Silviculture alters the genetic structure of an eastern hemlock forest in Maine, USA

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Abstract: We evaluated the influence of long-term silvicultural selection on the genetic structure of an eastern hemlock (*Tsuga canadensis* (L.) Carr.) forest at the Penobscot Experimental Forest, in Maine, USA. Plots in this forest received one of the following three treatments: (1) selection cuts in which small and poorly formed trees were preferentially removed in 1957 and 1977; (2) diameter-limit cuts in which trees at least 24 cm in diameter were removed in 1952, 1973, and 1994; or (3) no harvesting (an unmanaged control). Because of an association between the occurrence of rare alleles and tree phenotypes, phenotypically based tree removals were associated with a shift in allelic frequency. Where smaller trees with inferior phenotypes were preferentially removed (selection cut), the number of rare alleles and estimates of future genetic potential were lower than in the control group. Because of the theoretical long-term evolutionary benefit of unique gene forms, the loss of rare alleles could diminish the potential of populations to adapt to and survive ongoing environmental change. In contrast, alleles that were rare in the control group existed at a higher frequency in the diameter-limit cut. However, productivity was low in this stand, where the frequency of characteristically rare alleles was artificially amplified.

Résumé : Les auteurs ont évalué les effets de la sélection sylvicole pratiquée pendant une longue période sur la structure génétique d'un peuplement de pruche du Canada (*Tsuga canadensis* (L.) Carr.) à la forêt expérimentale de Penobscot dans le Maine, aux États-Unis. Les parcelles expérimentales de cette forêt ont reçu l'un des trois traitements suivants : (1) des coupes de jardinage où les arbres mal formés ou de faible dimension ont été préférentiellement récoltés en 1957 et 1977; (2) des coupes à diamètre limite où les arbres de 24 cm de diamètre et plus ont été récoltés en 1952, 1973 et 1994; ou (3) aucune récolte (parcelles témoins non aménagées). En raison d'une association entre la présence d'allèles rares et le phénotype des arbres, la récolte des arbres effectuée à partir d'une évaluation du phénotype était associée à un changement des fréquences d'allèles. Là où les petits arbres au phénotype inférieur étaient préférentiellement récoltés (coupe de jardinage), le nombre d'allèles rares et les estimations du potentiel génétique futur étaient plus faibles comparativement au traitement témoin. Étant donné le bénéfice théorique à long terme des formes alléliques uniques du point de vue évolutif, la perte des allèles rares pourrait réduire la capacité des populations à s'adapter et à survivre aux changements environnementaux actuels. À l'opposé, les allèles qui étaient rares au sein du traitement témoin avaient une fréquence plus élevée après la coupe à diamètre limite. Toutefois, la productivité était faible dans ce peuplement où la fréquence des allèles typiquement rares avait été artificiellement augmentée.

[Traduit par la Rédaction]

Introduction

The selective removal of individual trees and their genes from forest systems has the potential to alter the genetic structure of residual populations and levels of genetic diversity on which stand productivity, ecosystem stability, long-term survival, and evolution depend. Genetic structure can change as a result of the selective loss of specific genes, alterations in the frequency of genes, or disruptions of breeding systems within populations. Most north temperate conifers depend on outcrossing to maintain genetic variability and create new adaptive genotypes in response to changing environmental conditions. An important potential consequence of selective tree removal is an increase in inbreeding, which could reduce the reproductive output and viability of a population and possibly delay the development of new genotypes, which are the foundation of adaptation to changing environmental conditions (Ledig 1992).

Despite the potential for harvest-induced changes in population genetics, little empirical information has been generated concerning the influence of intensive forest management on genetic structure and diversity within forest stands. In addition, the few published reports that do exist provide conflicting indications of the impact of harvesting on genetic reserves. For example, Neale (1985) and Neale and Adams (1985) reported that shelterwood harvesting had little impact on the genetic structure of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. They attributed this resiliency to the high levels of genetic diversity inherent to Douglas-fir and the fact that the species occurs in almost pure, high-density stands.

