indexes for forest trees. *In:* Proc. Wkshp on Adv. Gen. Breeding: Current Status and Research Needs, June 6—7, 1984. pp. 17—20 (1986). —— Bridgwater, F. E. and Stonecypher, R. W.: Index selection for volume and straightness in a loblolly population. *In:* Proc. 15th So. For. Tree Improv., Starkville, MS. pp. 132—139 (1979). —— Falconer, D. S.: Introduction to Quantitative Genetics. Longman, London. 340 p. (1981). —— Lambeth, C. C., Dougherty, P. M., Gladstone, W. T., McCullough, R. B. and Wells, O. O.: Large-scale planting of North Carolina loblolly pine in Arkansas and Oklahoma: a case of gain versus risk. J. For. 82 (12): 736—741 (1984). —— McKeand, S. E.: Optimal age for family selection for growth in genetic tests of loblolly pine. For. Sci. 34 (2): 400—411 (1988). —— Miller, R. G.: Visual assessment of stem straightness in radiata pine. Austr. For. Res. 7*:* 45—46 (1975). —— Mullin, L. J., Barnes, R. D. and Prevost, M. J.: Review of the Southern Pines in Rhodesia. Rhod. Bull. For. Res. 7*:* 328 p. (1969). —— Namkoong, G.: Introduction to quantitative genetics in forestry. U.S.D.A. Forest Service Tech. Bull. No. 1588. 342 p. (1979). —— Paschke, J. L.: Age-age relationships in loblolly pine (*Pinus taeda* L.). Master of Science thesis, Dept. of Forestry, North Carolina State University, Raleigh, North Carolina. 49 p. (1979). —— Perry, T. O.: The inheritance of crooked stem form in loblolly pine form (*Pinus taeda* L.). J. For. 58*:* 943—947 (1960). —— Schroeder, J. G., Campbell, R. A. and Rodenbach, R. C.: Southern pine log grades for yard and structural lumber. U.S.D.A.-Forest Service Res. Pap. SE-39. 9 p. (1968). —— Shelbourne, C. J. A. and Namkoong, G.: Photogrammetric techniques for measuring bole straightness. Proc 8th So. For. Tree Improv. Conf., Savannah, GA. pp. 131—136 (1966). —— Shelbourne, C. J. A. and Stonecypher, R. W.: The inheritance of bole straightness in loblolly pine. Silv. Gen. 20 (5/6): 151—156 (1971). —— Snedecor, G. W. and Cochran, W. G.: Statistical Methods. Iowa State University Press (1967). —— Talbert, C. B.: An analysis of several approaches to multiple-trait index selection in loblolly pine (*Pinus taeda* L.). Ph. D. Dissertation, Dept. of For., N. C. State Univ., Raleigh, N. C. 106 pp. University Microfilms, Ann Arbor, MI. (1984). —— Talbert, J. T., Bridgwater, F. E. and Lambeth, C. C.: Tree improvement cooperative genetic testing manual. N. C. State-Industry Cooperative Tree Improvement Program, School of Forest Resources, North Carolina State University, Raleigh, N. C. 37 p. (1981).

Genotypic Differentiation at PGM in Engelmann Spruce from Wet and Dry Sites

By J. B. Mitton[1]), H. P. Stutz[1])[2]), W. S. Schuster[1])
and K. L. Shea[3])

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Summary

Microgeographic variation of PGM allozymes was examined in 999 Engelmann spruce from 6 population samples. Field sites were categorized as wet or dry, and genotypic frequencies were compared between adjacent wet and dry sites. Dry sites had higher proportions of heterozygotes than wet sites, and the value of F at dry sites was generally lower than at wet sites. Comparisons of genotypic frequencies between age classes suggests that PGM heterozygotes have lower viability than homozygotes in wet sites.

Key words: Engelmann spruce, microgeographic differentiation, allozymes, natural selection.

