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Genetic Structure of Marginally Located Pinus nigra var pallasiana Populations in Central Turkey

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Summary

To determine the genetic structure of marginally located populations of *Pinus nigra* var *pallasiana*, seedlings of open pollinated families from 7 populations were raised in Kizilcahamam nursery near Ankara for 2 years. Seed weight (SW) and cone weight (CW) for families, number of cotyledon per seedling (COT), timing of bud set in 1990 (BS90) and in 1991 (BS91), bud burst timing of seedlings in 1991 (BB91), height growth in 1991 (HT90) and final height growth in 1991 (HT91) and final diameter growth of seedlings (DM91) were recorded. Among the traits studied, the component of genetic variation attributed to regions (ranging from 0% to 5.7% of the total variation) and populations (ranging from 0% to 9%) made up very small portion of the total genetic variation while variation among the families within population was very high (ranging from 11.5% to 91.5%). The estimated family heritabilities were moderately high for the most of the traits, ranging from 0.28 for BB91 to 0.98 for SW. Correlations between seedling traits and topographic variables were not significant, suggesting that effects of aspect, slope and altitude on genetic differentiation of population are minor. In general, phenotypic and genetic correlations between seedling traits were generally the same sign and magnitude, however, genetic correlations between height growth and bud set timing were strongly negative (—0.54).

It was concluded that the marginal populations of Anatolian black pine maintain a large within population genetic variation in order to be able to adapt to the mosaics of micro-environments that exists in these locations. The implications of the findings in the study in terms of tree improvement and genetic adaptation mechanisms in the species are discussed in detail.

Key words: Pinus nigra var *pallasiana,* genetic variation, family heritability, marginal populations, genetic correlations, genetic adaptation.

FDC: 165.3; 165.5; 174.7 *Pinus nigra;* (560).

Introduction

European black pine (*Pinus nigra*) has a natural distribution in southern Europe, extending from Spain to Tur-

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key, however, the distribution across this range is fragmented. Previous studies have indicated that very distinct variations exist in numerous morphological, anatomical, genetic and physiological characters (RÖHRIG, 1966; CRITCHFIELD and LITTLE, 1966; VIDAKOVIC, 1974; ARBEZ et al., 1974; WILCOX and MILLER, 1975; WHEELER et al., 1976; READ, 1976; BONNET-MASIMBERT and BIKAY-BIKAY, 1978; KAYA et al., 1985; MATZIRIS, 1989; PORTFAIX, 1989). The Turkish variety (Anatolian black pine) of European black pine, *Pinus nigra* var *pallasiana*, is a widespread mid-elevation species in the Taurus, western Anatolia and northern Anatolian mountains. Anatolian black pine in Turkey is an important timber species and the first choice for afforesting the high Anatolian steppes.

In recent years, large areas in Turkey have been afforested with the species using seeds from available seed sources. Finding the suitable seed sources, especially for the central Turkish steppes is difficult since most of the Anatolian black pine stands have been reduced to the outskirts of high mountains due to centuries of extensive utilization of the wood and conversions of forest land to agriculture. Thus, marginal populations are most often used as seed sources for reforestation programs in central Turkey. Although there have been several studies dealing with geographic variation (ALPTEKIN, 1986; IŞIK, 1990; ECONOMU, 1990) in Anatolian black pine, there is an absence of information the concerning genetic structure of natural populations, especially marginal populations. Furthermore, although tree improvement work has begun by establishing seed stands (8350 ha) and seed orchards (19 clonal seed orchards with a total area of 95 ha) (Anonymous, 1989), there is a lack of basic information on the magnitude and pattern of genetic variation in natural populations of Anatolian black pine in Turkey. As suggested by REHFELDT (1991), a sound programs of gene resource management, including tree improvement programs, require an understanding of the system of genetic variability that exists in natural populations. In a preliminary study (KAYA and TEMERIT, 1993), we assessed the magnitude and pattern of genetic variation in natural stands of Anatolian black pine which were set aside as a "Seed Stands" by the Turkish Forest Service to provide seed from known sources for reforestation programs. This study showed that the component of total variation in seedling traits between seed stands was very low compared to within stands, however, the materials used in that study did not allow us to analyze the components of variation within the seed stands. Thus, the objective of the present study was to determine the magnitude and pattern of genetic variation existing among marginally located natural populations of the species. To meet this objective, open pollinated seeds from 45 trees (families) in each of 7 marginally located natural populations of Anatolian black pine in central Turkey were obtained. Seedlings from these seven populations were planted in a forest nursery as a randomized complete block design and were grown for two years.