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Table 1. Year silvicultural treatment was imposed, and amount of eastern hemlock removed.

Treatment and year of cut	No. of hemlock·ha^{-1} preharvest	No. of hemlock·ha^{-1} removed	% hemlock removed	% hemlock basal area removed
Diameter limit				
1952	140	30	21.4	41.7
1973	215	89	41.4	57.2
1992	169	83	49.1	65.0
Selection cut				
1957	350	107	30.6	44.3
1977	262	198	75.6	76.0

In contrast, Cheliak et al. (1988) found that phenotypically selected white spruce (*Picea glauca* (Moench) Voss) trees had on average only 75% of the genes found in randomly selected trees from the same population. Significant reductions in genetic diversity following harvests were also noted by Buchert et al. (1997) in virgin, old-growth eastern white pine (*Pinus strobus* L.) stands in central Ontario. Here, a 75% reduction in tree density was accompanied by a 25% decrease in the number of alleles, a 33% reduction in the proportion of polymorphic loci, a 40% loss of low-frequency alleles, and an 80% decrease in the number of rare alleles. It was estimated that the latent genetic potential of these stands was reduced by about 50% and that this loss likely compromised the ability of these gene pools to adapt to changing environmental conditions. Microsatellite DNA analysis by Rajora et al. (2000) on samples from the same study produced results similar to those reported by Buchert et al. (1997), who used allozyme analysis.

To better assess the influence of selective harvesting on the genetic resources of eastern hemlock (*Tsuga canadensis* (L.) Carr.), we measured the effect of two opposing silvicultural treatments — a diameter-limit cut and a selection cut — imposed repeatedly over 40 years, on the genetics of residual populations in a long-term study at the USDA Forest Service's Penobscot Experimental Forest (PEF), Bradley, Maine, USA.

Materials and methods

Stand history and plant material

Between 1952 and 1957, the USDA Forest Service established a replicated, long-term experiment at PEF in east-central Maine to examine the differential responses of a mixed northern conifer forest to several silvicultural treatments. Although the study area was never cleared for agriculture or grazing, it had been thinned, perhaps 20–40 years before 1950 (Safford et al. 1969). Red spruce (*Picea rubens* Sarg.) and eastern hemlock were the dominant long-lived conifers in these stands. However, because red spruce is more commercially valuable than eastern hemlock, it was favored as a residual tree for future harvest. Consequently, from the beginning of the experiment, eastern hemlock has been harvested at greater frequency than red spruce. Because of the greater selection pressure on eastern hemlock in these stands, it was selected for genetic assessments. Stand age structures were not determined when the experiment began. However, Kenefic and Seymour (2000) established that selected stands in the long-term silvicultural experiment are quite uneven aged, with eastern hemlock represented in almost every age-class from 10 to 210. In addition to an unmanaged control stand, silvicultural treatments in this long-term experiment included two opposing selection criteria: a diameter-limit cut and a selection cut.

The fixed diameter-limit cut was applied throughout a 10-ha stand and consisted of three harvests: June 1952, May 1973, and January 1994. When the experiment started, in 1952, eastern hemlock accounted for 18% of the trees in the stand and 25% of the basal area. All merchantable hemlock trees with diameter at breast height of ≥24 cm were removed. Other tree species had different diameter limits, and unmerchantable trees were not harvested. Approximately one-fifth to one-half of the hemlock trees were removed in each of the three cuts, which resulted in removal of 41%–65% of the basal area of hemlock per cut (Table 1). At the most recent inventory (1999), 31% of the trees in the stand were eastern hemlock, and they accounted for 40% of the stand basal area.

