	Elevation (m)
Haradstorp	SP55	Full sibs	8	55.96–56.22°	13.34–14.28	15–100
Reference cross	SP60	Full sibs	1	60.68	14.68	280
Domsjöänget	SP63	Full sibs	11	62.49–65.33	15.54–19.96	185–360
Brån	SP64	Full sibs	4	63.80–64.81	19.96–20.14	90–355
Östteg	SP65	Full sibs	9	64.49–64.85	17.51–19.61	220–435
Skatan	SP66	Full sibs	8	65.02–67.42	18.20–21.30	265–390
Skogsgård	SP57	Half sibs and full sibs[b]	8	57.42–57.69	14.74–15.62	140–184
Klocke	SP67	Half sibs and full sibs[b]	8	67.16–67.57	19.94–21.56	363–438
Långtora	S59[c]		Unknown	59.65	18.27	103
Askerud	S61[c]		Unknown	60.78	13.01	364

[a] Local lodgepole pine control seed-lots in Canadian test sites, named LPL in Tables 4 and 5, and in the text.
[b] Orchard polycrosses creating a mix of half-sib and full-sib families with 3 and 20 pollen parents, respectively.
[c] Bulk orchard collection with no family structure. There were 36 seed donors at Långtora and 43 at Askerud, and the pollen donors were either the clones in the orchard, or trees from outside the orchard.

Seedlings for the Canadian sites were grown in 1985 at the Balco Nursery (now Tolko Nursery) situated in Kamloops (latitude 50.6°N), British Columbia, and for the Swedish sites at the Faculty of Forestry nursery at the Swedish University of Agricultural Science in Umeå (latitude 63.8°N). In Sweden, seedlings were grown indoors until early July and material from southern latitudes was treated with prolonged nights after July 22.

Planting and test sites

Seedlings were planted in the spring of 1986 on five test sites in western Canada (four in British Columbia and one in Yukon; site codes CAN-54, -56, -57, -59 and -61) and two test sites in Sweden (site codes SWE-61 and -64) (Figure 1; Table 2). The test sites were selected to represent a wide range of geographic and climatic conditions. The Renberget site (SWE-64) was fenced to protect seedlings from moose (*Alces alces*) and reindeer (*Rangifer tarandus*), and the Fort St John site was fenced against cattle. At Garsås (SWE-61), both Scots pine and lodgepole pine were heavily damaged by pine weevil (*Hylobius abietis*) at a young age and by moose at an older age. Thus, based on the criterion that the plots should have more than 20 of 64 living trees to be selected for evaluation, only 45% of the plots were evaluated.

Table 2. Field tests included in the reciprocal transplant experiment with LP and SP.

Location	Site code	Latitude (°N)	Longitude(Can: °W, Swe: °E)	Elevation(m)	Soil type
Fort St James	CAN-54	54.45	124.05	855	Sandy, some gravel and silt. 1–3 cm organic layer
Mackenzie	CAN-56	55.50	123.72	680	Medium to coarse sand, some gravel. Ca. 1 cm organic layer
Fort St John	CAN-57	56.60	122.37	800	Medium to coarse sand with gravel. Partly thick organic layer
Fort Nelson	CAN-59	59.00	123.33	600	Silt clay (rather heavy)
Whitehorse	CAN-61	60.68	135.37	660	Silt soil, medium to fine sand. Little or no organic matter
Garsås	SWE-61	60.93	14.88	205	Sandy till. Thin organic layer
Renberget	SWE-64	64.25	19.80	225	Sandy till/fine sand. Some stony ground

Experimental design

Each site was established using a randomized complete block design with five blocks per site. At every site except SWE-61, blocks 1–4 were composed of 8 × 8 tree square plots with separate species and provenances. The number of plots (treatments) per block varied between 9 and 11. Block 5 was composed of single tree plots with mixed species, provenances and families. At SWE-61, 4 × 16 tree plots were used, instead of 8 × 8 tree square plots, in blocks 1–4. A 2 m × 2 m square spacing was used. The number of individuals per full-sib or half-sib family at each site was unbalanced and ranged from 2 to 61, with most families represented by between 8 and 40 individuals per site. Families were planted at random within provenance plots. In general, three rows of surround trees were planted around each trial.