Introduction

The high levels of outcrossing and the wind pollination common to all conifers produces the opportunity for high levels of gene flow among populations. Radioactively-labelled pollen has been observed to travel more than one kilometer, and pollen traps on ships 50 or more kilometers from shore capture conifer pollen (Wolfenbarger, 1946). The great distances traveled by pollen lead us to expect relatively little geographic differentiation in conifers, and this expectation is usually consistent with empirical results. For example, Hamrick (1983) examined modes of reproduction and patterns of population structure in different groups of plants, and found relatively little differentiation of populations in conifers. Despite the expectation of little differentiation among populations of conifers, biologists have found microgeographic differentiation among stands differing in elevation, aspect, or moisture availability. For example, white fir, *Abies concolor,* in the mountains of Colorado and New Mexico is polymorphic for female cone color. Some trees produce exclusively green cones, while others produce exclusively purple cones. Populations at low elevations (2000 meters to 2500 meters) have predominantly trees bearing green cones, while the most common trees at the upper edge of the elevational distribution bear purple cones. Strong shifts in phenotypic frequencies have been documented over elevational distances of 1200 meters, and lateral distances of 10 km (Sturgeon and Mitton, 1980; Farris and Mitton, 1985). There are also examples of differentiation of sites with respect to allelic frequencies for protein polymorphisms. For example, the peroxidase locus in ponderosa pine is differentiated both along elevational gradients and between adjacent north- and south-facing slopes (Mitton *et al.,* 1977; Beckman and Mitton, 1984), and peroxidases in both Engelmann spruce (*Picea engelmannii*) and subalpine fire (*Abies lasiocarpa*) are differentiated among krummholz, flag and spire trees at tree line (Grant and Mitton, 1977).

The high potential for gene flow in conifers helps us to identify the causes of microgeographic variation. Heterogeneity on a small scale that is not associated with environmental variation and is not replicable from site to site might well be attributed to familial structure in stands of forest trees (Linhart *et al.,* 1981). However, microgeographic patterns of differentiation that are repeatedly associated with environmental variation can be attributed to natural selection among heterogeneous environments.

This study of microgeographic variation follows comprehensive studies of inheritance, mating systems and microgeographic variation in both Engelmann spruce, (*Picea engelmannii*), and subalpine fir, (*Abies lasiocarpa*) Shea, 1985, 1987, 1988). Shea used six polymorphic allozyme loci in spruce to document variation in the mating system between sites and over years, and to reveal microgeogra-

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[1]) Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, Colorado 80309, USA

[2]) Swiss Federal Institute of Forestry Research, Birmensdorf, Switzerland

[3]) Department of Biology, St. Olaf College, Northfield, Minnesota 55057, USA

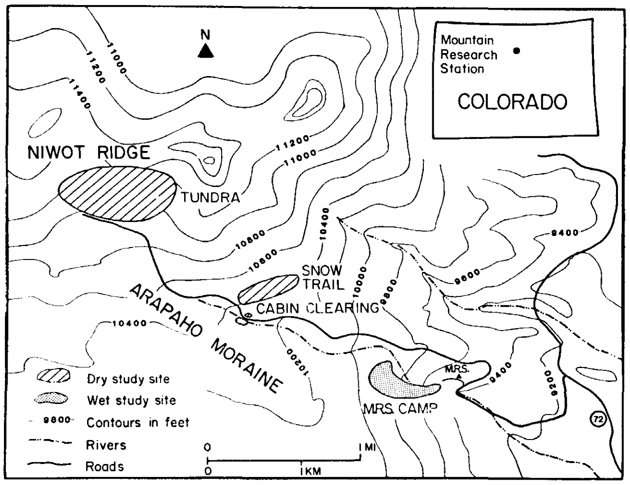

Figure 1a. — Collection localities on Niwot Ridge, Colorado, USA. Niwot Ridge is immediately east of the Continental Divide and approximately 25 km south of Rocky Mountain National Park.