The selection cut was applied throughout an 8-ha stand and consisted of two harvests prior to genetic assessments: May 1957 and January 1977. On the PEF, selection silviculture is practiced, and cutting cycles and stand structural goals are defined by the BDq method (Guldin 1991). In this study, the cutting cycle was 20 years, and the BDq goals were as follows: residual basal area (B), 18.4 m^2·ha^{-1}; residual maximum diameter (D), 40.6 cm; and the relationship between the number of trees across consecutive diameter-classes (q), 1.96 for 5-cm classes. Essentially, harvesting criteria were the opposite of those for the diameter-limit cut: across diameter-classes, phenotypically superior trees were retained, and trees with negative phenotypes (poor-risk, unmerchantable, and poor-quality trees) were preferentially removed. Nearly one-third of the eastern hemlock trees were removed in 1957, and an additional 75% were removed in 1977 (Table 1). Because the selection cut was administered twice rather than three times, the overall selection intensity was not as great for the selection cut as it was for the diameter-limit cut. After the genetic assessments were done, a third harvest was conducted; hemlock currently accounts for 22% of the trees in the stand and 30% of the basal area.

Seed was collected in the fall of 1994 from 40–50 randomly selected residual eastern hemlock trees from throughout each treatment. In addition, seed was also collected from 50 trees in an unmanaged control (approximately 2 ha in area) adjacent to the stands receiving silvicultural treatments.

Table 2. Measures of genetic diversity of residual eastern hemlock trees following two silvicultural treatments and for an unmanaged control stand.

	Treatment		
Genetic diversity parameter	Control	Diameter-limit cut	Selection cut
No. of trees	35	31	40
Total no. of alleles	42	44	39
Mean no. alleles per locus	1.56	1.63	1.44
Effective no. alleles per locus	1.20a	1.26b	1.18a
% loci polymorphic (95%)	18	41	26
Mean observed heterozygosity	8.7b	11.2a	8.3b
Mean expected heterozygosity	10.1	14.5	9.7
Mean fixation index	0.044	0.216	0.105
P^*	0.142	0.034	0.090

Note: Means within genetic diversity parameter followed by the same letter are not significantly different according to analysis of variance ($P < 0.05$).

*Probability of difference between observed and expected heterozygosity.

Because of variable germination, final genetic assessments were conducted on 31–40 individuals per treatment (Table 2). Using megagametophyte tissue, we were able to examine 62–80 gametes per locus, providing an average of >90% probability of detecting an allele of ≥4% frequency if it was present in the population (Brown and Moran 1981).

We compared genetic diversity assessments from the control stand with those from the treated stands to evaluate the effects of silvicultural treatments on stand genetics. Because silvicultural treatments were begun in the 1950s, it was not possible to confirm that stands were genetically similar prior to treatment. However, because of similar stand histories prior to the study and the random assignment of treatments, we made the assumption that contemporary differences in genetics primarily reflect differences in long-term silvicultural selection. This assumption and approach have been used by others to assess the influence of silviculture, domestication, and other anthropogenic factors on tree genetics (Neale 1985; Bergmann and Scholz 1987; Stoehr and El-Kassaby 1997; Adams et al. 1998).

Genetic assessments

Starch gel electrophoresis of megagametophyte tissue was used to assess genotypes and genetic variability of residual trees in treatment and control stands. A total of 106 individual trees were examined at 27 gene loci representing 19 enzyme systems. Electrophoretic data were also used to assess levels of inbreeding and outcrossing. Electrophoretic gel buffers and enzyme recipes were prepared according to procedures described by Jech and Wheeler (1984) and Cheliak and Pitel (1984) and included appropriate modifications made in our laboratory. Seed from individuals of known genotype that have been shown to be highly homozygous were included as standards in each electrophoretic run.

Data analyses

For each individual tree, multilocus genotypes and estimates of observed heterozygosity were obtained. For the unmanaged stand and residual stands from the two cutting regimes, genetic estimates included proportion of polymorphic loci, effective number of alleles per locus, percentage polymorphic loci, allelic frequencies, observed and expected heterozygosity, fixation indices, and single-locus estimations of inbreeding and outcrossing levels. We used BIOSYS-1 for most of the data analysis (Swofford and Selander 1989). Analysis of variance was used to test for differences among trees in the treated and control stands in observed heterozygosity, expected heterozygosity, and effective number of alleles per locus when individual locus measures were used as observations. The significance of allele frequency differences between trees in the treated and control stands was calculated by using χ^2 tests of heterogeneity (Workman and Niswander 1970). We calculated mean and individual locus fixation indices for each stand to determine to what extent homozygosity and heterozygosity deviated from those expected under Hardy–Weinberg equilibrium.