Materials and Methods

Six populations from the interior Taurus Mountains and 1 population from north-central Turkey were sampled. All 7 populations are located on the borders of the high Central Anatolian steppes. On average, the elevations of the sampled populations ranged from 1322.9 m (Taşlıca-2) to 1544.2 m (Çamlık). The slopes of the populations varied from 0 % to 40.2 %. Wherever possible populations were selected from different aspects to determine the influence of aspect on populations (*Table 1*). This is because there are contrasting differences in growth forms of stands located on different aspects. However, there was only one population available to be sampled from "Çamlık". Normally, open-pollinated seeds from 45 parent trees (families) for in each population were collected in September, 1989. Only 25 parent trees from "Çamlık" and 31 from "Taşlıca -2" populations were available for seed collection in satisfactory quantities. With the following restrictions, families were chosen in each population at random: (1) parent trees had to be separated by at least 150 m (most were widely separated) within each population; (2) elevational range of the parent trees had to be no greater than 300 m within any 1 population; and (3) parent trees had to be approximately at the same age. Topographical variables such as elevation, aspect and slope were also recorded for each parent tree. Parent trees identities were kept separate throughout the experiment.

Open-pollinated seeds from parent trees (families) were sown in 3 nursery beds in Kızılcahamam nursery (70 km northeast of Ankara, elevation: 1100 m, latitude: 32^0 38', and longitude: 31^0 26') in April 1990. Five seedling row plots of 281 families (45 families/population x 5 + 31 from "Taşlıca-2" + 25 families from „Çamlık") were randomly allocated to plots in a randomized complete block design with three replications. Nine traits expressing timing of bud set in 1990 (BS90) and 1991 (BS91), timing of bud burst in 1991 (BB91), total height growth in 1990 (HT90) and total height growth in 1991 (HT91), total diameter growth in 1991 (DM91), number of cotyledons per seedling within family (COT), seed weight (SW) and cone weights (CW) of

Table 1. — Description of the seed sources used in the study. The aspect, altitude and slope values are the average values derived from the values of families within populations.

Populations	Latitude	Longitude	Altitude	Slope	Aspect
Fadara-1 (Beyşehir)	37.75°	31.75°	1497.2m	38.67%	NE
Fadara-2 (Beyşehir)	37.75	31.75	1392.7m	40.20%	SW
İslibucak-1 (Beyşehir)	37.75	31.75	1342.8m	0%	Flat
İslibucak-2 (Beyşehir)	37.75	31.75	1446.7m	22.70%	NE
Taşlıca (Ilgın)	38.25	32.00	1329.3m	20.20%	SW
Taşlıca-2 (Ilgın)	38.25	32.00	1322.9m	22.70%	NE
Çamlık (Yozgat)	39.75	35.90	1544.2m	23.70%	N

Table 2. — Description of coded variables used in the study.

Code	Descriptions	Units
ASP	Aspect of each seed tree (family) within population (N=1, NE=2.. SW=6)	Codes
ALT	Altitude of each seed tree within population	meters
SLP	Slope of each seed tree within population	%
SW	Seed weight of each family(30 seeds)	grams
CW	Cone weight of each family (3 cones)	grams
COT	Cotyledon numbers of seedlings in each family within population	numbers
BS90	Bud set timing of seedlings in each family within population	days from Jan.1, 1990
HT90	Height growth of seedlings in each family within population in year of 1990	mm
BB91	Budburst timing of seedlings in each family within population	days from Jan. 1, 1991
BS91	Bud set timing of seedlings in each family within population	days from Jan. 1, 1991
HT91	Total height growth (cumulative of year 1990 and 1991)of seedlings in each family within population at the end of growing season of 1991	mm
DM91	Total diameter growth (cumulative of year 1990 and 1991) of seedlings in each family within population at the end of growing season of 1991 each family within population	mm

families were recorded (*Table 2*). The timing of bud set was determined as the number of days from the first day of the year (January 1st, 1990). Bud set was defined as the date when brown bud scales were first visible on the overwintering terminal bud. Observations were made weekly and began on August 1, 1990 in the first year and July 1, 1991 in the second year. Bud set observations were carried out weekly until 90% of seedlings set overwintering buds. Height growth in 1990 (HT90) and 1991 (HT91) were measured in November 1990 and 1991, respectively as the distance from the cotyledon scar to base of terminal bud.