Measurements

The measurements were made in 2010, when active growth was nearly complete (end of June and beginning of July) in Canada and after completion of seasonal growth (August and October to December) in Sweden. The status of each tree was recorded, along with diameter at breast height (DBH, one measure to the nearest half centimeter at 1.3 m above the ground) in blocks 1–4 for sites in Canada and all five blocks for the two Swedish sites. At the Canadian sites, the largest stem of double stems was measured, so productivity was slightly underestimated. Tree height was measured to the nearest decimeter of every 10th tree from each provenance (8 × 8 tree plot) using a vertex hypsometer and the average of three measurements per tree was recorded (HT). When a tree that was preselected for height growth measurement had abnormal form (e.g. a fork or broken top) the closest representative tree was selected in its place. There was substantial mortality caused by mountain pine beetle at Fort St James and Mackenzie (CAN-54 and CAN-56, respectively). We preferred to estimate total productivity without considering this extreme event, so both living trees and trees that had recently died (1–3 years before assessment) were assessed and measured for diameter.

Calculations of stem volume and top height

Individual tree stem volumes including bark over stump height (1% of tree height) were calculated for all trees for which height measurements were taken. For lodgepole pine and Scots pine trees with >5 cm DBH, volume functions presented by Eriksson (1973) and Brandel (1990) were used, respectively, while functions presented by Andersson (1954) were used for trees with smaller diameters.

Secondary volume functions were created for each species and site as a function of diameter (DBH) using the following equation:

$$\ln(\mathrm{VOL}) = b_0 + b_1 \times \ln(\mathrm{DBH} + 1) + b_2 \times \ln(\mathrm{DBH} + 1)^4, \tag{1}$$

where VOL = single tree stem volume according to the volume function and b_0–b_2 = coefficients estimated by regression on the basis of sample tree data.

The secondary volume equations were used to calculate individual tree stem volume for all trees and to estimate total stand volume.

Heights of individual trees not actually measured were estimated as a function of their diameter using second-degree polynomial height curves. Height curves were then used to estimate top height using average values for the 100 trees with the largest diameter per hectare.

In the comparison of the exotic species and the native species, we used the two most productive Scots pine (SP) and lodgepole pine (LP) provenances at each site. The percentage increase or decrease in production resulting from using the exotic species instead of the native species was thus 100 × (SP–LP)/LP for Canada and 100 × (LP–SP)/SP for Sweden. We also compared the two best provenances of the exotic species with the local material of the native species (local lodgepole pine (LPL) in Canada and the provenance with the nearest origin in Sweden).

Estimates of covariances among sites

Data for block 5 at all sites were dropped prior to the linear mixed-model analysis. Variance and covariance estimates were generated according to the following linear mixed model:

$$y = X\tau + Z_g u_g + Z_p u_p + e, \tag{2}$$

where y is a vector of observations, τ is a vector of fixed effects, u_g is a vector of random additive genetic effects, u_p is a vector of random non-additive effects, e is a vector of random residual effects, and X, Z_g and Z_p are incidence matrices for fixed, random additive genetic and random non-additive genetic effects, respectively. The fixed effects were composed of site, species, site-by-species interaction, provenance nested within species and the three-way interaction of site, species and provenance. The random effects (u_p) were composed of family (GCA), cross (SCA), block nested within site and the interactions of site with family and cross. Random factors were assumed to have a multivariate normal distribution

$$\begin{bmatrix} u \\ e \end{bmatrix} = N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}\right), \tag{3}$$

where G is the (co)variance matrix for random effects (u_g *and* u_p) and R is the (co)variance matrix for e. Restricted maximum likelihood (REML) analysis of the statistics software package ASReml-R (version 3) was used to estimate all variance and covariance components. Residuals for all traits were inspected visually and appeared to be normally distributed.

To estimate (co)variances among sites for DBH, a multi-environment trial analysis was conducted for each species, using an approximate reduced animal model (ARAM) (Quaas & Pollak 1980) in place of the full animal model. The ARAM is identical to the full animal model when there is no relatedness among parents. Using this model reduces computing time and memory usage (White et al. 2006). The additive genetic (co)variance among sites was estimated using a factor analytic model (Smith et al. 2001; Cullis et al. 2014) with three factors and the following R-matrix:

$$R = \begin{bmatrix} \sigma^2_{e_{iq}} I_{n_{iq}} & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & \sigma^2_{e_{jr}} I_{n_{jr}} \end{bmatrix}, \quad (4)$$

where $\sigma^2_{e_{iq}}$and $\sigma^2_{e_{jr}}$are the residual variances for sites i and j, respectively; I_N is an identity matrix of dimensions $N \times N$ (N = the number of trees); $q = 1$ to r; and r = the number of sites.