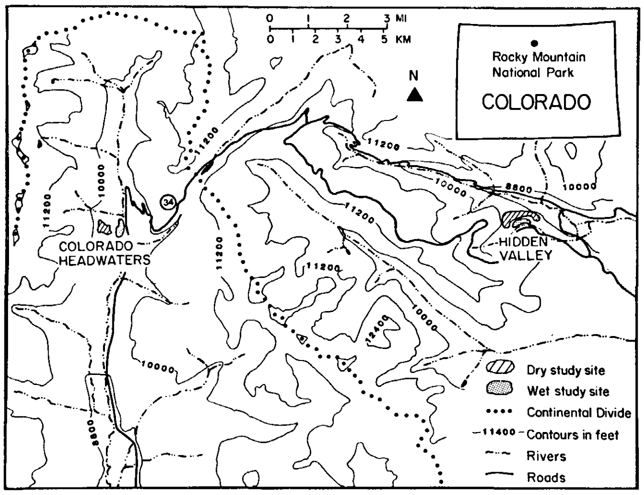

Figure 1b. — Collection localities in Rocky Mountain National Park, Colorado, USA.

phic variation between a wet and a dry site. From that array of six polymorphic loci we chose one polymorphism, phosphoglucomutase, for its striking pattern of differentiation between sites and within the life cycle. We have expanded the studies of microgeographic variation in Engelmann spruce, and here we report patterns of genetic differentiation at the phosphoglucomutase polymorphism between wet and dry sites.

Materials and Methods

Tissues of Engelmann spruce were sampled from six different locations within the Colorado Rocky Mountains. At three of these sites adjacent wet and dry habitats made it possible to compare spruce growing in contrasting environments across a relatively short distance (*Figure 1*). Two additional sites were sampled which represent spruce in relatively dry habitats, and one other site representing spruce in a wet habitat.

Sample Localities

Both seedlings and adult trees were sampled from adjacent wet and dry sites on the south slope of Niwot Ridge at an elevation of 2800 m (Shea, 1985). These sites will be referred to as the Cabin Clearing sites and are within 30 m of one another. The wet site has a braided stream running through it which flows throughout the spring, summer, and fall. The dry site is on higher ground, has a layer of needles and assorted litter, and a south-facing aspect. Spruce in both of these sites is co-dominant with subalpine fir, *Abies lasiocarpa*. More extensive description of the site, extensive genetic analyses of microgeographic variation, and quantitative mating system estimates for both Engelmann spruce and subalpine fir are presented in Shea (1985, 1987).

Mature Engelmann spruce were sampled from adjacent wet and dry sites at Hidded Valley, elevation 2800 m to 2950 m, on the eastern slope of the Continental Divide in Rocky Mountain National Park (*Figure 1*). The dry site is a steep slope with a south-eastern exposure. The wet site contains a marsh, a braided stream and a complex of beaver dams. These sites are approximately 30 m apart. Trees with diameters at breast height exceeding 20 cm were categorized as large, while all other trees (3 cm to 20 cm diameter at breast height) were listed as small.

Mature Engelmann spruce were sampled in Rocky Mountain National Park on the western slope of the Continental Divide, at an elevation of 2750 m to 2900 m, near the headwaters of the Colorado River (*Figure 1*). We refer to this site as Colorado Headwaters. The dry site is a scree slope covered with large boulders and lacking surface soil. The wet site is a marsh with a system of beaver ponds below the scree slope. The wet and dry sites are separated by approximately 100 m. Once again, trees at these sites were designated either large ($>$ 20 cm diameter at breast height) or small.

A set of mature trees was sampled on Niwot Ridge in a relatively larger geographic area west of the mountain research station on Niwot Ridge, and will be referred to as MRS Camp. These trees were not sampled randomly, but were chosen for large size in comparison to the trees around them. The majority of these trees are in very wet microsites, either in swampy areas or at the edges of streams.