For each stand, we calculated χ^2 goodness-of-fit values with BIOSYS-1 for each locus to test observed genotypic proportions against those expected under Hardy–Weinberg equilibrium. Uncommon (frequency of $0.25 > P > 0.05$) and rare ($P \leq 0.05$ frequency) alleles were determined, and the proportion of trees in each stand possessing rare alleles was calculated.

To evaluate the long-term influence of silvicultural treatments on the future genetic potential of these stands and to help define genetic diversity losses, we also compared several calculated measures of genetic potential for residual trees in the silvicultural treatments and control. Calculated parameters were latent genetic potential (which sums the differences between number of alleles per locus and expected number of alleles per locus), hypothetical gametic diversity (the product of effective number of alleles per locus for all loci), and genotypic multiplicity (the product of the potential number of alleles at each locus over all loci) (Bergmann et al. 1990). Although not commonly calculated for tree improvement research, these estimates have recently been used in evaluating the effects of anthropogenic selection on forest gene pools in numerous studies (e.g., Buchert et al. 1997; Rajora et al. 2000; Konnert and Ruetz 2003; Rajora and Pluhar 2003).

Results and discussion

Level of genetic diversity

Among the eastern hemlocks in the unmanaged control stand, 18% (95% criterion) of the 27 loci were polymorphic,

Table 3. Comparison of genetic diversity measures of residual eastern hemlock trees following two silvicultural treatments and for an unmanaged control stand.

	Treatment		
Genetic diversity parameter	Control	Diameter-limit cut	Selection cut
Total no. of rare alleles	9	5	4
Total no. of low-frequency alleles	2	8	4
Novel alleles relative to control	—	4	2
Lost alleles relative to control	—	2	5
% trees with rare alleles	29	68	34
% trees with ≥2 rare alleles	6	26	2
% trees with homozygous rare alleles	0	42	5
Latent genetic potential	9.6	9.9	7.1
Genotypic multiplicity	4.25×10^6	38.33×10^6	0.23×10^6
Hypothetical gametic diversity	36.9	159.7	31.8

and the mean and effective numbers of alleles per locus were 1.56 and 1.20, respectively (Table 2). Observed and expected heterozygosity levels in the unmanaged control stand were 8.7% and 10.1%, respectively. This somewhat higher expected than observed heterozygosity also resulted in a slightly positive stand mean fixation index in the unmanaged control stand, which indicates a small excess of homozygotes within this natural stand. However, results from the paired *t* test of observed versus expected heterozygosity and χ^2 tests for each locus were all nonsignificant, indicating that the control stand was in Hardy–Weinberg equilibrium. Our genetic assessments of this single eastern hemlock stand are considerably higher than those of Zabinski (1992), who, when using foliar tissue, reported only 1 of 10 loci to be polymorphic for 17 eastern hemlock populations.

Eastern hemlock remaining after two selection cuts that removed phenotypically inferior trees were similar to trees in the control stand in their level of genetic diversity and were not significantly different from trees in the control stand for any parameters we used to measure genetic diversity (Table 2). The mean fixation index for the selection cut was positive and slightly higher than that for the control. However, observed and expected heterozygosity levels were not significantly different, indicating that the selection cut stand was also in Hardy–Weinberg equilibrium.

