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Damage by pests, pathogens and mountain pine beetle in reciprocally planted Scots and lodgepole pine in Canada and Sweden after 25 years

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ABSTRACT

A combined species – provenance – family experiment with Scots pine and lodgepole pine was planted in Canada and Sweden. One aim of the experiment (addressed here using data collected 25 years after establishment) was to evaluate the two species' sensitivity to pathogens and insects in the non-native continent. In Canada, Scots pine had better survival than lodgepole pine, on average, but survival of trees from the best seed-lots was equal. The only common lodgepole pine pathogen in Canada that infected Scots pine to some extent was western gall rust. Mountain pine beetles attacked and killed Scots pine more frequently than lodgepole pine. At one of two sites in Sweden lodgepole pine had higher survival rates than Scots pine, both on average and among the best surviving seed-lots. At the other site the species' survival rates were equal, largely due to extensive moose damage to lodgepole pine. Adaptation to local conditions seemed to be important to resist stem breakage due to heavy snowfalls. Generally the exotic species seemed to resist the new threats in the first generation, but serious attacks by mountain pine beetle on Scots pine in Canada and moose on lodgepole pine at one Swedish site demonstrate the risks of using exotic species.

INTRODUCTION

Introduced plant species have been used for a long time and for many reasons. Indeed, most agricultural crops are widely cultivated exotically (Tigerstedt 1993) and forest trees have been used to improve production in commercial forestry, in afforestation programs and to establish shelter plantations (Rebele 1994). Another reason for introducing exotic tree species may be to spread risks by increasing species variation (Burdon 2010; Rosvall 2010), and many species have grown and performed well following planned introductions (Jaako Pöyry Oy 1987; Wang et al.

2006; Cubbage et al. 2014, Verhaegen et al. 2014). Some species may have much higher productivity in new environments than in their natural range. For example, Monterey pine (*Pinus radiata* D. Don) grows more rapidly (and is industrially important) in areas of Australia, New Zealand, Chile and Africa than in its native regions of California and Mexico (Piirto and Valkonen 2005).

A reason for performing better as exotic species can be that their growth is severely limited in their native environment by abiotic factors (e.g. climatic conditions) and/or abiotic factors (notably pests and pathogens). Thus, as stated by the "enemy release hypothesis", all species are regulated to some degree by natural enemies (pests and pathogens) within their native ranges, so they may grow better than indigenous species in a non-native environment due to the absence of those enemies (Mitchell & Power 2003). However, if a species depends on positive biotic interactions within its native range, its growth in new environments may be highly restricted by the absence of suitable associates (Pringle et al. 2009). Hence, the presence or absence of key biotic interactions in the non-native range may determine the success of introduced or invasive species (Mitchell et al. 2006). Silvicultural measures in the new environment may also improve possibilities for the success after an introduction (Tigerstedt 1993, Cubbage et al. 2014).

In experimental plantations with several exotic conifers in the 20th century has lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm), which is native to northwestern USA and western Canada, shown to be highly productive as compared to the native Scots pine (*Pinus sylvestris* L.; Elfving et al. 2001). Numerous mature field experiments indicate that it is approximately 36% more productive than Scots pine in Sweden, on average (Elfving & Norgren 1993), partly due to higher specific needle biomass (Norgren 1996). Another reason for the interest in lodgepole pine was its superior capacity to survive in harsh climates. In contrast, Scots pine is not used in North American forestry, although it has been experimentally planted (van der Kamp & Karlman 1993).

Despite its significant productivity benefits, lodgepole pine has been cautiously used in Sweden, due to uncertainties about ecological interactions, and fears of triggering outbreaks of fungal or insect diseases, in either the native species or the exotic species (Karlman et al. 1997). Accordingly, planting of lodgepole pine was reduced in the 1980s following a severe epidemic outbreak of scleroderris canker, caused by *Gremminiella abietina* Lagerb., a pathogen not native to western Canada, in northern Sweden (Karlman et al. 1994). Formal restrictions on its use were thus imposed by the Swedish Forest Agency in 1987. Nevertheless, since 1970 areas covering more than 600000 ha in northern and central Sweden have been planted with lodgepole pine (Skogsstyrelsen 2013). The general risks associated with introducing the species to Sweden have been thoroughly reviewed by Karlman (1981, 2001) and Hansson and Karlman (1997).

In its natural range in the interior of British Columbia lodgepole pine is susceptible to rusts and various other parasitic fungi, most commonly western gall rust (*Endocronartium harknessii*), a pine-to-pine rust that does not require an alternate host (van der Kamp 1989, van der Kamp et al. 1995, Krebill 1975). Infections occur on both branches and the stem, where the fungus produces globose swellings (Ziller 1974). This rust and other fungi pose potential risks to Scots pine if the pine is introduced in Canada or the fungi occur in Sweden. Mountain pine beetle (*Dendroctonous ponderosae*) also poses a major threat, as it is considered the most destructive of all western forest insects (Furniss & Carolin 1977) and routinely causes widespread disturbances during outbreaks in North American forests. In British Columbia lodgepole pine is the most threatened species. Outbreaks there have been regulated by the cold winter climate, although certain life stages of the beetle survive (Robertson et al. 2009). However, in the last 15 years favorable winters and increasing spatial connections between suitable habitats in lodgepole pine stands thanks to forest fire suppression triggered an extreme outbreak.

In order to evaluate risks of pests or parasites spreading from Scots pine to lodgepole pine or vice versa and possible epidemic outbreaks, and to compare the productivity of the species, a transcontinental reciprocal transplant experiment was established in five sites in western Canada (British Columbia and Yukon) and two in Sweden (A Joint Swedish – Canadian 1987; Lindgren & Lindgren 1990). The materials used in the experiment included full-sib and half-sib families of the two species, together with operational seed-lots. Early results from the Canadian test sites have been published by Lindgren and Lindgren (1990), van der Kamp et al. (1995) and Karlman et al. (1997).

