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Old-growth red spruce forests as reservoirs of genetic diversity and reproductive fitness

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Abstract Old-growth forests are assumed to be potential reservoirs of genetic diversity for the dominant tree species, yet there is little empirical evidence for this assumption. Our aim was to characterize the relationship of stand traits, such as age, height and stem diameter, with the genetic and reproductive status of old-growth and older second-growth stands of red spruce (*Picea rubens* Sarg.) in eastern Canada. We found strong relationships between height growth (a fitness trait) and measures of genetic diversity based on allozyme analyses in red spruce. The negative relationship between height and the proportion of rare alleles suggests that high proportions of these rare alleles may be deleterious to growth performance. Latent genetic potential, however, showed a significant and positive relationship with height. Stand age was not correlated to height, but was correlated to seedling progeny height. In late-successional species such as red spruce, age and size (e.g., height and stem diameter) relationships may be strongly influenced by local stand disturbance dynamics that determine availability of light, growing space, moisture and nutrients. In larger and older stands, age appeared to provide a good surrogate measure or indicator for genetic diversity and progeny height growth. However, in smaller and more isolated populations, these age and fitness relationships may be strongly influenced by the effects of inbreeding and genetic drift. Therefore, older populations or old-growth forests may represent superior seed sources, but only if they are also of sufficient size and structure (e.g., stem density and spatial family structure) to avoid the effects of inbreeding and genetic drift. Thus, larger and older forests appear to have an important evolutionary role as reservoirs of both genetic diversity and reproductive fitness. Given the rapid environmental changes anticipated (as a result of climate change, increasing population isolation through fragmentation, or following the introduction of exotic pests and diseases) these older populations of trees may have a valuable function in maintaining the adaptive potential of tree species.

Keywords Conservation · Genetic diversity · Inbreeding · Old-growth forests · Reproductive fitness

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Introduction

Genetic diversity provides the evolutionary potential for sustaining forest health in the face of environmental change. Therefore, conserving the genetic diversity of native trees, as the dominant life forms of forested ecosystems, has special significance. Old-growth forests are considered to have great value for species conservation (Anonymous 2000) by providing a special habitat for an array of forest-dependent wildlife. These older populations may also serve as reservoirs of genetic diversity and reproductive fitness, important for maintaining populations of native trees under pressure from environmental changes. However, there is very little empirical evidence supporting the assumption that old-growth forests serve as reservoirs of genetic diversity or fitness.

The Acadian Forest Region (AFR) covers most of the Maritime provinces (Nova Scotia, New Brunswick and Prince Edward Island) of Canada (Rowe 1972). Except for a small area of boreal forest, the forest cover is typical of much of the Temperate Zone of northeastern North America, where natural forest succession, in the absence of stand-replacing disturbances such as fire, tends towards the development of late-successional forest types composed of long-lived, relatively shade-tolerant trees, such as eastern hemlock (*Tsuga canadensis*), red spruce

(*Picea rubens*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*). One of the most important distinguishing features of the AFR is the high proportion of red spruce (Loucks 1962; Rowe 1972), a species adapted to the high atmospheric moisture that prevails in the AFR. Red spruce is commonly associated with the red spruce-eastern hemlock-eastern white pine (*Pinus strobus*) species complex, which comprises a mostly shade-tolerant coniferous tree species association, with eastern white pine as a legacy from an earlier successional stage. Red spruce also occurs within mixedwood forests, together with shade-tolerant hardwood trees. These climatic climax associations are most commonly found on xeric to mesic lowland sites and, to a lesser extent, in upland areas of Atlantic Canada.

Several hundred years of land clearing for agriculture and timber harvesting has eliminated most of the old-growth forest in the AFR and throughout the northeastern temperate forests of North America (Korstian 1937; Gordon 1994; Davis 1996). In this older forest, the average age of the dominant trees exceeds 150 years and the oldest trees are approaching their maximum longevity of 300–400 years (Cogbill 1996; Mosseler et al. 2000). What little old-growth forest remains is largely restricted to small isolated stands, often found in steep gorges that were inaccessible to harvesting and agriculture, or areas that either were protected or escaped harvesting. Late-successional, old-growth forest types, dominated by shade-tolerant conifers such as red spruce, are becoming increasingly rare. These forest types have great commercial value and, because of their ecophysiological adaptations, present the forest industry with important silvicultural alternatives to clearcutting, and the intensive forest management regimes that normally follow complete forest clearing. The conservation of these declining red spruce-dominated forest types has become an important issue in temperate forests such as the AFR and further west into the Great Lakes – St. Lawrence Forest Region of Ontario. The reproductive and genetic status of the red spruce component of these late-successional forests has been characterized across the Canadian range, from Nova Scotia to the geographically disjunct populations of Ontario in the northwestern portion of the species' range (Mosseler et al. 2000; Rajora et al. 2000).