A sample of mature trees was taken near tree line on the south slope of Niwot Ridge. One portion of these trees, labeled Tundra, were krummholz or elfinwood trees, growing above tree line. Another sample, labeled Snow Trail, was taken approximately 200 m below tree line and just over 1 km away, and these were all of the normal spire form typical of subalpine forests. Tundra and Snow Trail are steep or well-drained sites, generally at the dry end of the range of sites occupied by Engelmann spruce.

Sample Preparation and Electrophoresis

PGM genotypes were observed either in undifferentiated tissue dissected from dormant buds or from mature leaf tissue ground in liquid nitrogen and mixed with a grinding solution (Mitton *et al.*, 1979). Homogenates from either buds or needles were stored at -70^0 C for several days before electrophoresis. Material from buds and needle tissues give identical results, but buds are available only from October through March.

The PGM scored here is the PGM-1 of Shea (1985, 1988). This locus segregates 1 rare and 2 common alleles, and segregation of alleles in haploid megagametophytes in heterozygous trees fits Mendelian expectations (Shea, 1988).

Statistics

Heterogeneity of allelic frequencies was tested by the method of Workman and Niswander (1970). The fit of observed to expected frequencies under the assumptions of the Hardy-Weinberg law were tested with a Chi-square test. F, the inbreeding coefficient, was calculated as

$$F = 1 - \frac{\text{observed heterozygosity}}{\text{expected hetrozygosity}}$$

The standard error of F is the square root of the variance of F, calculated as in Brown (1970). Heterogeneity of genotypic proportions was tested with a test of equality of proportions (Zar, 1984, pp. 395—397).

Results

The PGM polymorphism segregates two common alleles and one rare allele. The rare, fastest-migrating allele does not exceed 0.01 in any of the population samples examined here, and it is not present in all of them. To simplify the analyses of the data, the rare allele has been pooled with allele 2, which has the most similar electrophoretic mobility.

Allelic frequencies do not differ between krummholz trees and the normal spire-shaped trees typical of the subalpine forest. The frequency of the 2 allele is 0.53 in a sample of krummholz trees at Tundra, and 0.52 in a random sample of spire trees taken about 200 m below tree line at Snow Trail. Neither allelic frequencies nor genotypic proportions differ between these two population samples, so they have been pooled and are referred to as Tree Line in subsequent analyses.

Wet and dry sites from a locality tend to have similar allelic frequencies. The available comparisons include wet and dry sites at Cabin Clearing, MRS Camp (wet) and Tree Line (dry), and wet and dry sites at both Hidden Valley and Colorado Headwaters (*Figure 1*). In these 4 comparisons, allelic frequencies differ between wet and dry sites only at Cabin Clearing (*Table 1*). The frequency of the 2 allele is higher at the dry site at Cabin Clearing ($P < 0.05$), but there is no hint of this pattern at other localities.

In contrast to the relative homogeneity of allelic frequencies, genotypic frequencies show a reliable pattern with moisture regime (*Table 1*). In each of the comparisons, the proportion of heterozygous genotypes (H) is higher in the dry site than in the wet site. These contrasts are statistically significant ($P < 0.05$) in the comparison of MRS Camp ($H = 0.344 \pm 0.044$) and Tree line ($H = 0.512 \pm 0.038$) and in the comparison of the wet ($H = 0.448 \pm 0.044$) and dry ($H = 0.581 \pm 0.053$) at Hidden Valley. This repeated pattern of microgeographic differentiation is also reflected in the pattern of F among wet and dry sites; in each comparison, F is greater in the wet site than in the dry site. Once again, this pattern reaches statistical significance in the comparison of MRS Camp ($F = 0.306 \pm 0.088$) with Tree Line ($F = -0.026 \pm 0.077$) and in the comparison of wet ($F = 0.067 \pm 0.090$) and dry ($F = -0.216 \pm 0.102$) sites at Hidden Valley.