A previous paper addressed variations in productivity between species and sites (Fries et al. 2015). However, few studies have adequately evaluated the damage by pathogens, insects and animals at a higher age and the aim with the present study was to: (1) evaluate the occurrence of damage by various fungi, insects and mammals on the two species as native and exotic species, (2) evaluate differences between provenances and between plus tree progenies and operational stand collections in susceptibility to those threats, and also damage by snow and wind, (3) evaluate genetic differences in susceptibility to western gall rust and mountain pine beetle, and (4) judge the risks of severe consequences due to large-scale outbreaks of diseases or insects when lodgepole pine or Scots pine is used exotically in forestry in Sweden or Canada.

MATERIAL AND METHODS

The experiment is described in detail in Fries et al. (2015), and briefly summarized below.

Plant material

The plant material was for lodgepole pine seed-lots of plus tree progenies (designated LP) and seed-lots from operational seed collections in natural stands close to the test sites (designated L). The plus tree seed-lots were either full-sib families from controlled crosses in seed orchards or half-sib families from open pollinated plus trees in natural stands. The seed-lots of Scots pine were all plus tree progenies and designated SP. All abbreviations were followed by a number designated their latitudinal origin. Each seed-lot represents one provenance and the term seed-lot and provenance are used equally.

Seedlings were planted in the spring of 1986 at five test sites in western Canada (four in British Columbia and one in Yukon) and two sites in Sweden (Fig. 1; Table 1).

Experimental design

The field tests had a randomized complete block design with five blocks per site. At every site except Garsås, blocks 1 to 4 were composed of 8×8 tree square plots with separate species and provenances, and block 5 was composed of single tree plots with mixed species, provenances and families. Blocks 1 to 4 at Garsås were 4×16 tree plots. In the present study all 5 blocks were included except for growth data which only used block 1-4. Spacing was 2 m×2 m.

Measurements

Volume

Growth measurements presented and described by Fries et al. (2015) were used in the analyses of western gall rust effects on volume production. At the southern Swedish site, Garsås, both species were heavily damaged by pine weevil (*Hylobius abietis*) at a young age, then later by moose: only 35% of the plots had more than 20 of 64 living trees and only these plots were evaluated. The results from this site should thus be treated with caution.

Survival

At the Ft St James and Mackenzie sites most mortality was due to mountain pine beetle. To assess probable survival capacity in the absence of an extreme outbreak of a pest like mountain pine beetle, at these sites trees killed by mountain pine beetle were included in the surviving trees. At the other sites the survivors were exclusively those that were still surviving at the time of the surveys.

Disease and insect survey

In 2010 (end of June/beginning of July at the Canadian sites, August and October to December at the Swedish sites), when the trees were 25 years old they were assessed for infection by mountain pine beetle (*Dendroctonous ponderosae*) and several conifer pathogens: western gall rust (*Endocronartium harknessii*), atropellis canker (*Atropellis piniphilla*), elytroderma (*Elytroderma deformans*), comandra blister rust (*Cronartium comandrae*) and stalactiform blister rust (*Cronartium stalactiforme*). The presence of mountain pine beetle was recorded if pitch tubes, or entrance and exit holes, were observed in the bark. Sometimes the bark was removed and the presence of mountain pine beetle was confirmed by the presence of beetle galleries. The occurrence of western gall rust was recorded if galls were detected on a tree's stem or branches, regardless of their abundance. Atropellis canker infection was recorded if considerable resin exudation was observed, and confirmed by the presence of black fruiting bodies and black staining in the wood beneath the bark at the point of exudation. Elytroderma infection was recorded if elongated black fruiting bodies on needles were observed, or either excessively swollen branches or elongated stem cankers with rough bark and no region of cambial mortality (which would be characteristic of blister rust infections).

Comandra and stalactiform blister rusts were identified by the presence of stem cankers which often included a region of cambial mortality in the centre. The fungi were distinguished by size and shape with comandra cankers having a height to width ratio of one while the ratio for stalactiform cankers was much higher than one.

Stem form and animal damage

Tree top damage and stem form abnormalities were assessed by recording the propensity to fork. Two classes of stem forks were recorded, <1.3 m and > 1.3 m above the ground. In addition, at the Ft. Nelson site trees with broken tops and uprooted trees were recorded. Signs of animal damage beside attacks by mountain pine beetle were also recorded.

Statistical analysis

Microsoft Excel 2010 was used for frequency calculations. For other statistical analyses procedures implemented in SAS Enterprise version 4.3, including Proc TTest, were used, except for estimates of variance components and heritabilities (for which restricted maximum likelihood analysis, REML, was applied, as implemented in ASReml-R version 3 software). Fixed effect models were applied to the data in the analysis of genetic parameters. The genetic parameters for western gall rust were calculated using the following model where provenance (or prov) corresponds to seed-lot:

[1] $Y_{ijk} = \mu + block_i + prov_j + block_i \times prov_j + fam(prov)_k + block_i \times fam(prov)_k + e_{ijk},$

Where

Y_{ijk} = individual observation of each trait of the ijk^{th} plant position,

$block_i$ = fixed effect of the i^{th} block, i = 1-4,

$prov_j$ = fixed effect of the j^{th} provenance: for lodgepole pine j =1-10 (*F*t St James, Ft St John, Mackenzie and Ft Nelson) and 1-11 (Whitehorse); for Scots pine j =1-8 (Ft St James, Ft Nelson and Whitehorse), 1-6 (Ft St John) and 1-7 (Mackenzie)

$fam(prov)_k$ = random effect of the k^{th} family within-provenance: for lodgepole pine k =1-30 (Ft St James), 1-36 (Ft St John, Ft Nelson and Whitehorse) and 1-34 (Mackenzie); for Scots pine k =1-32 (Ft St James, Mackenzie and Whitehorse), 1-24 (Ft St John), and 1-33 (Ft Nelson),

e_{ijk} = random residual (*res*) (assuming normal independent distribution) with different σ^2_e for each site and species, ijk = 1-n, according to Table 8.