Results

Species productivity

On average for all sites in Canada, SP had larger DBH and higher survival (mortality due to mountain pine beetle not included) and volume (5.5%, 28.4% and 22.4%, respectively), but lower top height (−10.4%) than LP, when all provenances were included (Table 3). SP had higher survival but lower top height than LP across all sites, while for volume and DBH, the ranking of species varied. At the Renberget site (SWE-64), the exotic species (LP) had higher top height, survival and volume (11.3%, 27.3% and 47.8%, respectively), but lower diameter (−2.1%) than the native species (SP). At Garsås (SWE-61), the species produced equally much and the production was much lower than at SWE-64. When data for both Swedish sites were combined, the superiority of top height and volume for LP was reduced by 50%. The exotic species produced on average more than the native species in both Canada and Sweden, with the largest effect in Sweden, but the effect differed considerably between sites. The two best provenances of SP produced 34.6% and 13.7% more volume than the two best provenances of LP at CAN-56 and CAN-57, respectively, but 14.4%, 10.7% and 6.1% lower volume at the other three Canadian sites (Figure 2). At SWE-64, the two best LP provenances produced 43.1% more volume than the two best SP provenances. When comparing with the LPL seed-lot, the exotic SP also had higher production than the native in CAN-59.

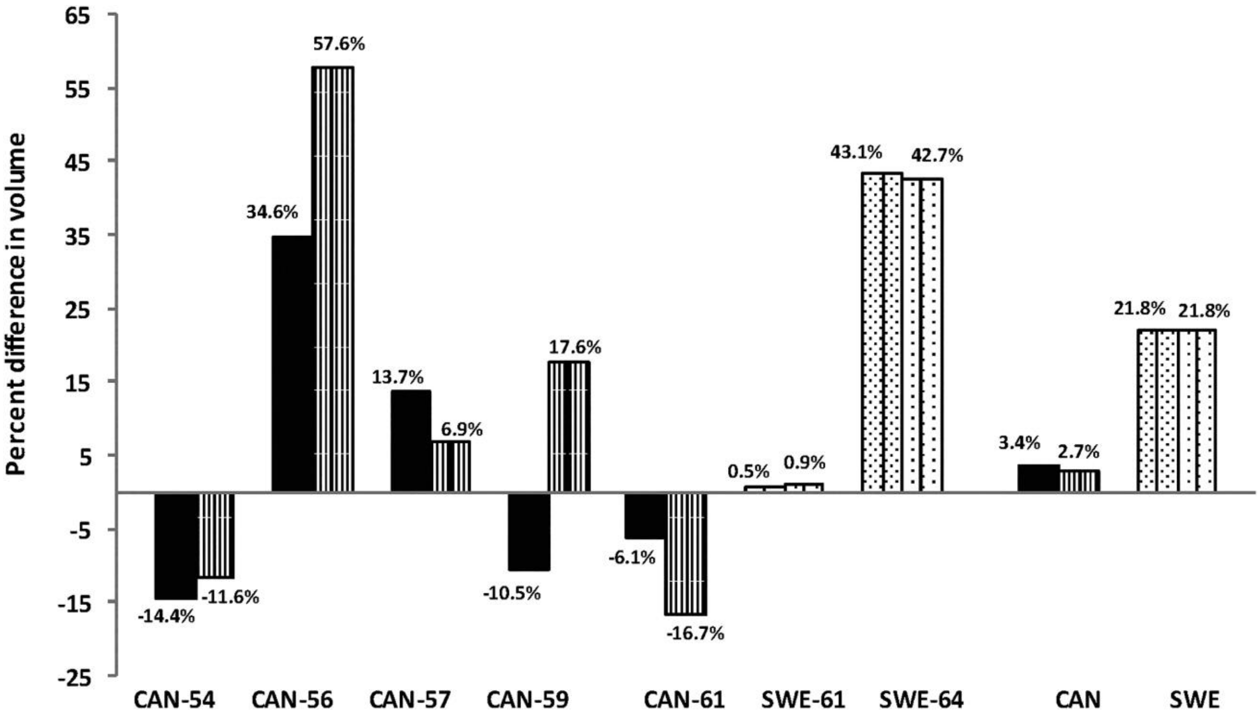

Figure 2. The percent differences in volume production of the two best seed-lots of the exotic species compared with the two best of the native species including the operational controls (left bar in each pair). The difference between the two best seed-lots of the exotic species and the local seed-lot (right bar).