From a genetic perspective, very little attention has been given to the implications of the loss of late-successional tree species and forest types and, in particular, the oldest stages of forest development. Most forest genetics literature has focused on genetic aspects related to tree improvement and selective breeding activities.

High levels of genetic diversity are generally accepted as essential for facilitating the adaptive responses required to adjust to anticipated climate and other environmental changes. The objective of this study was to examine relationships between stand traits, such as tree age, stem height and stem diameter, in ten natural populations of red spruce with: (1) genetic diversity parameters, (2) reproductive fitness traits, and (3) progeny growth. These relationships help us to understand what these older populations represent in terms of genetic resources and as potential reservoirs of genetic diversity and reproductive fitness.

Materials and methods

Red spruce populations and sampling

Ten red spruce populations, five from New Brunswick and Nova Scotia, and five from Ontario (Table 1), were studied as described in Mosseler et al. (2000) and Rajora et al. (2000). The sampled populations were all located within a similar range of latitude and elevation. Maritime populations consisted of large, extensive stands that normally contained several thousand mature trees contributing to the reproductive gene pool. Ontario red spruce populations, however, generally consisted of much smaller stands occurring as remnant patches, often with fewer than 50 mature trees that were sometimes isolated from adjacent stands by distances that would be expected to restrict pollination or seed dispersal among stands. As most of the Ontario stands had only 15 to 20 red spruce trees bearing a cone crop, we limited our sampling to about 15 trees per population in order to keep relatively uniform sample sizes. This sample size represented an almost complete (80–90%) female reproductive census and 35–65% of the total red spruce individuals from the Ontario populations. The Nova Scotia red spruce populations at Abraham Lake and Rossignol Lake represent relatively undisturbed, old-growth forest stands dominated by red spruce of all ages, including trees presumed to be well over 300 years of age, as determined from wood increment corings. Data on height, diameter and age of individual sampled trees were recorded (Mosseler et al. 2000).

Seed processing, germination and seedling growth

Cones were collected from individual sampled trees and the seeds were processed as described in Mosseler et al. (2000). Various cone and seed traits, including the total number of seeds, the number and proportion of empty and filled seeds per cone, and the proportion of filled to developed seeds, were measured and calculated, as were population means for these traits. Seed was germinated from individual open-pollinated families under glasshouse conditions and seedling height was measured to the nearest 5 mm 169 days after sowing.

Genetic diversity analysis

Genetic diversity parameters of the populations were determined by assaying 37 allozyme loci, coding for 15 enzymes in haploid megagametophytes as described in Rajora et al. (2000). Of the 37 loci studied, eight were invariant (monomorphic) in all ten red spruce populations and 29 were polymorphic. The traits examined include: (1) the percentage of monomorphic loci, (2) the percentage of polymorphic loci, (3) the mean number of alleles per locus, (4) the latent genetic potential, (5) the proportion of rare alleles, and (6) the mean observed heterozygosity.

Statistical analyses

The regional (Ontario versus Maritime) effect was tested in a covariance analysis to examine tree height growth in relation to various genetic diversity traits in a way analogous to the analysis of covariance of female effects presented by Major and Johnsen (1996), using the model $Y_{ij} = B_0 + B_{0i} + B_1X_{ij} + B_{1i}X_{ij} + e_{ij}$, where Y_{ij} is tree height of the j^{th} population of the i^{th} region, B_0 and B_1 are average regression coefficients, B_{0i} and B_{1i} are region coeffi-

Table 1 Geographic coordinates, elevation, and population abbreviations for sampled red spruce populations