Mountain pine beetle is known to attack trees with a large diameter (Björklund & Lindgren 2009). Thus, the following model including DBH as a random effect was used for mountain pine beetle attacks:

[2] $Y_{ijkl} = \mu + block_i + prov_j + block_i \times prov_j + fam(prov)_k + block_i fam(prov)_k + DBH_l + e_{ijkl}$

where

DBH_l = random effect of stem diameter at breast height on individual stem observations of the $ijkl^{th}$ plant position.

As the data for the analysed traits were binary (living/dead, attack/no attack or occurrence/no occurrence) the “logit” function in ASReml (Gilmour et al. 2002) was used (see also Yanchuk et al. 2008). Using this method narrow-sense individual heritability was calculated as follows:

[3] $\hat{h}_i^2 = 4\hat{\sigma}^2_{fam(prov)} / (3.29 + \hat{\sigma}^2_{block \times fam(prov)} + \hat{\sigma}^2_{fam(prov)})$.

RESULTS

Survival

In Canada there were no significant differences in survival rates between the plus tree seed-lots (LP) and operational seed-lots (L) of lodgepole pine, thus pooled data were used in the comparisons with Scots pine. As shown in Table 2a, survival rates were, with the exception of Whitehorse, significantly higher for Scots pine than lodgepole pine ($p<0.05$-0.001). Furthermore, if the two southernmost provenances (SP57 and SP59) are excluded, survival rates of Scots pine were also higher at Whitehorse ($p<0.01$). When comparing the 'best' seed lots (those with >10% higher than mean survival rates; Table 2b), Scots pine had significantly higher survival rates than lodgepole pines at only two sites: Mackenzie and Whitehorse ($p<0.05$) (note: if no seed-lot met this criterion, the three best were used, except at Ft Nelson, where one with >10% higher than mean survival and the second best were used). At the Renberget site lodgepole pine had significantly higher survival, only when comparing the 'best' provenances, and at Garsås survived Scot pine slightly better.

Stem damage

Forking

At the Canadian sites there were neither below nor above 1.3 m significant differences in forking frequencies between plus tree seed-lots and operational seed-lots of lodgepole pine (Table 3). Frequencies of forking at >1.3 m differed significantly between the species only at Ft Nelson and Renberget, where forking was more frequent among lodgepole pines than Scots pines ($p<0.05$ and 0.01, respectively).

Scots pine had significantly more forks <1.3 m than lodgepole pine at the four southern sites in Canada (45-58% for Scots pine compared to 2-33% for lodgepole pine; $p<0.01$). In Whitehorse, however, there was no significant difference between the species and the frequencies were low.

Broken stems and uprooting

At the Fort Nelson site heavy snowfalls resulted in considerable frequencies of broken stems and uprooting in the spring of the measurement year, and both types of damage were more frequent among plus tree seed-lots of lodgepole pine than among the Scots pine seed-lots ($p<0.01$; Table 4). In addition, stem breakage was significantly more common than uprooting in lodgepole pine ($p<0.05$). Among operational seed-lots of lodgepole pine, frequencies of broken stems were lower for origins from the same region as the site (L57 and L58; cf. Fig 1) than for more distant origins and plus tree seed-lots (3.15% on average, versus 20.7% and 12.8 %, respectively). The frequencies of Scots pines with broken stems were similar to those of lodgepole pines originating from local seed-lots. Frequencies of uprooting did not differ significantly between species and not between trees originating from local and more distant operational seed-lots. Among Scots pine the southernmost seed-lot had significantly higher frequencies than the others ($p<0.001$) (11.3% compared to 2.6%, data not shown).

At Renberget were frequencies of uprooted trees higher among plus tree seed-lots of lodgepole pine than among operational stand seed-lots and among Scots pine (14.8% uprooted compared to 2.2% and 6.6%, respectively; $p<0.001$ for both comparisons) (data not shown). The latter differed also significantly ($p<0.05$).

Western gall rust

Western gall rust was observed at all Canadian sites, although at very low frequencies at the most northern site, Whitehorse, and none at the Swedish sites. Lodgepole pine was significantly more frequently infected than Scots pine at the four southern Canadian sites ($p<0.001$). For lodgepole pine varied the occurrence of western gall rust between 19 and 100% (average 78%) among seed-lots, while the range for Scots pine was 0-30% (average 10.4%) (Table 5). There were no significant differences in frequency of infections between plus-tree seed-lots and operational seed-lots of lodgepole pine. The operational seed-lot L57 had lowest infection rate at all sites. At the four southern sites 49.2% of trees of seed-lot L57 were infected, compared to 81.2% for those originating from other operational seed-lots. Based on the production data reported by Fries et al. (2015), western gall rust caused ca. 25% growth reductions of both lodgepole and Scots pine trees (Table 6).