Table 3. Stand data and difference between the exotic and native species based on data for all provenances at 25 years from planting. Averages for each species (LP = lodgepole pine; SP = Scots pine) and difference between the exotic and native species.

	DBH over bark[a] (mm)			Top height (m)			Survival[b] (%)			VOL (m^3ha^{-1})		
8.5	LP	SP	Exotic vs. native species (%)[c]	LP	SP	Exotic vs. native species (%)[c]	LP	SP	Exotic vs. native species (%)[c]	LP	SP	Exotic vs. native species (%)[c]
CAN-54	163	170	4.3	10.7	9.0	−15.9	93	96	3.2	141	126	−10.6
CAN-56	136	134	−1.5	8.7	8.0	−8.0	58	93	60.3	44	66	50.0
CAN-57	158	182	15.2	10.4	9.5	−8.7	68	91	33.8	70	130	85.7
CAN-59	172	191	11.0	11.8	10.1	−14.4	68	88	29.4	102	120	17.6
CAN-61	98	89	−9.2	6.6	6.2	−6.1	59	75	27.1	12	10	−16.7
Average CAN	145	153	5.5	9.6	8.6	−10.4	69.1	88.7	28.4	73.7	90.2	22.4
	LP	SP	Exotic vs. native species (%)[d]	LP	SP	Exotic vs. native species (%)[d]	LP	SP	Exotic vs. native species (%)[d]	LP	SP	Exotic vs. native species (%)[d]
SWE-61	170	173	−1.7	11.4	11.5	−0.9				99	102	−2.9
SWE-64	183	187	−2.1	12.8	11.5	11.3	84	66	27.3	170	115	47.8
Average SWE	176	180	−2.0	12.1	11.5	5.2	67	62	8.1	135	108	24.2
Weighted average CAN+SWE	154	161		10.3	9.4		68.5	81.1		91.1	95.4	

[a] DBH is the average DBH of the 100 tallest trees per hectare (trees with heights estimated by diameter included), that is, top height; VOL is volume production per hectare.

[b] Trees recently killed by mountain pine beetle were included among living trees (see materials and methods).

[c] Species difference based on all provenances in Canada, (SP-LP)/LP (%).

[d] Species difference based on all provenances in Sweden, (LP-SP)/SP (%).

At the SWE-64 site, LP produced 229 m^3ha^{-1} and SP 110 m^3ha^{-1} (108% higher production for LP) when planted in the block where the species, provenances and families were mixed (block 5), while in the uniform 64-tree plots (blocks 1–4), the corresponding volumes were 173 m^3ha^{-1} for LP and 118 m^3ha^{-1} for SP (47% higher production) (data not shown).

Provenance variation

Among the LP provenances planted in Canada (excluding local seed-lots, LPL), LP57 had the highest volume at all sites, and its relative volume production compared with LPL ranged from −26% to +25% (Table 4). LPL had the highest production in two sites (CAN-57 and CAN-59) and 4–20% lower than the top provenance in the other three. The SP provenance from 63° latitude (SP63) had the highest volume production of all provenance materials at the three northern sites in Canada, where its relative volume production compared with LPL ranged from −20% to +42%. The top SP provenance at site CAN-54 was SP59 (−11% compared to LPL), while at CAN-56 SP61 performed best (+59%). In Sweden, the LP provenance with the most southern origin (LP55) had the highest volume at both sites. For SP, SP63 had the highest volume at the southern Swedish site (SWE-61) and SP65 the highest volume at the northern site (SWE-64). At CAN-59, heavy snowfall caused considerable stem damage in the spring of the year of measurement. The LPL operational control seed-lot (LPL), which had the highest volume, had less damage than transferred LP provenances, but the least damage occurred on SP (Table 5).

Genetic correlations among sites

Type B genetic correlations (genetic correlations among sites) were calculated for DBH. For LP in Canada, the four southern sites had rather high correlations, which increased with decreasing distance between the sites (from 0.69 to 0.99) (Table 6; Figure 3). CAN-61 was poorly correlated with the southernmost Canadian site (CAN-54), but also here the correlation increased with decreasing difference in latitude (from 0.24 to 0.70). There was no correlation between CAN-61 and the Swedish sites. Growth of LP in the two Swedish sites was highly correlated (0.82) and it was relatively highly correlated with the two southern Canadian sites. For SP, the four southern Canadian sites were all highly correlated. CAN-61 had very low correlations with the four southern Canadian sites and SWE-61, but rather high correlation with SWE-64. The two Swedish sites were highly correlated with each other (0.96). SP in the Swedish sites showed similar correlations with the four southern Canadian sites, but with generally lower correlations for SWE-64 than for SWE-61.