Location of populations (population abbreviation)	Latitude	Longitude	Elevation (m)
Maritimes:			
1. Rossignol Lake, NS (RL)	45°08′	65°14′	100
2. Abraham Lake, NS (AL)	45°10′	62°38′	185
3. Quiddy River, NB (QR)	45°31′	65°12′	100
4. Hurlett Road, NB (HR)	46°07′	66°39′	185
5. Blowdown Brook, NB (BB)	46°41′	67°36′	380
Ontario:			
6. Gloucester Township (GT)	45°21′	75°32′	80
7. Haliburton Forest (HF)	45°13′	78°35′	185
8. Bruton Clyde Reserve (BCR)	45°17′	78°17′	460
9. Centennial Ridges (CR)	45°34′	78°25′	510
10. Blythe Township (BT)	46°32′	79°32′	380

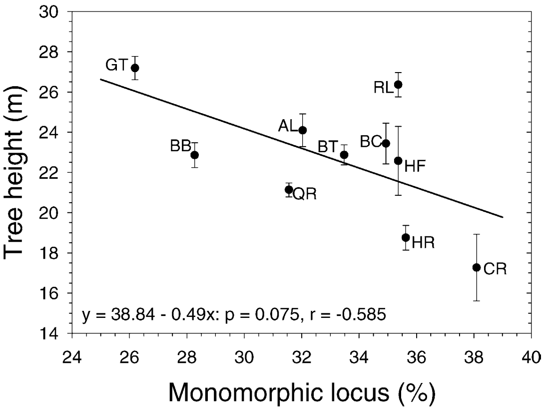

Fig. 1 Relationship between tree height (mean and SE) and percentage of monomorphic loci by population (see Table 1 for population abbreviations)

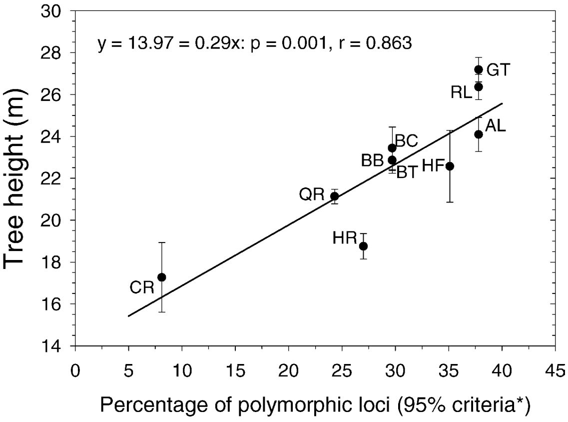

Fig. 2 Relationship between tree height (mean and SE) and percentage of polymorphic loci (genetic diversity) at the 95% criterion by population (see Table 1 for population abbreviations). *A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95

cients, X_{ij} is the independent variable (e.g., genetic diversity traits such as the percentage of poly- and mono-morphic loci, the mean number of alleles per locus, the latent genetic potential, the proportion of rare alleles, and heterozygosity), and e_{ji} is the error term. In this analysis, three sources of variation are identified: (1) genetic diversity trait (covariate), (2) region, and (3) region × covariate. Significant region effects indicate differences in region means (i.e., differences in B_{0i} coefficients, if B_{1i} coefficients are similar) and significant region × covariate effects indicate differences in the slopes (B_{1i} coefficients) between regions.

The relationships (*r*-value) and significance (*p*-value) of stand age, tree height, tree diameter and height of the open-pollinated progeny with genetic diversity parameters were determined by correlation analysis based on the population means for these traits. Two-dimensional plots with *p*- and *r*-values were constructed to portray these relationships for the stands identified in Table 1.

Results

Correlations between stand averages for traits such as tree height, diameter and age resulted in no significant relationships among these traits (data not shown). For instance, average stand height showed no relationship to average stand age ($p = 0.685$). However, average stand height was significantly correlated with a number of genetic diversity traits. The region effect (e.g., Ontario vs Maritimes) was not significant for any of the genetic diversity traits examined. Mean stand height was negatively correlated to percent monomorphic loci ($r = -0.585$) (Fig. 1). The Gloucester Township (Ontario) population was monomorphic for eight of the allozyme loci that were normally polymorphic in most of the other populations. The Centennial Ridges (Ontario) population was monomorphic for 19 loci that were normally polymorphic in most of the other populations. Rossignol Lake (Nova Scotia) appears to be an outlier in this relationship between percent monomorphism and average stand height growth.