Analyses of traits were based on plot means. There were three plots with no seedlings in family plots, thus, analysis of variance for all traits were carried out by using a generalized least square procedure (SAS Inst., SAS/STAT User's guide, 1988). A GLM-SAS procedure was used which gives unbiased estimates of all mean squares when a data set has missing plots. According to the geographical origin of sampled populations, the 7 populations were grouped as regions. The populations originated from 3 regions (Çamlık, Beyşehir and Ilgın). There were 4 populations from Beyşehir, 2 from Ilgın and 1 from Çamlık. These groupings were necessary to determine if regions and populations within regions varied genetically. For this reason, the following statistical model has been used during the data analysis.

$$Z_{ijkl} = \mu + B_k + R_l + (P_{(l)j} + F_{(j)i} + e_{ijkl}$$

where μ is the experimental mean, Z_{ijkl} is the mean performance of the i th family in the j th population in the l th region and in the k th replication; B_k = the effects of replication; R_l = the effects of regions; $P_{(l)j}$ = the effects of populations within region; $F_{(j)i}$ = the effects of families within populations; e_{ijkl} = the experimental error.

Components of variance and covariance of regions, populations within regions and families within populations were estimated according to the expectations from the analysis of variances. Heritabilities were estimated from the components of variance as in NAMKOONG (1979). Family heritabilities (h^2_f) were estimated by using the following equation:

$$h^2_{fx} = \frac{\sigma^2_{f(x)}}{\sigma^2_e / r + \sigma^2_{f(x)}}$$

where $\sigma^2_{f(x)}$ = family component of total variance for trait x, r = 2.98, σ^2_e = error variance.

Genetic correlations were estimated from the component of variance and covariance (FALCONER, 1981) substituted into the standard equation for the product moment correlation coefficient.

$$\text{Genetic correlation } (Rg_{(x,y)}) = \frac{COV_{f(x,y)}}{\sqrt{\sigma^2_{f(x)}}\sqrt{\sigma^2_{f(y)}}}$$

Table 3. — A) The results of analysis of variance, experimental means and family heritabilities (h^2_f), df= degrees of freedom. B) Region means for the traits.

A-ANALYSIS OF VARIANCE

	MEAN SQUARES						
Traits	Replication df= 2	Regions df=2	Populations within Regions df=4	Families within Populations df=274	Error df= 560	Means	h^2_f
SW	0.0015	0.104ns	0.123**	0.035**	0.0004	0.60	0.98
vc		0%	5.4%	91.5%	3.1%		
CW	15.49	2867.16ns	1678.90**	269.53**	21.03	41.10	0.92
vc		5.7%	9%	68%	17.3%		
COT	0.396	3.04ns	0.380ns	0.540**	0.280	8.25	0.51
vc		3.2%	0%	23.2%	73.6%		
HT90	2278.59	232.08ns	188.62*	56.08**	29.84	25.91	0.47
vc		0.9%	2.5%	22%	74.6%		
BS90	1396.79	199.84ns	48.00*	19.31ns	16.09	265.54	0.49
vc		2.7%	0.3%	23.5%	73.5%		
BB91	70.52	23.82ns	12.89ns	7.92*	5.71	116.67	0.28
vc		0.9%	0.6%	11.3%	87.2%		
BS91	1991.30	989.60ns	767.61*	238.37**	133.95	267.87	0.44
vc		0.9%	2.3%	20.1%	76.7%		
HT91	100547.67	8153.76ns	55591.86**	14680.15**	8155.20	563.45	0.45
vc		0%	3%	20.5%	76.5%		
DM91	194.50	79.91ns	22.42*	8.61**	4.81	11.75	0.44
vc		4.4%	1.6%	19.7%	74.3%		

B-REGION MEANS FOR THE TRAITS

	REGIONS		
Traits	Fadara-İslibucak(Beyşehir)	Taşlıca (Ilgın)	Çamlık (Yozgat)
SW	0.79a#	0.67a	0.66a
CW	42.78a	36.84a	42.10a
COT	8.29a	8.25a	7.99a
HT90	25.51a	24.04a	23.82a
BS90	265.63a	266.82a	264.42a
BB91	115.65a	116.03a	116.36a
BS91	262.72a	261.74a	257.17a
HT91	575.53a	575.28a	560.06a
DM91	11.69a	10.98a	10.40a

ns= not statistically significant;
*) significant at $p<0.05$; **) significant at $p<0.01$
#) Region means labeled with the same letters are not significantly different from each other.

where $Rg_{(x,y)}$ = estimated genetic correlation between trait x and y, $\sigma^2_{f(x)}$ = estimated components of variance of families within populations for trait x, $\sigma^2_{f(y)}$ = estimated components of variance of families within populations for trait y and $COV_{f(x,y)}$ = estimated component of covariance of families within populations between traits x and y, estimated from covariance analysis.

The phenotypic correlation between traits x and y were calculated from family mean squares and mean cross products for the traits according to KAYA et al. (1989).