Table 4. Volume production (m^3ha^{-1}) of different provenances of LP and SP in blocks 1–4 at indicated test sites in Canada (CAN) and Sweden (SWE).

Provenance	CAN-54	CAN-56	CAN-57	CAN-59	CAN-61	CAN	SWE-61	SWE-64	SWE
LP55	154 (2) *a*	52 (18) *bcd*	85 (−35) *bc*		8 (−33)		133	194 *a*	
LP57	157 (4) *a*	52 (18) *cd*	115 (−12) *ab*	141 (−26) *abc*	15 (25)		94	177 *ab*	
LP59	101 (−33) *d*	26 (−41) *e*	69 (−47) *bc*	124 (−35) *bcd*	15 (25)		80	176 *ab*	
LP61			20 (−85) *d*	33 (−83) *e*	11 (−8)		76	171 *abc*	
LP63			5 (−96) *d*	22 (−88) *e*	10 (−10)			134 *abcd*	
LPL	151 *ab*	44 *d*	130 *a*	191 *a*	12				
SP55	121 (−20) *cd*						82		
SP57	132 (−13) *abc*	66 (50) *abc*	122 (−6) *a*				87		
SP59	135 (−11) *abc*	69 (57) *ab*	138 (6) *a*	140 (−27) *abc*	6 (−50)		100		
SP61		70 (59) *a*	132 (2) *a*	144 (−25) *ab*				89 *d*	
SP63	125 (−17) *bcd*	65 (48) *abc*	140 (8) *a*	152 (−20) *ab*	17 (42)		125	123 *bcd*	

Table 4, cd.									
Provenance	CAN-54	CAN-56	CAN-57	CAN-59	CAN-61	CAN	SWE-61	SWE-64	SWE
SP65	116 (−23) *cd*	59 (34) *abcd*	116 (−11) *ab*	120 (−37) *bcd*	9 (−25)		94	137 *abcd*	
SP66				88 (−54) *cd*	11 (−8)			105 *cd*	
SP67				75 (−61) *de*	8 (−33)			121 *bcd*	
Mean (excl. LPL) LP	137.5 (−9)	58.4 (33)	43.3 (−67)	79.7 (−58)	11.8 (−2)		95.5	170.3	
Mean (incl. LPL) LP	140.8	43.5	70.7	102.2	11.8		95.5	170.3	
SP	125.9 (−17)	65.9 (50)	129.6 (0)	119.9 (−37)	10.1 (−16)		97.5	114.8	
Two best (incl. LPL) LP	155.6	52.0	122.2	165.7	14.7	102.4	113.0	185.4	149.2
Two best SP	133.2 (−12)	70.0 (59)	139.0 (6)	148.0 (−23)	13.8 (15)	100.8	112.4	129.6	121

Notes: Figures followed by different letters are significantly different and numbers within brackets are percent differences from the LP operational control seed-lots (LPL). For the CAN-61 and SWE-61 test sites, no differences were significant.

Table 5. Stem damage for LP, the local operational seed-lot (LPL) and SP at Fort Nelson (CAN-59).

Provenance	Percent broken stem	Percent toppled	Sum
LP57 – LP63	16.3	9.3	25.5
LPL	2.9	7.0	9.9
SP59 – SP67	1.4	3.2	5.9