Average stand height was strongly ($p = 0.001$) and positively ($r = 0.863$) correlated with the percent polymorphic loci (Fig. 2), when a locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95 (95% criterion). There was also a significant positive correlation ($p = 0.02$, $r = 0.725$) between mean stand height and percent polymorphic loci, when a locus was considered polymorphic if the frequency of the most common allele did not exceed 0.99 (99% criterion) (data not shown). The populations at Gloucester Township, Rossignol Lake and Abraham Lake (Nova Scotia) were among the most polymorphic. The ranking of the ten different populations was relatively consistent regardless of whether the percentage of polymorphic loci was calculated based on the 95% or 99% criteria.

Average stand height was also strongly and positively correlated to the mean number of alleles per locus (Fig. 3A) ($r = 0.750$, $p = 0.012$) and latent genetic potential (Fig. 3B) ($r = 0.718$, $p = 0.019$). However, the relationship between the average tree height within a stand

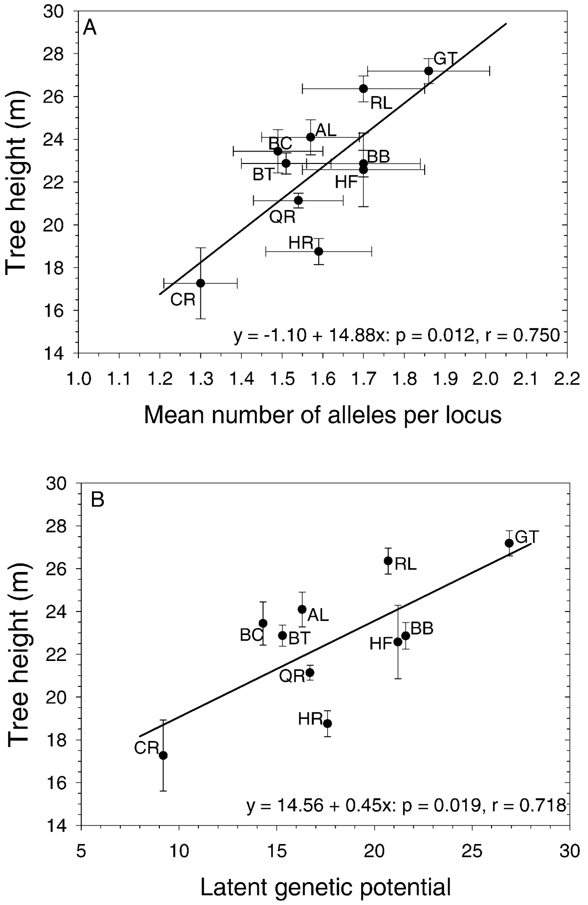

Fig. 3 Relationship between tree height (mean and SE) and (**A**) mean number of alleles per locus, and (**B**) latent genetic potential by population (see Table 1 for population abbreviations)

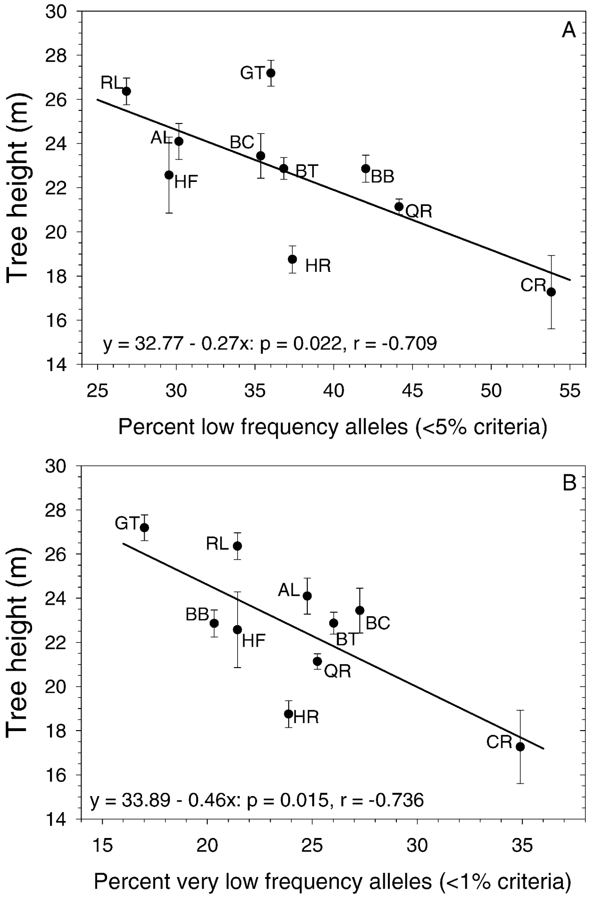

Fig. 4 Relationship between tree height (mean and SE) and rare alleles at (**A**) 5% criterion, and (**B**) 1% criterion, by population (see Table 1 for population abbreviations)

and the percentage of rare alleles (Fig. 4A and B) showed a strong decline in height growth with increasing proportions of rare alleles. The ranking of individual populations was somewhat different when comparing the 1% and 5% criteria as the frequency threshold for rare alleles (Fig. 4A and B).