After three treatment cycles, residual trees in the diameter-limit treatment were significantly higher in genetic diversity measures than trees in the control and selection cut stands (Table 2). Observed heterozygosity was >25% higher than in trees in the control stand and nearly 35% higher than in selection cut stand trees, and more than twice as many loci were polymorphic in the stand receiving repeated diameter-limit cuts than in the control. Even greater differences were found between stand treatments when expected heterozygosity was examined. Diameter-limit treatment trees had 43% and 50% higher levels of expected heterozygosity than control and selection cut trees, respectively. The mean fixation index for the diameter-limit stand was positive and considerably higher than those of control and selection cut treatments. The χ^2 tests revealed that 36% of the variable loci were out of Hardy–Weinberg equilibrium in the diameter- limit treatment, and a paired *t* test indicated that observed heterozygosity was significantly lower than expected after a generation of random mating (Table 2). The positive fixation index indicates an excess of homozygotes in the stand. In this diameter-limit cut, repeated removal of the most vigorous trees in the stand was associated with a dramatic increase in genetic diversity and an alteration in the genetic structure in the residual population relative to the control.

Allele frequency differences

Although differences in genetic diversity were evident among stands, differences in the frequencies of rare and uncommon alleles among stands were substantial and likely the underlying cause of genetic diversity differences. Trees in the control stand had nine rare ($P \leq 0.05$ frequency) and two uncommon ($0.25 > P > 0.05$) alleles (Table 3). The stand modified by a series of diameter-limit cuts contained fewer rare alleles (five) but more uncommon alleles (eight) than the control. The selection cut stand also had fewer rare alleles than the control (four vs. nine) and five alleles that were no longer detected. Eastern hemlock in the selection stand also had a slightly higher number of uncommon alleles (four) than the control stand (two).

The higher number of uncommon alleles and lower number of rare alleles in the diameter-limit cut stand compared with the control occurred primarily because alleles that were rare in the control existed at a higher frequency in the diameter-limit stand and, thus, moved into the uncommon allele category (Table 4). For example, 26% of the trees in the unmanaged control contained rare alleles, whereas 68% of the trees receiving the diameter-limit cut possessed alleles that were rare in the unmanaged control (Table 3). Only 6% of the trees in the unmanaged control contained at least two rare alleles, whereas 26% of the trees in the diameter-limit cut contained at least two rare alleles. More than 40% of the trees in the diameter-limit cut were homozygous for alleles that were rare in the control; this represents a dramatic difference. For example, none of the trees from the control were homozygous for rare alleles (Table 3). Furthermore, four alleles found in the stand receiving the diameter-limit cut were not detected in the control stand. Presumably, these alleles were associated with the selection to retain slow-growing, poorly formed trees that would normally be expected to be eliminated by the natural thinning process. Three out of four of these alleles were rare, and the remaining allele occurred in high enough frequency to be considered uncommon.

As frequencies of typically rare genes increased, so did measures of genetic diversity (Table 2). This treatment-associated shift in gene frequency likely resulted from the dispropor-

Table 4. Rare ($P \leq 0.05$) and uncommon ($0.05 < P < 0.25$) allele frequency distribution among silvicultural treatments and control.

Locus and allele	Control	Diameter-limit cut	Selection cut
6PG-1 B	Not detected	Rare	Not detected
6PG-1 C	Rare	Not detected*	Not detected*
ATT-1 B	Rare	Uncommon	Not detected*
ACP-1 C	Rare	Rare	Not detected*
BST-1	Not detected	Uncommon	Not detected
DIA-1 C	Not detected	Rare	Not detected
G3P-1 C	Rare	Not detected*	Not detected*
IDH-1 B	Not detected	Rare	Not detected
LAP-1 C	Uncommon	Uncommon	Uncommon
LAP-2 B	Rare	Uncommon	Uncommon
LAP-2 C	Not detected	Not detected	Rare
MDH-1 B	Rare	Uncommon	Rare
MDH-2 B	Not detected	Not detected	Rare
PGI-1 B	Uncommon	Uncommon	Uncommon
PGI-1 C	Rare	Rare	Not detected*
PGI-1 B	Rare	Uncommon	Uncommon
UGP-1 B	Rare	Uncommon	Rare

*Not detected, but present in the control stand.

tionate concentration of rare gene forms in the phenotypically inferior trees preferentially retained under diameter-limit selection criteria. With repeated removal of larger competitors, gene forms that were rare following natural selection (the dominant selective force in the control) were allowed to persist in the diameter-limit stand and increase in relative frequency.