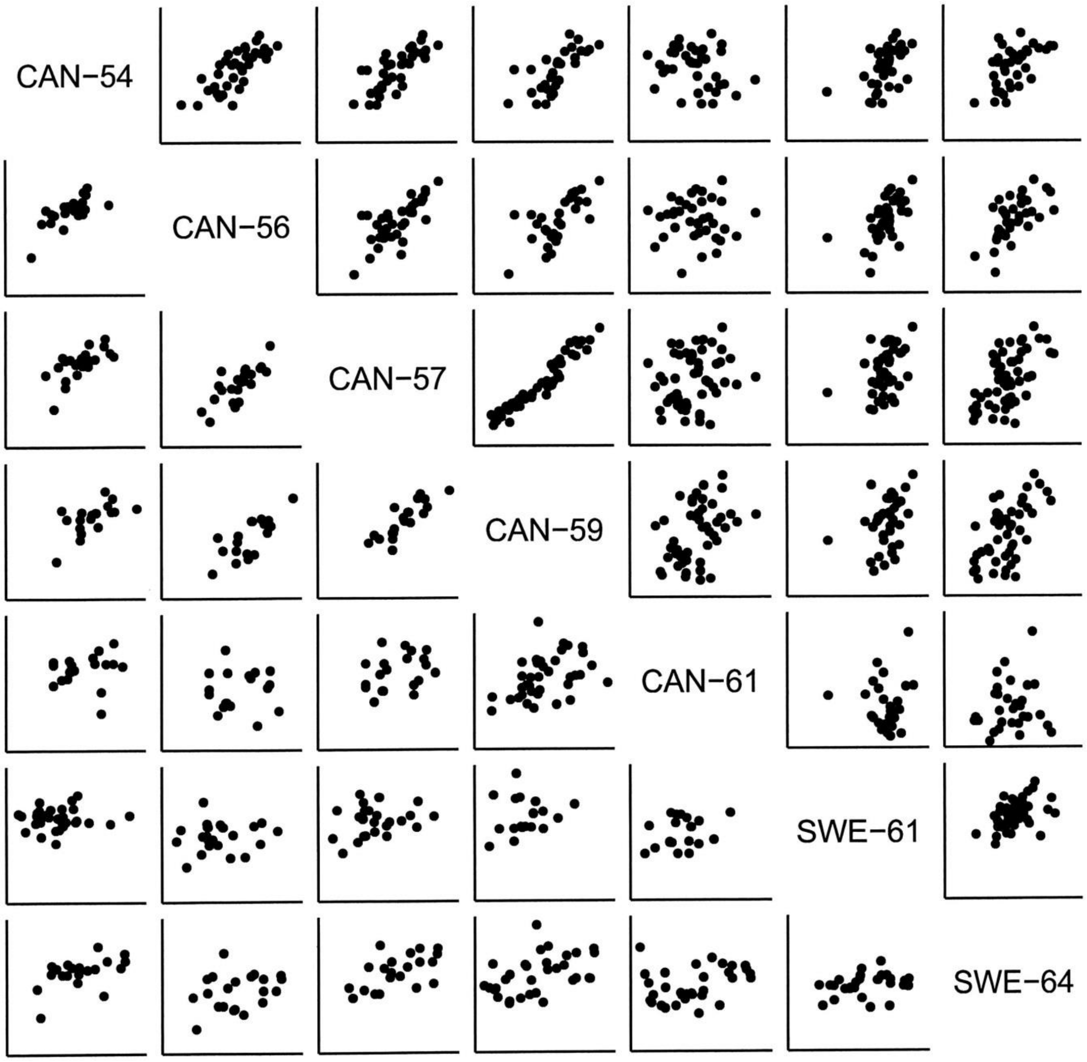

Figure 3. Scatterplots for genetic correlations between sites for DBH of LP (above diagonal) and SP (below diagonal). The *x*- and *y*-axes indicate DBH of the seed-lots in the sites each plot refers to.

Table 6. Genetic correlations between sites (type B genetic correlations) for DBH of LP (above diagonal) and SP (below diagonal).

	CAN-54	CAN-56	CAN-57	CAN-59	CAN-61	SWE-61	SWE-64
CAN-54		0.93	0.76	0.69	0.24	0.96	0.77
CAN-56	0.90		0.94	0.90	0.47	0.86	0.68
CAN-57	0.91	0.84		0.99	0.66	0.63	0.47
CAN-59	0.72	0.74	0.94		0.70	0.55	0.40
CAN-61	0.11	–0.28	0.25	0.21		0.09	0.03
SWE-61	0.86	0.60	0.90	0.76	0.59		0.82
SWE-64	0.72	0.36	0.74	0.57	0.77	0.96	

Discussion

Exotic vs. native species

Based on the two best producing seed-lots, the exotic species (LP) had higher production than the native SP in one of the Swedish sites (SWE-64), while it was equal in the other (SWE-61) (Table 4; Figure 2). SWE-61 was, however, severely damaged by pine weevil, which caused a high mortality at an early age. At the latitude of SWE-61, the expected survival of local material of SP is ca 68% (Eriksson et al. 1980). The low survival in this site and comparatively slow height growth in our inventory, only 45% of the plots had more than 20 of 64 surviving trees, are quite exceptional. In 44 replicated Swedish experiments with both species examined by Elfving and Norgren (1993), LP survived better in most experiments and grew faster in 43 of them. The considerably higher production of LP compared to SP at SWE-64 may, however, be a result of the release of Canadian pathogens, but contributing factors could be a higher growth capacity and that the Swedish soil has shown to provide better biota for LP than the Canadian soil (Gundale et al. 2014) and that the Swedish soil has lower net nitrogen immobilization than soils in Canadian LP stands (McIntosh et al. 2012).