A strong positive relationship was detected between stand tree height and mean observed heterozygosity (Fig. 5) (r = 0.698, p = 0.025). Populations from Gloucester Township, Rossignol Lake and Abraham Lake once again showed some of the highest genetic diversity in terms of observed heterozygosity.

There was a strong negative relationship between the proportion of empty seeds, which is a measure of reproductive fitness, and average stand age (r = –0.731, p = 0.016) (Fig. 6A). Covariate analysis indicated no significant regional effect (p = 0.764) or region × age interaction (p = 0.362). There was a strong positive correlation between average seedling progeny height, which is a measure of genetic fitness, and the average stand age of their parents (r = 0.568) (Fig. 6B). Covariate analysis indicated no significant regional effect (p = 0.528) or region × age interaction (p = 0.255).

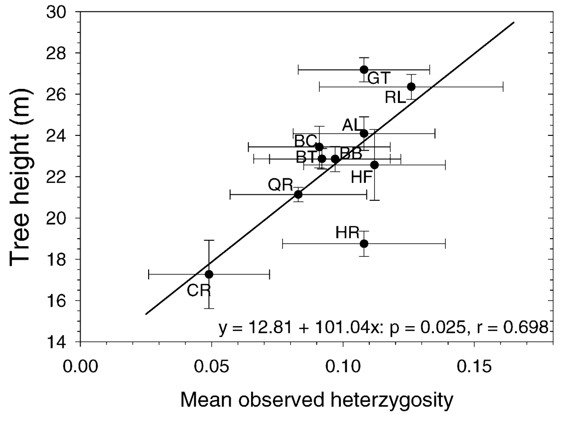

Fig. 5 Relationship between tree height (mean and SE) and mean observed heterozygosity by population (see Table 1 for population abbreviations)

Correlations between average parental population diversity traits and average seedling progeny height resulted in no significant relationships (p > 0.300, data not shown).

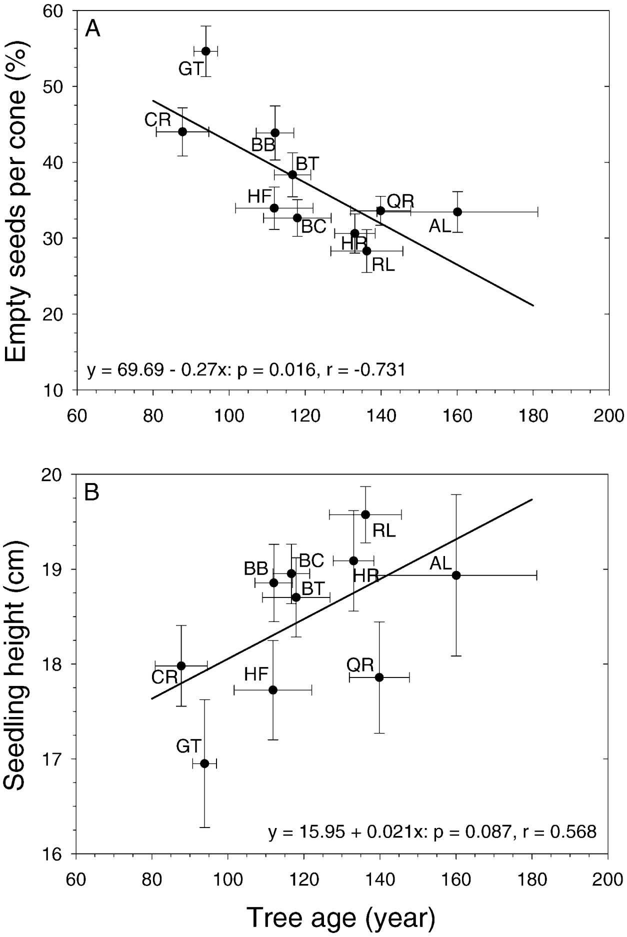

Fig. 6 Relationship between (**A**) empty seeds production per cone, and (**B**) seedling progeny height growth, to stand age by population (see Table 1 for population abbreviations)