Other pathogens

Stalactiform blister rust was observed in Ft St James and Mackenzie. In Ft St James seven of 10 seed-lots of lodgepole pine had infections (range 0-7%, average 1.2%; not shown in table), and at Mackenzie six out of nine seed-lots had infections (range 4-20%, average 6.3%). Infections on Scots pine occurred on only one and two trees, respectively. Comandra blister rust was also detected at these sites (and at Whitehorse), but in very low frequencies and not on Scots pine. Atropellis canker was recorded on all seed-lots of lodgepole pine in Ft St James and in six out of ten seed-lots of lodgepole pine in Mackenzie (range 7-81%, average of 40.2% and range 4-24%, average 12.3%, respectively; not in table). Infections were more frequent on southern origins. In addition were a few lodgepole pines infected at Whitehorse. Notably, at Ft St James 26% (6 of 23) of the trees originating from one Scots pine seed-lot, SP60, were infected by atropellis canker. Otherwise, infections were only observed in single Scots pine trees.

Elytroderma occurred only in Mackenzie and there all lodgepole pine seed-lots except two (represented with very few plants) were infected (range 10-72%, average 42.7%; not in table). Infected was recorded on only one Scots pine tree.

Mountain pine beetle

Numerous trees of both species were attacked by mountain pine beetle at Mackenzie, and substantial numbers at Ft St James. At both sites significantly higher proportions of Scots pines than lodgepole pines were attacked ($p<0.01$) while there were no significant differences between plus tree seed-lots and operational stand seed-lots of lodgepole pine (Table 7). At Mackenzie the frequencies among Scots pines seed-lots ranged from 85 to 100% (average 95%), while frequencies among lodgepole pine plus tree seed-lots or operational seed-lots ranged from 0 to 100% (average 59%). At the time for inventory, 40% of the attacked lodgepole pines were dead and 90% of the Scots pines. At Ft St James the frequencies of attacks were lower among both Scots pine seed-lots (28-88%, average 53%) and lodgepole pine seed-lots (3-57%, average 21%). Mortality at inventory was 70 and 85%, respectively. There was no latitudinal trend among seed-lots in attack frequency by mountain pine beetle and there were no among-seed-lot correlations between Ft St James and Mackenzie in attack frequency.

Animal damage

Damage caused by animals except mountain pine beetle was negligible at Ft St James and Mackenzie, but sapsuckers (*Sphyrapicus* spp.) damaged substantial numbers of trees at Ft St John and Ft Nelson, and mammals (deer, porcupine or hare) in a few cases (less than 1%) stripped bark, browsed and rasped shoots at Whitehorse. Significantly higher ($p<0.001$) proportions of Scots pines than lodgepole pines were damaged by sapsucker (54% and 1.1%, on average, respectively). At Garsås both species were equally much damaged by pine weevil (*Hylobius abietis*) at a young age, then later by moose: only 35% of the plots had more than 20 of 64 living trees. At the time for inventory moose damage was identified on 45% of the lodgepole pines but only 2% of the Scots pines (data not shown). Renberget was fenced and had very limited damage from animals.

Genetic parameters

For both species was the block effect on western gall rust infection larger than the family effect at the three southern sites, but lower at Ft Nelson (Table 8). The heritabilities were similar for both species: h^2=0.14-0.26 except for lodgepole pine at Ft Nelson (h^2=0.05) and Scots pine at Mackenzie ($h^2=6.7\times10^{-8}$).

For mountain pine beetle attacks the effect of stem diameter (DBH) was negligible in Ft St James and Mackenzie, and heritabilities were low for Scots pine (h^2= 0.12 and 0.053, respectively) and negligible for lodgepole pine.

DISCUSSION

Survival

Survival rates of the exotic species were higher than those of the native species at most sites. This is consistent with the "enemy release hypothesis" (Mitchell and Power 2003), i.e. that an exotic tree species in a new environment may have higher fitness than an indigenous species due to the absence of restrictive pests and pathogens endemic in its native range. However, the exotic species have less clearly superior survival rates when the 10% best seed-lots are compared, indicating that it may be possible to find sufficiently well adapted materials of either exotic or indigenous species to ensure good survival and also production rates (Fries et al. 2015).

At Renberget, the Swedish site where development was acceptable, lodgepole pine seemed to cope with very long northern transfer, as survival rates for material of all origins were 80-90%, indicating that for lodgepole pine similarity of climatic conditions between source and transfer sites is more important than similarity of light climate. A northern transport is possible since lodgepole pine stands lower temperatures during the growth period (Christersson et al. 1987) and becomes hardy earlier in the autumn (Lindgren & Nilsson 1992). Its better survival at Renberget can probably also be attributed to the fewer potential threats to lodgepole pine. At Garsås, the high mortality rates were caused by outbreaks of pine weevil and later damage by moose. Moose seems to prefer Scots pine over lodgepole pine at fertile sites, but prefer lodgepole pine at poor sites (Niemelä & Danell 1988). Top height, stem diameter and volume production were all lower at Garsås, despite its more southern location than at Renberget (Fries et al. 2015) indicating that Garsås is a relatively poor site, which may explain the frequent damage on lodgepole pine. It also shows that exotic species may get considerable damage by unexpected agents, suggesting that their use should be extended cautiously.

Stem damage

Forking below breast height was more common in the exotic species at all Canadian and Swedish sites except Whitehorse, and lodgepole pine was more frequently forked above breast height than Scots pine in Sweden (Table 3). This may have been at least partly due to the exotic lodgepole pine having greater mean heights (see Fries et al. 2015) and longer, more vulnerable top shoots. It also allocates smaller amounts of the biomass to the stem (Elfving et al. 2001). There were no significant differences in frequency of broken stems between operational seed-lots and plus tree seed-lots, except that frequency of stem breakage was considerably rarer in local operational seed-lots than in distant operational seed-lots and plus tree seed-lots at Ft Nelson (Table 4). The area where the site is located has a relatively more maritime climate with heavy and wet snow. Thus, local adaptation to these conditions may have been a key factor for avoiding stem damage and the limited damage to Scots pine may reflect its adaptation to the more maritime climate in Scandinavia and at Ft Nelson.