Further insight into the pattern of genotypic differentiation with moisture regime can begained by comparing individuals from separate age classes. The degree of differentiation between wet and dry sites differs with the age class at Cabin Clearing (*Table 2, Figure 2*). At both sites, seedlings have a moderate value of F, consistent with a small amount of inbreeding in Engelmann spruce (Shea, 1987). While the values of F are similar in seedlings (wet $F = 0.062 \pm 0.127$; dry $F = 0.088 \pm 0.161$), the values are significantly different in mature trees (wet $F = 0.470 \pm 0.172$; dry $F = -0.020 \pm 0.132$).

A comparison of age classes reveals a similar shift in genotypic frequencies at Colorado Headwaters. Small and large trees on the dry site have nearly identical values of F. But on the wet site, there is a significant difference in the value of F between small and large trees. Small trees have a value of F of -0.234, but this increases to 0.004 in the large trees ($P < 0.05$).

Discussion

We conclude that selection differs between wet and dry sites in Engelmann spruce. Patterns of genotypic differentiation are similar between wet and dry sites at collection localities; in each comparison of wet and dry sites, the proportion of heterozygous genotypes is higher, and the inbreeding coefficient is lower in dry sites (*Table 1*). Comparisons of genotypic frequencies among age classes revealed similar patterns at Cabin Clearing (*Figure 2*) and Colorado Headwaters (*Table 2*); in wet sites, older trees were more homozygous than younger trees, suggesting selection against heterozygotes in wet sites. At Hidden Valley, although trees from the wet site were less heterozygous than

Table 1. — Allelic and genotypic frequencies and proportions of heterozygotes at PGM in Engelmann spruce from wet and dry sites.

Site	Environment	PGM Genotype 22	23	33	N	p ± SE		H ± SE		F ± SE	
Cabin Clearing	Wet	26	36	27	89	.494	.037	.404	.052	.191	.104
Cabin Clearing	Dry	39	44	14	97	.629	.035	.454	.051	.028	.102
MRS Camp	Wet	44	41	34	119	.542	.032	.344	.044	.306	.088
Tree Line	Dry	46	87	37	170	.526	.027	.512	.038	-.026	.077
Hidden Valley	Wet	47	56	22	125	.600	.031	.448	.044	.067	.090
Hidden Valley	Dry	27	50	9	86	.605	.037	.581	.053	-.216	.102
Colorado Headwaters	Wet	49	98	33	180	.544	.026	.544	.037	-.098	.074
Colorado Headwaters	Dry	30	77	26	133	.515	.031	.579	.043	-.159	.086

Note: p is the frequency of the 2 allele, H is the proportion of heterozygous genotypes, F is the inbreeding coefficient, and SE's are standard errors.

Table 2. — PGM genotypic frequencies in wet and dry environments, and in trees differing in size.

Locality	Type	Size	PGM Genotype 22	23	33	N	P ± SE	H ± SE	F ± SE
Cabin Clearing	wet	seedlings	18	29	15	62	.524 ± .045	.468 ± .063	.062 ± .127
	wet	adult	8	7	12	27	.426 ± .067	.259 ± .084	.470 ± .172
Cabin Clearing	dry	seedlings	19	16	5	40	.675 ± .052	.400 ± .077	.088 ± .161
	dry	adult	20	28	9	57	.596 ± .046	.491 ± .066	-.020 ± .132
Hidden Valley	wet	small	20	27	11	58	.578 ± .046	.466 ± .065	.046 ± .131
	wet	large	27	29	11	67	.619 ± .042	.433 ± .061	.082 ± .123
Hidden Valley	dry	small	18	33	5	56	.616 ± .046	.589 ± .066	-.246 ± .124
	dry	large	9	17	4	30	.583 ± .064	.567 ± .090	-.166 ± .178
Colorado Headwaters	wet	small	19	47	11	77	.551 ± .041	.610 ± .056	-.234 ± .110
	wet	large	30	51	22	103	.539 ± .035	.495 ± .049	.004 ± .093
Colorado Headwaters	dry	small	17	42	14	73	.520 ± .041	.575 ± .058	-.153 ± .116
	dry	large	13	35	12	60	.508 ± .046	.583 ± .064	-.167 ± .127