Discussion

Old-growth forest is a stage of forest development that represents a unique physical environment in terms of light availability, atmospheric moisture, nutrient regime, biomass structure and temporal stability of biomass structure. The declining representation of the old-growth stage of forest development has become a conservation issue because of the perceived ecological value and role of old-growth forests in biodiversity conservation (Cogbill 1996; Meier et al. 1996; Selva 1996). However, the role of these forests as important gene pools and seed sources has received much less attention. Our study indicates that old-growth red spruce populations may also serve as important reservoirs of genetic diversity and reproductive fitness.

The negative relationship between average stand height and percent monomorphic loci (Fig. 1), the strong positive correlations between average stand height and the percentage of polymorphic loci (Fig. 2), measures of allelic richness (Fig. 3A and B) and observed heterozygosity (Fig. 5), support the relationship between growth and genetic diversity in red spruce. In pitch pine (*Pinus rigida*), the positive relationship between tree diameter and heterozygosity also increased with stand age (Ledig et al. 1983). Increased genetic diversity (e.g., individual heterozygosity) may confer some inherent superiority in individual fitness and the capacity to buffer against environmental changes (Lerner 1954; Ledig et al. 1983; Mitton and Grant 1984; Allendorf and Leary 1986). Allozyme heterozygosity was found to be associated with stem diameter in trembling aspen, *Populus tremuloides* (Mitton et al. 1981), whereas no such relationship was observed in Ponderosa pine, *Pinus ponderosa*, and Lodgepole pine, *Pinus contorta* (Mitton et al. 1981). Most allozyme variation is thought to be largely neutral with respect to fitness (Kimura 1979). However, its selective value has not been adequately determined in forest trees. Nevertheless, we assumed that allozyme variation corresponded with variation at adaptively significant genes, and that its relationship with growth and other measures of fitness may be particularly important in a species with such low genetic diversity as red spruce (Morgenstern et al. 1981; Fowler et al. 1988; Eckert 1989; Bobola et al. 1992; Hawley and DeHayes 1994; Perron et al. 1995; Rajora et al. 2000) in comparison with most other trees for which allozyme-based estimates of genetic diversity are available (Hamrick and Godt 1990). The relatively low genetic diversity found in red spruce has been implicated in its decline (DeHayes and Hawley 1988, 1992).

The negative relationship between height growth and the proportion of rare alleles (Fig. 4A and B) suggests that high proportions of these rare alleles may be deleterious to height growth, as was observed in pitch pine (Bush and Smouse 1992). Although showing a negative effect, under an adaptive gene action hypothesis, the rare alleles in a population may also represent much of the genetic potential required for population adaptation to environmental changes. Latent genetic potential (LGP), which is the difference between the total number of alleles and the effective number of alleles summed over all loci (Bergmann et al. 1990), is a measure of allelic richness that emphasizes richness in terms of low frequency or rare alleles.

In most short-lived, early successional tree species, growing in open (fully exposed) environments, tree diameter growth is normally correlated with height growth. Intuitively, height and diameter growth could be considered as potential surrogate measures for age, but we detected no correlation between height and age. There are several reasons why this relationship between height and age might not hold in long-lived, late-successional trees such as red spruce. In long-lived, shade-tolerant trees, adapted to natural regeneration and growth under an established forest canopy, diameter growth fluctuates dramatically in relation to light levels created by the presence or absence of their nearest neighbors within a stand. In the case of red spruce, this phenomenon was quite evident when aging individual trees was based on stem increment cores (Mosseler et al.

2000). Growth (stem diameter) profiles varied dramatically over the lifespan of an individual, with alternating random episodes of suppression and release based on the effects of highly localized canopy gap disturbance events, such as the death of neighboring trees or small groups of trees.