In Sweden, uprooting was significantly more common among plus tree seed-lots of lodgepole pine than among operational seed-lots of lodgepole pine and Scots pine. Plants originating from seed orchards generally grow well in early stages, due to the high quality of seeds. A consequence of this for lodgepole pine is a risk of spiral roots developing in the plant containers, a well-documented problem in Sweden during the years when this experiment was established (Lindström & Rune 1999). Such spiraling affects the later development of the roots, and reduces their stability, as also shown for jack pine (*Pinus banksiana* Lamb.) by Chapman & Colombo (2006).

Western gall rust

Western gall rust occurred at all sites except Whitehorse in both 2010 and 1993 (Karlman et al. 1997). Significantly higher proportions of lodgepole pines than Scots pines were infected, but there was no difference in this respect between operational seed-lots and plus tree progenies of lodgepole pine (Table 5). The incidence on lodgepole pine had increased since the registrations in 1993; the average frequency of infected trees increased from 45-49% in 1993 to 60-94% in 2010 at the three southern sites (cf. Karlman et al. 1997) and at Ft Nelson only 4.5% of the trees were attacked in 1993 while 68% had been attacked in 2010. Furthermore, a tendency for fewer trees of northern origins to be attacked, recorded in 1993, had disappeared in 2010. Clearly, infections by western gall rust can continue for at least nearly 30 years and relatively resistant materials can be infected if the infection pressure is high enough. Nevertheless, the operational seed-lot L57 had the lowest infection rate at all four sites indicating higher resistance.

For Scots pine there was only a limited increase in western gall rust infection frequencies, from less than 5% in 1993 to nearly 10% in 2010, and it remained low at Ft Nelson (5%). Although conditions for infections of western gall rust were favorable, as manifested by the increase in numbers of infected lodgepole pines, infection frequencies remained low in Scots pine. However, since infection by western gall rust may occur at any age (cf. https://fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5341326.pdf [May 2015]) additional infections of Scots pine may occur in the future. Still, the severity of future infections should decrease with increasing age since the likelihood of stem-encircling infections, which can girdle the trees, should decline (Blenis & Duncan 1997).

Trees infected by western gall rust had 25% lower volume than uninfected trees (Table 6). This may have been at least partly due to the rust tending to infect small trees more frequently, but infections (especially stem infections) are also likely to depress growth rates as they cause the death of water-conducting tissues. Stem infections were also reported to reduce growth of Monterey pine (Zagory 1979). The observed growth reductions are large compared to previous reports, for example Bella and Navratil (1988) detected reductions in volume of 3-15%. Woods et al. (2000) also observed a small negative effect of western gall rust alone, but a stronger effect (up to 7% reductions) in combination with comandra blister rust. Differences in site productivity and exposure (Bella and Navratil 1988; Woods et al. 2000) may contribute to the variations in observed effects.

Heritabilities for infection by western gall rust were similar for both species and varied between 0.14 and 0.27, except for two sites where heritabilities were very low. Similar heritability (h^2=0.21) was obtained in a trial involving inoculating lodgepole pine with western gall rust (Kojwang 1994) and fusiform rust (*Cronartium quercum* f.sp. *fusiforme*) (Kayihan et al. 2010). However, Wu & Ying (1997) obtained higher estimates of heritability for western gall rust (h^2=0.50), and slightly lower estimates for stalactiform blister rust (h^2=0.32). Inoculation tests reported by Hoff (1991) have also indicated high heritability (h^2=0.76) for resistance to the disease in ponderosa pine (*Pinus ponderosa* Laws.). It is obvious that there is a potential for genetic improvement of lodgepole pine in resistance against rust fungi.

Other pathogens

Atropellis canker occurs on the bole below the crown base and is more common in dense than in widely spaced stands (Stanek et al. 1986). Unlike comandra and stalactiform blister rust, it seems to be capable of infecting mature trees, as well as young trees (van der Kamp 1994). Beside killing trees at high infection rates it may cause reductions in their modulus of elasticity (Nevill et al. 1990). Atropellis was frequent at two sites, Ft St James and Mackenzie, at which stalactiform and comandra blister rust also occurred, and thus seem to be in an area with generally high infection pressure. Despite the high atropellis infection rates at these two sites it was not detected in the other sites, presumably because its dispersal over long distances requires transportation of plant material, while it can spread over short distances via aeciospores, which are mostly dispersed by wind and rain (EFSA 2014). The finding that northern materials were more resistant indicates that trees that are under climatic stress may be more susceptible to the fungus. It is also noteworthy that these rust fungi occurred in sites of attacks by mountain pine beetle. The apparent associations between atropellis canker and mountain pine beetle and stalactiform and comandera blister rusts are consistent with statements regarding lodgepole pine infections by Rocchini et al. (1999). They found that such associations could be due to the fungus wounding the bark, which increases the possibility of insect attack. However, given the enormous outbreak of mountain pine beetle in British Columbia starting around year 2000 (Robertson et al. 2009; Chen 2014), is this cause–effect process however probably not the determining factor here.
Elytroderma was quite frequent on all seed-lots of lodgepole pine except two, so our data provide limited scope for drawing conclusions regarding optimal provenances. However, Wallis et al. (2010) claim that exposed populations develop genetic resistance to elytroderma over time, and material from areas where lodgepole pine is not a dominant species were generally more susceptible. This hypothesis is supported by findings by Wallis et al. (2010) that trees' capacity to resist elytroderma is connected to foliar levels of defense-associated compounds (lignin, phenolics and tannins), amounts of which are genetically determined (Fries et al. 2000).