Coincident with nearly opposite tree removal criteria, the selective removal criteria (favoring plus trees) had an influence on rare and uncommon allele frequencies antithetical to that of criteria used for the diameter-limit stand. Alleles that were rare in the control stand generally did not occur at a higher frequency in the selection stand (Table 4). Instead, the selection stand included fewer rare alleles, with five alleles that were rare in the unmanaged control stand no longer detected. Once again, there appeared to be an association between poor phenotypes and rare alleles: the preferential removal of small, poorly formed trees in the selection treatment was associated with a residual stand with few rare alleles. Because the opposite selection criteria coincided with inverse frequencies of rare alleles in residual stands, it seems likely that rare alleles were disproportionately present in and, in part, responsible for the poor phenotypes (slow growth, poor form) used as the basis for silvicultural selection.

Unique vulnerability of rare alleles to silvicultural manipulation

Because they occur at such low frequencies, rare alleles may be mathematically prone to meaningful alterations in frequency as a result of directional anthropogenic selection. In these eastern hemlock stands, the apparent overlap of rare alleles with phenotypic traits used to make harvesting decisions resulted in selections that were associated with either increases (the diameter-limit treatment) or reductions (the selection treatment) in the frequencies of typically rare alleles. However, the association of rare alleles with phenotypic characteristics used for selection is not unique to eastern hemlock. Indeed, because of a consistent association between negative phenotypes and rare alleles for a range of coniferous species, several recent studies support our observation that rare alleles may be particularly susceptible to silvicultural manipulation. Buchert et al. (1997) found that when eastern white pine underwent a 75% density reduction harvest that preferentially retained trees with old-growth characteristics (e.g., large size), the total number of alleles was reduced by 25%, and the percentage polymorphic loci decreased by 33%. Importantly, this phenotypically directed harvest resulted in an 80% reduction in rare alleles and a 40% reduction in low-frequency alleles. This preferential loss of rare alleles was also found when microsatellite DNA analysis was used to evaluate the genetic effects of harvesting this species (Rajora et al. 2000). For coastal Douglas-fir, Adams et al. (1998) reported fewer alleles in a shelterwood treatment (that preferentially removed low-quality trees) than in an unmanaged control. The alleles absent from the shelterwood stand were rare in the control stand (Adams et al. 1998).

Evidence of the alteration of rare allele frequencies through phenotypic selection also comes from studies involving the domestication of forest tree species. Stoehr and El-Kassaby (1997) compared genetic variation of natural stands with that of seed orchards for interior spruce (*P. glauca* × *Picea engelmannii* Parry ex Engelm.). They found fewer rare alleles in seed orchards than in natural stands and even fewer rare alleles when the seed orchards were thinned on the basis of progeny productivity. In a study comparing the genetics of phenotypically selected white spruce with that of natural stands, Cheliak et al. (1988) found that the selection group had only 75% of the total number of alleles that existed in natural populations.

Numerous studies indicate that because of an apparent association of rare alleles with negative phenotypes (e.g., slow growth, poor form), management options that preferentially remove these phenotypes also tend to eliminate rare alleles. However, our data suggest that the opposite also appears possible: management that selectively favors inferior phenotypes (e.g., our diameter-limit treatment) can increase the frequency of some alleles above natural levels. Because they occur at very low frequencies, rare alleles appear uniquely vulnerable to either potential loss or measurable increases in frequency and potential influence now and into the future. Although it is important to define this propensity for manipulating allele frequency, it is also instructive to consider the potential consequences of these alterations to the productivity and health of forest populations now and into the future. Because of the likelihood of allelic losses through management and domestication, numerous strategies have been proposed to preserve the genetic richness of forest tree species (e.g., Yang and Yeh 1992; Burdon 2001).