In Canada the sites CAN-54 and CAN-56 were attacked by mountain pine beetle prior to measurements, and SP was considerably more damaged than LP (53% compared to 21% and 95% compared to 53% in CAN-54 and CAN-56, respectively). The trees killed by mountain pine beetle were included when production was calculated and their potential growth 1–3 years prior to measurements was thus not included. Therefore, their estimated productivity was somewhat underestimated and since SP was more frequently killed by mountain pine beetle, calculated production in those sites became more reduced for SP than for LP. Based on the two best seed-lots of each species, exotic SP produced more than the native LP in two sites (CAN-56 and CAN-57), while LP grew better in three. Based on all seed-lots, the exotic SP had higher production at CAN-59 and on average produced more than LP. LP had higher top height in Canada (Table 3), which indicated higher production potential, but the higher production potential is not obvious here and one reason could be the more damage it suffers, which thereby reduces its growth. Thus, the simultaneous inventory of diseases showed that in Canada all pathogen species occurring on LP except western gall rust were missing or occurred only in single infections on SP (Fries unpublished data). The same situation could sometimes occur for LP in Sweden: its superiority in production in SWE-64 and often in Sweden (Elfving & Norgren 1993) could be because the native SP is more severely affected by pests and pathogens occurring in Sweden. We suggest thus that the result in some sites in the present study may follow the “enemy release hypothesis” described in Mitchell and Power (2003) and Mitchell et al. (2006). The higher production of LP than SP at three of the Canadian sites shows, however, that it is possible to find native well-adapted materials with high production.

The much larger mortality among SP due to mountain pine beetle in two Canadian sites demonstrates the risks with species introduction. Furthermore, in general the risk with disease or insect attack may in future increase due to adaptation of the disease or insect to also attack the exotic species (Karlman 2001; Garbelotto & Pautasso 2012). A similar example to mountain pine beetle is attacks by *Gremmeniella abietina* on LP in parts of northern Sweden. After severe snow conditions in the winter 1993/94, infection of *Gremmeniella* was very frequent and caused high mortality on LP, while SP suffered much less (Hansson & Karlman 1997). On the other hand, in the same study snow blight *(Phacidium infestans*) infected the native SP to a considerably higher degree than LP. These opposite results for LP demonstrate not only the potential risks, but also possibilities with introduced species.

Block five, with mixed species and provenances, was only measured at SWE-64. In this site monocultural blocks with LP produced 47% more than those with SP. In block five the volume of LP was 108% larger than that of SP. This indicates that when planted together, LP will have a significant competitive advantage over SP.

Provenance variation

The climate in northern Sweden has a substantial maritime influence originating from the west from the Gulf Stream of the Atlantic Ocean west of Norway and, to a minor extent, from the Gulf of Bothnia to the east. In Sweden, LP is therefore planted in sites with a less continental climate than east of the Coastal Mountains in Canada from where much of the LP is taken. Further south in British Columbia, the climate is milder. Provenances from these areas had higher volume production in the site in north Sweden (SWE-64) than provenances from more northern latitudes. This indicates that climatic similarities, rather than latitude or elevation, are more suitable for matching provenances in Canada with breeding zones in Sweden (cf. Kreyling et al. 2015). This is also consistent with recommendations in Sweden for the selection of LP provenances (http://www.kunskapdirekt.se/sv/KunskapDirekt/Alla-Verktyg/Planters-guide-2/ [July 2016]).

British Columbia has considerable environmental and climatic variation (Pojar et al. 1987), which according to Mátyás (1996) result in steep genetic clines for the native species. Large geographic transfers often result in a high degree of stress and increased susceptibility to damage, pests and pathogens (Karlman 2001; La Porta et al. 2008). This has resulted in large population-level variation for LP, with specialized adaptation to local biotic and abiotic factors, and maladaptation is probably a reason for the greater snow damage on the non-local lodgepole pine than on the local seed-lot at

CAN-59 (Table 5). This highlights the importance of local adaptation of the species in Canada. Nevertheless, SP seems to be even better adapted to heavy snow (Table 5), a trait that has probably evolved under the maritime climate in Sweden. The larger needle biomass of LP compared to SP making it more sensitive to snow and wind may, thus, reduce the potentially higher productivity of LP. Furthermore, the different SP provenances show similar relationships to the LPL at the different sites, indicating that the species has higher phenotypic stability over environmental gradients than LP.