Note: see *Table 1.*

on the dry site (*Table 1*), we found no significant differences between small and large trees. Our sampling design at Hidden Valley contrasted trees smaller and larger than 20 cm dbh. This sampling design would not detect differences if the events differentiating wet and dry sites occurred early in the life cycle.

Small trees (< 20 cm dbh) on the dry site at Hidden Valley and from both sites at Colorado Headwaters have higher proportions of heterozygotes than would be expected with random outcrossing (*Table 2*). These excesses of heterozygotes may have been produced by selection acting upon seedlings and young trees, but there are other possibilities as well. For example, if the pollen producing these trees originated in stands with distinctly different allelic frequencies, seedlings would be expected to exhibit excesses of hetrozygotes. That is, when males and females have different allelic frequencies, their offspring will have heterozygosity in excess of Hardy-Weinberg expectations. This is always a possibility in a wind- pollinated species with the potential for long-distance gene flow.

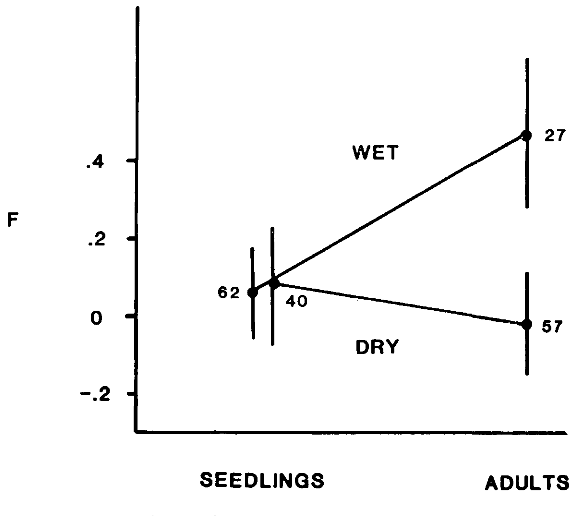

Figure 2. — The inbreding coefficient, F, in Engelmann spruce from adjacent wet and dry collection sites at Cabin Creek, on Niwot Ridge. Values of F are similar in seedlings, but are significantly different in mature trees. Vertical bars indicate ± 1 standard error.

The distances between sites at Cabin Clearing, Hidden Valley, and Colorado headwaters are all less than 50 m, while the distance between MRS Camp and Snow Trail is less than 2 km. Gene flow mediated by wind-borne pollen is expected to prohibit genetic differentiation between these sites. The consistent differences that we observed were probably produced by selection.

Selection may be acting directly upon the PGM locus, or it may be acting upon loci in linkage disequilibrium with PGM. Although we have successfully identified sites perceived by Engelmann spruce to be different selective environments, the gradient which we perceive as a wet versus dry gradient may not be the factor that is important in determining genetic differentiation. Wet and dry sites would also differ with respect to temperature, amount of oxygen in the soil, and pH. Any of these variables individually or in combination might be more important than soil moisture in producing the observed patterns of differentiation.

Apparently, enzyme polymorphisms such as PGM and peroxidase in Engelmann spruce exhibit independent patterns of microgeographic variation. Engelmann spruce is strikingly differentiated across tree line for a peroxidase locus, with allelic frequencies of 0.78, 0.51, and 0.35 in samples of krummholz, flag trees, and spire trees respectively (Mitton and Grant, 1977). Peroxidases play an antifungal role in many species of plants (Lehrer, 1969), and Wardle (1968) discussed the importance of snow molds in the formation of the krummholz growth form in Engelmann spruce. These observations led Grant and Mitton (1977) to propose that the peroxidase differentiation across tree line was a response to selection imposed by snow molds. In contrast to this striking pattern of differentiation, allelic frequencies at PGM, UDPG pyrophosphorylase, glutamate dehydrogenase, and isocitrate dehydrogenase do not differ across tree line (Mitton, unpublished). While the PGM locus is not differentiated across tree line, it exhibits a pattern of microgeographic variation associated with moisture.