Implications for current fitness and future adaptive potential

Rare alleles arise from random gene mutations that are generally thought to have deleterious effects on growth and overall fitness in the short term and to have little adaptive value under current environmental conditions (Bush and Smouse 1992). As a result of the reduced fitness they may convey, most novel alleles remain rare because they are selected against (Rajora and Mosseler 2001). Although the

majority of mutations are expected to be disadvantageous in the homozygous form, they typically exist at such low frequencies that they are of little negative consequence to the population as a whole. However, some factors (e.g., inbreeding and genetic drift) can result in an increased frequency of rare alleles, thereby elevating the genetic load of a population.

Several empirical studies have identified a fitness disadvantage under current environmental conditions for individuals possessing alleles that are generally rare in the population overall. For example, Bush and Smouse (1992) showed that for loblolly pine (*Pinus taeda* L.), there was intense selection against individuals with low-frequency alleles in both the heterozygous and the homozygous forms. Bergmann and Scholz (1987) documented that pollution-sensitive Norway spruce (*Picea abies* (L.) Karst.) had a disproportionate concentration of rare alleles compared with pollution-tolerant individuals. Furthermore, Bongarten et al. (1985) found a significant negative relationship between the number of rare alleles and growth rate for Douglas-fir.

If rare alleles generally have deleterious effects on growth, then the removal of phenotypically inferior trees (a potential reservoir of rare alleles) should result in a reduction of rare alleles within the residual population. This is consistent with data from the selection cut stand, which had fewer rare alleles and was missing alleles relative to the control (Table 3). Presumably, this decline in the number of rare and potentially deleterious alleles would increase the mean fitness of the stand in the near term, given stable environmental conditions. When the experiment began, the stands used in this study were similar in structure and composition (Kenefic et al. 2005). However, now, after three harvests in each treatment, they are markedly different. The selection stand now has significantly more sawtimber-sized trees and greater total stand basal area. Projections 20 years into the future indicate that the selection treatment will be able to sustain a harvest similar to the most recent one, whereas the diameter-limit treatment will have only 88% of the target harvest volume (Kenefic et al. 2005). Although greater productivity in the selection cut reflects the influence of preferentially retaining larger trees, it is also likely that these trees were large, in part because they contained few rare alleles (Table 3).

In contrast to residual trees in the selection treatment, trees remaining in the diameter-limit stand had higher frequencies of alleles that were rare in the control. Indeed, many of these alleles became so common that they were no longer rare in this stand (Table 3). Again, considering the presumed fitness disadvantage conveyed by typically rare alleles, the enhanced presence of unusual gene forms within the diameter-limit treatment would be expected to reduce current stand fitness. Although we do not have data from eastern hemlock, Sokol et al. (2004) compared growth rates of red spruce in the same stands over a 100-year period and showed that residual trees in the diameter-limit cut stands grew more slowly than trees in the selection cut stands. Their results indicate that diameter-limit cutting can select against optimal productivity.

Although numerous studies have demonstrated the possible disadvantage of rare alleles under current environmental conditions, rare alleles are also thought to be a genetic reservoir that accommodates future adaptation, survival, and health as environmental conditions change. The value of rare alleles in supporting population persistence, despite implications of negative short-term fitness, has been widely documented for a variety of life forms, including bacteria (antibiotic resistance; Abramson and Sexton 1999), herbaceous "weeds" (herbicide resistance; Heap 1997), insects (insecticide resistance; Georghiou 1991), and trees (e.g., pollution and pathogen resistance; Berrang et al. 1989; Griffin 2000). Because they can act as a reserve for altered gene expression that may be of adaptive benefit under new environmental and competitive conditions, rare alleles contribute to latent genetic potential that may be vital to long-term population and species survival (Bergmann et al. 1990; Buchert et al. 1997; Rajora and Mosseler 2001). Thus, the loss of genetic diversity, and particularly rare alleles, could diminish the potential of populations to successfully adapt and survive ongoing environmental change and altered competitive pressures (Ledig 1986; Millar and Libby 1991).