In regions with significant environmental heterogeneity, a policy to use local seed-lots for reforestation will exploit local adaptation to minimize the risk of damage by biotic and abiotic factors, but may not allow the optimization of volume production. However, with adequate information from well-designed provenance tests and multispecies trials, it should be possible to optimize volume production through species and population selection. In the current study, at three sites in Canada, CAN-56, CAN-57 and CAN-61, the best performing seed-lot was a SP seed-lot. Their average gain in volume over the local seed-lots (LPL) was 36% (Table 4). At one site (CAN-54), the best performing seed-lot was a transferred LP provenance with a volume gain of 4%, and at one site (CAN-59), the local seed-lot had the highest volume production of all LP and SP seed-lots (26% higher production than the second best). Furthermore, the use of the optimum LP seed-lot instead of the local operational seed-lot (LPL) would have resulted in an average gain in volume of 9.4%. This agrees with modeling with LP by Wang et al. (2006b), suggesting that seed-lot selection can be used to mitigate the negative impacts of climate change and optimize volume production in LP; it was reported that an increase in volume of 14–36% can be achieved with seed-lot selection and moderate levels of climate change. In addition, our data show that if SP seed-lots are included for selection, the potential gain could be 23%.

These results after 25 years are of course only indicative. Final conclusions cannot be drawn before optimum rotation age, which can vary between 70 and 100 years for the different sites and species in the study. The heavy attack by mountain pine beetle has destroyed a meaningful continuation of this experiment and demonstrates the difficulties to evaluate forest productivity by long-term field experiments. Long-term evaluation of productivity must be based on growth modeling.

Correlations between sites and phenotypic stability

Given the pattern of the genetic correlations between sites (type B genetic correlations) for LP in northwestern Canada (Table 6), there is a need for multiple breeding zones in Yukon and Canada. The northernmost zone should be the Whitehorse area (CAN-61). The clinal increase in correlation with decreasing distance between the other four sites did, on the other hand, not indicate any clear boundary, with the possible exception of a boundary between the Mackenzie and Fort St John area (CAN-56 and CAN-57). The more stable type B genetic correlations for SP than LP between Canadian and Swedish sites indicated that SP is less affected by changes in the climatic, biotic and abiotic factors across northern British Columbia. Seven out of 10 correlations between the Canadian and Swedish sites were 0.60 or higher and with a total variation of between 0.36 and 0.90 for SP, while 5 out of 10 correlations for LP in Sweden were 0.60 or higher (total variation 0.03–0.96). This suggests a higher degree of phenotypic stability of SP than of LP, which may be the result of adaptation to lower variation in the biotic environments in Sweden (Mátyás 1996) than in western Canada. CAN-54 was the site in Canada with the highest type B genetic correlation with SWE-64 for LP. This indicates that there are similarities between southern locations in western Canada and regions in northern Sweden. Thus, selection results from the CAN-54 site and the CAN-56 site are most appropriate for supporting the LP breeding program in northern Sweden.

Conclusions

One goal of this transcontinental reciprocal transplant experiment was to compare the overall productivity of LP and SP in their native and exotic environments. In some sites, the introduced species (LP in Sweden and SP in Canada) provided higher volume production than the native species, but in others the native species produced more. The higher production of LP than SP in one Swedish site, and frequently in Swedish forestry, may be due to its higher production capacity but contributing is probably that damage by pathogens and insects are fewer, thus in accordance with the so-called enemy release theory. Also, the Swedish soil seems to provide better biota and nitrogen availability for LP than the Canadian soil.

Despite higher production of the exotic SP than LP in some sites in western Canada, there are many LP populations that can be utilized to maximize productivity on managed forest lands. Good performance of the less continental southern provenances of LP in the Swedish sites demonstrates that climatic similarities, rather than latitude or elevation, should be used for matching provenances in Canada with breeding zones in Sweden. High correlation between Canadian and Swedish sites for SP indicates its relatively high phenotypic stability. More severe damage by mountain pine beetle on SP than on LP in Canada, together with previous outbreaks of *Gremmeniella* on LP in Sweden, indicates, however, risks with species introductions.

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