Literature Cited

Beckman, J. S. and **Mitton, J. B.**: Peroxidase allozyme differentiation among successional stands of ponderosa pine. Amer. Midl. Nat. **112**, 43—49 (1984). —— **Brown, A. H. D.**: The estimation of

WRIGHT's fixation index from genotypic frequencies. Genetica **41**, 399—406 (1970). —— FARRIS, M. A. and MITTON, J. B.: The effects of a cone color dimorphism on the reproductive output of white fir growing along elevational gradients. Amer. J. Bot. **72**, 1719—1725 (1985). —— GRANT, M. C. and MITTON, J. B.: Genetic differentiation among growth forms of Engelmann spruce and subalpine fir at tree line. Arctic and Alpine Res. **9**: 259—263 (1977). —— HAMRICK, J. L.: The distribution of genetic diversity within and among natural plant populations. pp. 335—348. In: SCHONEWALD-COX, C. M., CHAMBERS, S., MACBRYDE, B. and THOMAS, W. (eds.): Genetics and Conservation. Benjamin/Cummings Publishing Co., Inc. (1983). —— LEHRER, R. I.: Antifungal effects of peroxidase system. J. Bacteriol. **99**, 361—365 (1969). —— LINHART, Y. B., MITTON, J. B., STURGEON, K. B. and DAVIS, M. L.: Genetic variation in space and time in a population of ponderosa pine. Heredity **46**, 407—426 (1981). —— MITTON, J. B., LINHART, Y. B., HAMRICK, J. L. and BECKMAN, J. S.: Observations on the genetic structure and mating system of ponderosa pine in the Colorado Front Range. Theor. Appl. Genet. **57**, 5—13 (1977). —— MITTON, J. B. and GRANT, M. C.: Relationships among protein heterozygosity, growth rate, and developmental stability. Ann. Rev. Ecol. Syst. **15**, 479—499 (1984). —— MITTON, J. B. and JEFFERS, R. M.: The genetic consequences of mass selection for growth rate in Engelmann spruce. Silvae Genetica **38**, 6—12 (1989). —— MITTON, J. B., LINHART, Y. B., STURGEON, K. B. and HAMRICK, J. L.: Allozyme polymorphisms detected in mature needle tissue of ponderosa pine. J. of Hered. **70**, 86—89 (1979). —— PITEL, J. A. and CHELIAK, W. M.: Effect of extraction buffers on characterization of isoenzymes from vegetative tissues of five conifer species: A user's manual. Information Report PI-X-34, Petawawa Natonal Forestry Institute (1984). —— SHEA, K. L.: Mating systems and population structure in Engelmann spruce and subalpine fir. Ph. D. dissertation, University of Colorado (1985). —— SHEA, K. L.: Effects of population structure and cone production on outcrossing rates in Engelmann spruce and subalpine fir. Evolution **41**, 124—136 (1987). —— SHEA, K. L.: Segregation of allozyme loci in megagametophytes of Engelmann spruce and subalpine fir. Genome **30**, 103—107 (1988). —— STURGEON, K. B. and MITTON, J. B.: Cone color polymorphism associated with elevation in white fir, *Abies concolor*, in Southern Colorado. Am. J. Bot. **67**, 1040—1045 (1980). —— STUTZ, H. P. and MITTON, J. B.: Genotypic proportion in Engelmann spruce associated with variation in soil moisture. Arct. Alp. Res. **20**, 461—465 (1988). —— WARDLE, P.: Engelmann spruce (*Picea engelmannii* ENGEL.) at its upper limits on the Front Range, Colorado. Ecology **49**, 483—495 (1968). —— WOLFENBARGER, D. O.: Dispersion of small organisms. Am. Mid. Nat. **35** (1), 1—151 (1946). —— WORKMAN, P. L. and NISWANDER, J. D.: Population studies on southwestern Indian tribes. II. Local differentiation in the Papago. Am. J. Hum. Genet. **22**, 24—49 (1970). —— ZAR, J. H.: Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliff. 718 pp. (1984).