At the Renberget site in Sweden the survival of lodgepole pine at age 9 was 92% which was much higher than for Scots pine (69%). In Canada seven years after planting were, however, the average survival rates of both species nearly 95%. The low survival for Scots pine in northern Sweden is well documented (Näslund 1986). A probable reason for the higher survival of lodgepole pine in northern Sweden is its ability to avoid or survive attacks by some of the pests and pathogens that cause mortality in Scots pine. They include snow blight (*Phacidium infestans*)

(Fries 1993), pine twisting rust (*Melampsora pinitorqua*) and resin top disease (*Cronartium flaccidum*) (Näslund 1986). Indeed, lodgepole pine growing in Sweden, in consistence with the ‘enemy release hypothesis’, has less pathogen infection than in most stands in Canada. Noteworthy, however, is that it was seriously affected by the outbreak of scleroderris canker caused by *Gremminiella abietina* Lagerb. (Karlman et al. 1994).

Mountain pine beetle

Attacks by mountain pine beetle were frequent at Ft St James and even more frequent at Mackenzie. This was expected since both sites are located in areas where lodgepole pine was the dominating conifer and the most intensive attacks occurred in 2007-2008 (Chen 2014). In contrast, Ft St John is located close to the boundary of attacks in those years, and no attacks were recorded there in 2010. Contributing to this may be that the area around this site not is dominated by lodgepole pine, which is likely to reduce the probability of attack. At Ft St James and Mackenzie the beetle attacked Scots pine more frequently than lodgepole pine (Table 7), which could be explained by the rougher bark of Scots pine. Thus, Ferrenberg & Mitton (2014) found that beetle attacks were considerably more frequent on rough bark than on smooth bark of *P. flexilis*. Findings presented here indicate that genetic factors weakly influence mountain pine beetle resistance; narrow-sense heritabilities were negligible for lodgepole pine and only 0.12 and 0.053 for Scots pine at Ft St James and Mackenzie, respectively. However, the mating design in this study covered limited relationships, which reduces the efficiency for estimating genetic parameters. Thus, Yanchuk et al. (2008) obtained higher heritabilities for occurrence and number of pitch tubes of h_i^2=0.26 and 0.15, respectively, from a trial with open-pollinated progenies. Wu & Ying (1997) found similar heritability for frequency of attack (h^2=0.21) by another insect, pitch moth (*Synanthedon sequoiae*). One genetically regulated factor that may contribute to the difference in attack frequency between the species is the abundance of resin ducts and amounts of wood extractives; Ferrenberg et al. (2014) found that resistant trees generally have considerably more resin ducts and Franceschi et al. (2005) emphasizes the genetic component in this aspect. Furthermore, Rosner & Hannrup (2004) recorded generally high broad sense heritabilities at four sites with Norway spruce clones (H^2=0.28, 0.81, 0.77 and 0.71) for abundance of resin ducts and resins, Fries et al. (2000) presented high heritabilities in Scots pine for amounts of resin acids (h^2=0.55-0.60) and Ott et al. (2011) showed that amounts of terpenes and terpenoids are under strong genetic control in lodgepole pine (h^2=0.12-0.58, average 0.28). All these substances are important for defense against beetle attacks by acting both as hydrophobic barriers and fungitoxins (Hart 1981; Pearce 1996; Ferrenberg et al. 2014).

Summary

When comparing lodgepole pine and Scots pine as exotic and native species the pattern was that survival was higher for the exotic species both in Canada and Sweden. There were, however, exceptions. At one Swedish site pine weevil and moose caused equal mortality, and at the site in Canada with the harshest climate was survival also equal. Furthermore, the differences between the exotic and native species were limited when comparing the origins with the highest survival. The infection rate on Scots pine of the native pathogens in Canada was very low, although they frequently attacked lodgepole pine. Earlier data has shown high mortality at low age for Scots pine in Sweden which was largely due to the native pathogens. They did however not seem to affect the exotic lodgepole pine. The low infection rates of Scots pine in Canada and lodgepole pine in Sweden are consistent with the "enemy release hypothesis" (Mitchell and Power 2003), i.e. that an exotic tree species in a new environment have higher fitness than an indigenous species due to the absence of restrictive pests and pathogens.

There were however important exceptions with the native pathogen or animal preferring the exotic species. The more severe outbreaks of mountain pine beetle on Scots pine than on lodgepole pine and the considerable moose damage on lodgepole pine at one Swedish site, and also the serious damage by scleroderris on lodgepole pine in Sweden in the 1980s are example of risks associated with species introductions. Noteworthy is also the higher frequency of damage by sapsucker on Scots pine than on lodgepole pine in Ft St John (54% compared to 1.1%) indicating preference of the exotic species.

The study presents results from first generation introductions before mid-rotation age and there is certainly a risk that the diseases in future adapt to attack also the introduced species. E.g. may the registered infections by western gall rust of Scots pine be a basis for an adaptation and increase in pathogeny.

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Table 1. Field tests included in the reciprocal transplant experiment with lodgepole pine and Scots pine.

Location	Latitude	Longitude	Elevation
Canada			
Fort St. James	54.45	124.05	855
Mackenzie	55.50	123.72	680
Fort St. John	56.60	122.37	800
Fort Nelson	59.00	123.33	600
Whitehorse	60.68	135.37	660
Sweden			
Garsås	60.93	14.88	205
Renberget	64.25	19.80	225

Table 2.

Survival rates, in terms of percentages of surviving trees. The “surviving trees” at Ft St James and Mackenzie include trees recently attacked and killed by mountain pine beetle. LP, L and SP refer to lodgepole pine plus tree progeny, lodgepole pine originating from operational seed-lots and Scots pine plus tree progeny, respectively. Mv is mean values, and figures followed by different letters are significantly different. *a)* All seed-lots; *b)* The ‘best’ seed-lots (see text for definition of ‘best’).