To better understand the potential long-term impact of treatment-associated differences in the frequencies of rare and uncommon alleles, we compared the latent genetic potential, hypothetical gametic diversity, and genotypic multiplicity of trees in the control with those of residual trees following the silvicultural treatments. Compared with trees in the control, those in the selection treatment had lower values for latent genetic potential, genotypic multiplicity, and hypothetical gametic diversity (Table 3). The estimates of low future genetic diversity in the selection treatment indicate that the preferential removal of weaker phenotypes may have depleted some of the long-term evolutionary potential of the stand. Buchert et al. (1997) and Rajora et al. (2000) documented similar losses in genetic potential following harvests in old-growth eastern white pine forests. Residual trees in the diameter-limit cut showed a different pattern of potential long-term genetic alteration. Although the latent genetic potential within the diameter-limit cut was only slightly higher, the levels of hypothetical gametic diversity and genotypic multiplicity were projected to be substantially greater than in the control (Table 3). These increases in potential new genotypes following random mating within the residual stand suggest that the evolutionary potential of this stand had been elevated. However, any increase in long-term evolutionary flexibility within the diameter-limit treatment was likely countered by a loss in short-term productivity and current fitness.

Because rare alleles may be a source for both reduced fitness under current conditions and enhanced adaptive potential in an altered competitive environment, they are prominent components of the tradeoff within forests between short- and long-term productivity and health. A balance between these opposing benefits and costs is critical to stand productivity and ecosystem function across a range of time horizons. This balance is determined and maintained through the combined influence of forces such as gene mutation, gene flow, and natural selection. Although many of these factors have shown signs of anthropogenic alteration (e.g., DeHayes et al. 2000; Rajora and Mosseler 2001), our study highlights the potential of intensive management to overshadow natural selection and shift gene frequencies.

The disruption of the balance between current fitness and adaptive potential has been noted by others who found that management activities can alter the frequencies of rare alleles.

For example, Adams et al. (1998) noted that the shelterwood harvest of Douglas-fir resulted in a reduction of potentially deleterious rare alleles. However, they cautioned that currently deleterious alleles might be valuable for adaptation in future environments. Similarly, Stoehr and El-Kassaby (1997) reported that seed orchard populations of interior spruce contained fewer rare alleles than natural stands. They speculated that this loss of rare alleles would not be problematic, because rare alleles contribute little to fitness and are usually the result of deleterious mutations. However, they also noted the limitations of this approach and called for nursery practices that avoid allelic losses. In a similar study, Cheliak et al. (1988) found that phenotypically selected white spruce contained about 25% fewer alleles than native trees. Because important variation may have been lost in the phenotypically selected group, they suggested that this group would be unsuitable for conservation purposes. Furthermore, we recently genotyped 220 eastern white pine trees in a natural stand in central Vermont and found that trees with a high number of rare alleles were disproportionately represented in the suppressed crown class, suggesting both a positive relationship between rare alleles and inferior phenotypes and a vulnerability to the disproportionate amplification or removal of these gene forms through selective harvests (Nijensohn et al. 2005).

Conclusions

Because of the likely association of negative phenotypes and the presence of rare alleles, both silvicultural treatments applied in this study resulted in altered allele frequencies for treated stands relative to the unmanaged control. Repeated diameter-limit cuts that preferentially retained smaller trees with negative phenotypes were associated with a residual stand containing a high proportion of alleles that were rare in the control stand. In contrast, when small, poorly formed trees were preferentially removed in the selection treatment, the resulting stand contained few rare alleles, and some alleles present in the control were no longer detected. Inverse impacts on the frequencies of rare alleles coincident with the implementation of opposing selection criteria support the possibility of a causative relationship between treatment imposition and resulting stand genetics. Our results with eastern hemlock support observations for other species that indicate frequencies of rare alleles are prone to alteration through intensive management. Because rare alleles are likely both a constraint on current stand fitness and a reservoir of gene forms that could be adaptively beneficial at some future time, anthropogenic alteration of rare allele frequencies could disrupt the tradeoff between short- and long-term fitness that preserves stand productivity across time scales.

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