Effective Population Sizes, Genetic Variability, and Mating System in Natural Stands and Seed Orchards of Pinus sylvestris

By O. MUONA and A. HARJU

Department of Genetics, University of Oulu,
SF-90570 Oulu, Finland

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Summary

Genetic variation at allozyme loci and outcrossing rates were estimated in three natural populations and two seed orchards of *Pinus sylvestris* L. in Finland. For the seed orchards, effective population sizes were estimated based on male strobilus and cone production, and predictions were made regarding levels of genetic variability and inbreeding in the offspring generation. The seed orchard crops had as much variation as the natural stands despite decreased effective population sizes due to variation in the number of ramets per clone and variation in gamete production between clones. Multilocus estimates of outcrossing in natural stands ($\hat{t}_m = 0.94$) and seed orchards ($\hat{t}_m = 0.98$) were higher than have been found using single locus methods. The level of inbreeding as measured by average fixation indices was low both in natural stands and seed orchards.

Key words: *Pinus sylvestris*, seed orchard, mating system, effective population size.

Zusammenfassung

Genetische Variabilität wurde in zwei Samenplantagen und drei natürlichen Beständen von *Pinus sylvestris* studiert. In den Samenplantagen wurde die effektive Populationsgröße auf Grund der Blühvariation geschätzt. Es gab keine Unterschiede in der Variabilität zwischen Samenplantagen und natürlichen Beständen mit Allozymloci gemessen, trotz kleiner effektiver Populationsgröße, jedoch wegen großer Unterschiede zwischen Klonen in der Gametenproduktion. Die Fremdbefruchtungsraten in natürlichen Beständen ($\hat{t}_m = 0{,}94$) und Samenplantagen ($\hat{t}_m = 0{,}98$) waren höher mit der Multilokusmethode als mit Einzellokusmethoden. Es gab auch weniger Inzuchteffekte, sowohl in natürlichen Beständen als auch in Samenplantagen, als dies früher gefunden worden ist.

Introduction

Many commercially important tree species are still found primarily as natural stands and are only in the early stages of domestication. This is also true of most of Scots pine (*Pinus sylvestris* L.). For instance, in Finland more than 80% of the extant stands have originated through natural regeneration. At present, seedlings derived from seed orchards are used only for a small part of the regeneration, but the proportion is increasing. This represents a considerable change from the natural system of reproduction. The possible dangers of reduction in genetic variability or increases in the level of inbreeding have been discussed frequently (e.g. FAULKNER, 1975; ADAMS, 1981).

Scots pine is wind pollinated and in natural stands produces heavy flower crops. Pollen migration is considerable (KOSKI, 1970), and effective population sizes are expected to be large. Consequently Scots pine, like many other conifers, harbors large amounts of genetic variability at enzyme loci (MITTON, 1983; MUONA and SZMIDT, 1985; and references therein, GULLBERG *et al.*, 1985). Some seed is the result of fertilization by self-pollen (see SARVAS, 1962, for a description of the reproductive cycle), and despite embryonic mortality (see KOSKI, 1971), some selfs occur even among mature seed. Using rare isozyme markers, the percentage of viable selfed seed in the progeny of natural stands has been found to be low, varying between 5% and 10% (MÜLLER, 1977; YAZDANI *et al.*, 1985a; RUDIN *et al.*, 1986; and references therein). In the juvenile stages of develop-