	Ft St James	Ft St John	Mackenzie	Ft Nelson	Whitehorse	Garsås	Renberget	Mv	
								Can	Swe
a)									
LP	88.95*a*	59.98*a*	57.38*a*	66.88*a*	59.06*a*	50.47*a*	84.00*a*	64.45	49.82
L	88.03*a*	63.78*a*	59.37*a*	62.70*a*	71.00*a*			68.98	
SP	96.00*b*	88.60*b*	92.03*b*	80.38*b*	76.*48a*	58.12*a*	66.25*b*	86.70	54.25
b)									
LP+L	98.17*a*	82.96*a*	76.89*a*	85.01*a*	77.24*a*	60.54*a*	88.90*a*	84.054	67.89
SP	98.26*a*	91.64*a*	95.41*b*	88.47*a*	87.97*b*	69.14*a*	76.71*a*	92.350	72.21

Table 3.

Frequencies of forking above and below breast height (1.3 m). Abbreviations: see Table 2.

	Ft St James	**Ft St John**	**Macken-zie**	**Ft Nelson**	**White-horse**	**Garsås**	**Renberget**	**Mv Canada**	**Mv Sweden**
>1.3m									
LP	3.45 *a*	3.00	3.07 *a*	3.22 *a*	10.94	4.18 *a*	3.89 *a*	4.74 *a*	4.03 *a*
L	2.55 *a*	6.20	5.81 *a*	1.43 *a*	16.35	–	23.89 *b*	6.47 *a*	23.89 *b*
SP	1.91 *a*	1.93	1.68 *a*	0.52 *b*	10.86	1.77 *a*	0.72 *c*	3.38 *a*	1.25 *c*
<1.3m									
LP	9.95 *a*	22.84	20.54 *a*	16.68	3.82 *a*	29.55 *a*	3.51 *a*	14.77 *a*	16.53 *a*
L	1.88 *a*	29.56	33.34 *a*	12.70	4.06 *a*	–	3.24 *a*	16.31 *a*	3.24 *b*
SP	45.48 *b*	57.61 *b*	54.61 *b*	52.18	1.88 *a*	2.63 *b*	1.26 *b*	42.35 *b*	1.94 *c*

Table 4.

Mean percentages of broken or uprooted trees at the Fort Nelson site among lodgepole pine and Scots pine plus tree progenies, and trees originating from both local operational seed-lots (L57 and L58) and those with more distant origins (L60-L63). Abbreviations: see Table 2.

	Fort Nelson	
	Broken	**Uprooted**
L57	3.70	0
L58	2.6	6.3
L60-	20.67	3.91
LP	12.76 *a*	7.65 *a*
SP	2.67 *b*	3.73 *b*

Table 5. Percentages of trees originating from indicated seed-lots infected by western gall rust at indicated sites. Abbreviations: see Table 2.

			Ft St James 54.45^{o}	**Ft St John 56.60^{o}**	**Mackenzie 55.50^{o}**	**Ft Nelson 59.00^{o}**	**Whitehorse 60.68^{o}**
Lodgepole pine	Plus tree seed-lots	LP55	69.7	92.3	91.4	79.2	0.5
		LP57	54.5	79.3	71.7	55.6	0.9
		LP59	78.9	99.3	93.9	59.5	0.0
		LP61	77.4	100.0	82.4	83.0	0.6
		LP63	78.7	97.6	100.0	92.4	0.0
	Operational seed-lots	L54	75.3	100.0	92.3	–	–
		L55	68.0	100.0	92.8	–	–
		L57	19.2	66.9	70.0	40.9	0.0
		L58	43.3	88.9	76.5	57.0	0.0
		L60	91.7	89.3	92.3	60.9	0.6
		L62	–	–	–	76.2	0.0
		L63	–	–	–	77.8	0.0
Scots pine	Plus tree progenies	SP55	11.6	–	3.6	–	–
		SP57	6.5	8.9	11.9	4.3	0.0
		SP59	7.7	15.7	11.2	4.8	0.6
		SP60	30.4	–	–	–	–
		SP61	11.7	14.1	9.2	13.1	0.0
		SP63	7.2	9.4	9.8	5.5	0.0
		SP64	3.4	6.9	3.7	0.0	0.0
		SP65	4.6	10.4	5.3	4.2	0.0
		SP66	–	–	–	9.4	1.4
		SP67	–	–	–	1.9	0.0
		Mean	71.9 *a*	93.7 *a*	87.9 *a*	73.9 *a*	0.4 *a*
		Mean	59.5 *a*	89.0 *a*	84.8 *a*	62.6 *a*	0.1 *a*
		Mean	10.4 *b*	10.9 *b*	7.8 *b*	5.4 *b*	0.3 *a*

Table 6.

Mean volumes of lodgepole pine (LP) and Scots pine (SP) trees infected with western gall rust (WGR) and uninfected trees at the four southern Canadian sites. Only trees in block 1-4 are included since growth was not measured in block 5.

Species	**Mean volume, dm³**		**Volume reduction**
	without WGR (a)	**with WGR (b)**	**by WGR (1–b/a),%**
LP	56	42	25.0
SP	48	36	25.0

Table 7.

Frequencies of trees attacked by mountain pine beetle of indicated seed-lots. Abbreviations: see Table 2.