Although the Gloucester Township population from Ontario was one of the tallest and most genetically diverse of the sampled populations, it was also the smallest and most isolated population with only 36 reproductively mature individuals. There was strong evidence from a previous study that this stand had experienced genetic drift based on the unusually high frequency of chlorophyll-deficient seedlings (Mosseler et al. 2000). This population produced seedling progeny with the lowest vigor in terms of height growth (Fig. 6B), suggesting increased inbreeding and inbreeding depression due to the effects of small population size and isolation. These differences between the genetic status of the parental population and its seedling progeny indicate that the decline of red spruce in Ontario may be a relatively recent phenomenon, having occurred within the past several generations following a period of intensive logging activity in Ontario coinciding with European settlement. Thus, the extant Gloucester Township population may represent a small remnant of a much larger population that existed before the extensive logging that accompanied European settlement.

The mixed mating and breeding system of conifers (Sorensen 1982) and the existence of close family structure in natural populations, may increase levels of self-fertilization and consanguineous mating, respectively (Rajora et al. 2000). Inbreeding affects all traits by increasing homozygosity within individuals and populations. In natural populations of red spruce, both reproductive and vegetative fitness traits are affected simultaneously by inbreeding and inbreeding depression (Mosseler et al. 2000). The largest and oldest stands of old-growth red spruce, located at Rossignol Lake and Abraham Lake in Nova Scotia, had among the highest genetic diversity, and also had among the tallest and oldest trees. These populations also produced the fastest growing (tallest) seedling progeny. Thus, age in these large, old-growth stands may be a good surrogate measure for genetic diversity and progeny growth performance; whereas in the smaller, isolated populations of Ontario (such as Gloucester Township) and elsewhere in the Maritimes, these age and fitness relationships may be obscured by the effects of inbreeding (e.g., Gloucester Township). We hypothesize that the better performing progeny have greater genetic diversity (e.g., heterozygosity and allelic richness). This has been demonstrated in eastern white pine, where fixation rates in the filial seed population increased in smaller, isolated and more widely spaced (lower density) populations (Rajora et al. 2002). The high proportion of empty seeds in the Gloucester Township population demonstrates the effects of inbreeding on reproductive fitness (e.g., filled seed production) and in the poor growth performance of the resulting seedling population, whereas the extant parental population appears to have maintained its genetic integrity. Therefore, old-growth forests can represent superior seed sources, but only if they are also of a sufficient size and density to avoid the effects of inbreeding and genetic drift.

The loss of genetic diversity can play a decisive role in species persistence over the longer term because such diversity allows species to remain fit and adapt to changing environments (Lande 1996). The Fundamental Theorem of Natural Selection (Fisher 1930) states that the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness. Thus, the conservation and maintenance of genetic diversity in natural populations is critical to their adaptation and survival, particularly in rapidly changing environments. Earlier studies have shown that both old growth and older second-growth red spruce populations had lower genetic diversity than other conifers with similar life history traits (Hamrick and Godt 1990; Rajora et al. 2000).

Our results on the reproductive and genetic status of red spruce demonstrate significant positive relationships between average population age and genetic fitness in traits related to reproductive success (Fig. 6A) and seedling progeny height growth (Fig. 6B). Older trees produced not only better quality seed in terms of height growth in the resulting progeny but also produced less empty seed. Therefore, a direct relationship may exist between the age of the parent tree and its reproductive and genetic fitness. These results suggest that older populations of red spruce may have special genetic characteristics or processes that maintain or promote the genetic potential of their progeny in terms of growth performance, and also the reproductive capacity of natural populations. As populations age, one might expect the average level of genetic diversity to increase as natural selection against inbred individuals, due to the effects of inbreeding depression, reduces the number of inbred trees (Rajora et al. 2002). We know from earlier work (Mosseler et al. 2000; Rajora et al. 2000) that high levels of inbreeding occur in red spruce and that such high levels of inbreeding are tolerated in the viable seed produced by red spruce trees.

Older forests may have an important role as reservoirs of genetic diversity and reproductive capacity, by ensuring that populations maintain the genetic potential for adaptation to rapidly changing climate conditions and landscape patterns due to human impacts, and following the introduction of diseases and pests. However, the potential genetic advantages of older populations, as reservoirs of genetic diversity, can be undermined by inbreeding and genetic drift in small, isolated populations. The relationships observed among reproductive, genetic, and progeny fitness traits in red spruce are important because reproductive success and growth performance are the main components of fitness driving species survival and evolution. These relationships within old-growth red spruce stands present some of the strongest biological arguments in support of old-growth forest protection. A concerted effort should be made to maintain an adequate proportion of these older populations as reservoirs of genetic diversity and reproductive fitness to ensure the dispersal of genetically diverse seed across a landscape of changing environments.

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