			Ft St	**Mackenzie**
Lodgepole pine	Plus tree progenies	LP55	13.0	69.8
		LP57	21.4	77.5
		LP59	15.1	54.6
		LP61	3.2	36.7
		LP63	4.3	0.0
	Operational seed-lots	L54	5.4	100.0
		L55	36.0	45.2
		L57	46.2	100.0
		L58	56.7	87.5
		L60	8.3	16.7
Scots	Plus tree progenies	SP55	45.0	100
		SP57	47.9	97.6
		SP59	60.9	96.1
		SP60	52.2	–
		SP61	88.3	95.4
		SP63	52.8	88.5
		SP64	48.3	100.0
		SP65	27.7	84.9
Mean LP			11.4 *a*	47.7 *a*
Mean L			30.5 *a*	69.9 *a*
Mean SP			52.9 *b*	94.6 *b*

Table 8. Genetic parameters for infection by western gall rust (WGR) and attacks by mountain pine beetle (MPB). Prov, Provenance; Fam, family; Var.comp, variance component; stdev, standard deviation; h^2, narrow-sense heritabilities; N, number of plants; DBH, stem diameter at breast height. a) Western gall rust; *b*) mountain pine beetle.

***a*) WGR**

	Ft St James		Ft St John		Mackenzie		Ft Nelson	
	Var. comp	Var.comp/ stdev	Var. comp	Var.comp/ stdev	Var. comp	Var.comp/ stdev	Var. comp	Var.comp/ stdev
Block	4.38	1.23	2.27	1.18	1.32	1.18	0.035	0.17
Prov	0.18	0.73	3.67	1.46	0.76	1.1	0.83	1.21
Block × Prov	0.29	1.54	6.9×10^{-8}	0	5.6×10^{-8}	0	0.99	2.31
Block × Fam	2.8×10^{-8}	0	0.073	0.51	2.8×10^{-7}	0	0.053	0.38
Fam (Prov)	0.64	2.94	0.53	1.75	0.92	2.11	0.17	1.06
Residual	1	0	1	0	1	0	1	0
h^2	0.16		0.14		0.22		0.048	
N	1174		1519		829		1357	

Block	7.25	2.24	6.89	2.13	1.95	4.8×10^{-8}	0
Prov	4.7×10^{-7}	0	0.03	0.01	0.05	0.47	0.14
Block × Prov	0.40	0.12	0.08	0.03	0.13	0.00	0
Block × Fam	2.2×10^{-7}	0	1.1×10^{-6}	0	0.31	9.6×10^{-7}	0
Fam (Prov)	0.81	0.25	0.70	0.22	0	1.18	0.36
Residual	1	0.28	1	0.30	0.29	1	0.66
h^2	0.20		0.18			0.26	
N	1303		1233			1647	

***b*) MPB**	**Lodgepole pine**				**Scots pine**			
	Ft St James		Mackenzie		Ft St James		Mackenzie	
	Var. comp	Var.comp/ stdev	Var. comp	Var.comp/ stdev	Var. Comp.	Var.comp/ stdev	Var. Comp.	Var.comp/ stdev
DBH	6.0×10^{-4}	0.65	2.3×10^{-3}	0.7	0.01	0	4.75×10^{-3}	0
Block	42.0	1.29	21.3	1.32	28.7	8.86	20.6	6.36
Prov	4.8×10^{-8}	0	0.46	0.96	1.76×10^{-6}	0	0.64	0.20
Block × Prov	2.10	1.71	0.31	1.28	7.6	2.34	0.08	0.03
Block × Fam	8.8×10^{-8}	0	0.094	0.43	2.48×10^{-7}	0	0.43	0.13
Fam (Prov)	4.2×10^{-8}	0	8.8×10^{-8}	0	0.46	0.14	0.21	0.06
Residual	1	0	1	0	1	0.08	1	0.13
h^2	1.3×10^{-8}		2.6×10^{-8}		0.12		0.053	
N	1083		768		1483		1524	

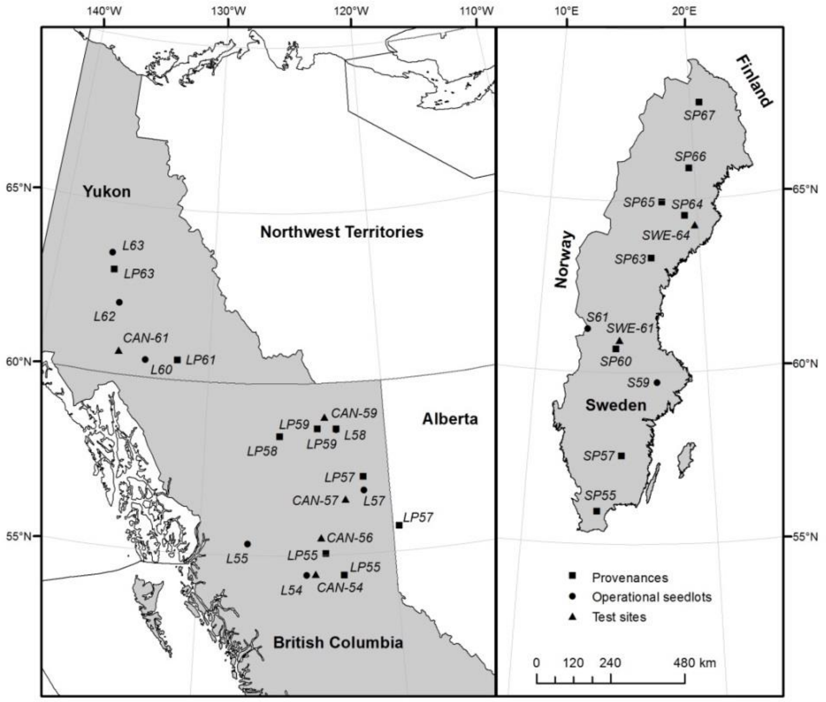

Figure 1.

Locations of the test sites, and origins of provenances and operational control seed-lots used in the multi-species transcontinental family provenance trial established in Canada and Sweden. The provenances and operational control seed-lots were collected from the areas surrounding the point sources shown on the map. See Table 2 for definitions of the abbreviations.