Correlation coefficients between seedlings traits and topographical variables were calculated from family means by using the PEARSON correlation coefficient procedure in SAS statistical package.

Results

Pattern of genetic variation

Differences between regions were not statistically significant. The component of total variation which is attributable to regions made up a very small portion of the total variance for all traits studied. The variation attributed to the regions was not greater than 6% for all traits (*Table 3*). The range of the regional means for the traits studied was very small for all seedling traits. Populations within regions were significantly different in SW, CW, HT90, BS90, BS91, HT91, and MD91 while populations within region did not show any significant variation for COT and BB91. The component of total variation attributed to populations within regions was generally low (less than 6%), except for CW where it was 9% (*Table 3*). Families within populations showed significant variation in all traits studied, except for the date of bud burst in 1991. The component of total variance attributed to the families within populations made up considerable amount of total variance which varied from 11.3% in BB91 to 91.5% in SW (*Table 3*). The effects of aspects within each location (i.e., Fadara, Islibucak, Taşlıca) were significant for some traits, but this was not consistent in all locations (*Table 4*). When the data were analyzed to see if south-west *vs* north to north-east aspect effected seedlings traits, no statistically significant differences in the traits were found (*Table 4*).

Heritabilities

Estimated family heritabilities were high and ranged from 0.28 in BB91 to 0.98 in SW (*Table 3*). Although family heritabilities for seedling traits were moderately high, for BB91, the estimated family heritability was low. To determine if there was any effect of pooling families from 7 populations on the estimation of genetic variance, family heritability estimates for the traits studied were calculated for each population separately (data not presented). It was clear from this analysis that when family heritability estimations for BB91 were calculated within each population, either there was a lack of family variance or only a very low family variance. Only in the Çamlık population was family heritability high for BB91 (h^2_f = 0.54).

Genetic and phenotypic correlations between traits, and correlation coefficients between traits and topographical variables

The values of genetic and phenotypic correlations between traits were generally of a similar sign and magnitude, but genetic correlation and phenotypic correlation between bud burst timing (BB91) and bud set timing (BS91) in the second year were not of the same magnitude. The phenotypic correlation between these traits was —0.03 while the genetic correlation between the same traits was —0.54 (*Table 5*), thus, only genetic correlations between traits will be reported. Genetic correlations between SW and height growth in first year (HT90) were strong (0.52). That is, families with heavy seeds had greater height growth in the first year. Also, families with a greater number of cotyledon had more height growth in the first year (Rg = 0.41 between COT and HT90). The amount of height growth during the growing season and timing of bud burst or bud set of families were not strongly correlated. The genetic correlations between phenological traits and growth traits were not very strong (*Table 5*). In fact, in the second year (1991), there was a negative genetic correlation between BS91 and HT91 (Rg = —0.30). Thus, the families with later bud set were not the tallest. Genetic and phenotypic correlations between traits were also estimated for each population separately to determine if there was any effect of pooling the family data from populations on estimates of genetic correlations. Estimated genetic and phenotypic correlations between traits within population showed similar patterns i.e., strong genetic correlations between SW and HT90, and low or negative genetic correlations between height growth traits and phenological traits (data not presented here). Topographical variables did not have any significant effect on seedling traits of Anatolian black pine since correlations between seedling

Table 4. — Population means for the seedling traits studied. Population means and aspect means labeled with the same letters are not statistically significant at $p<0.05$, the otherwise they are significant at $p<0.05$.

	TRAITS								
Populations	SW	CW	COT	HT90	BS90	BB91	BS91	HT91	DM91
Fadara-1	0.69a	42.9a	8.4a	25.4ab	266.6ab	115.9a	265.3a	578.1abc	12.1a
Fadara-2	0.68a	39.5a	8.3a	25.6ab	265.5cb	115.1a	263.6ab	569.4bc	11.6a
İslibucak-1	0.67a	40.2a	8.2a	24.2cb	265.3cb	115.8a	261.3bc	558.1c	11.4a
İslibucak-2	0.75b	48.5b	8.3a	26.8a	265.2cb	115.8a	260.7bc	596.7ab	12.2a
Taşlıca-1	0.68a	37.1c	8.3a	25.3ab	267.3a	115.9a	259.0cd	602.0a	11.7a
Taşlıca-2	0.66a	36.7c	8.2a	23.1c	266.6a	116.1a	263.7abd	556.6c	10.8b
Çamlık	0.66a	42.1a	8.0a	23.8cb	264.4c	116.4a	257.2d	560.1c	10.6b
N-NE Aspect	0.69a	42.1a	8.3a	24.7a	265.6a	116.1a	261.7a	572.9a	11.4a
SW Aspect	0.68a	38.3a	8.3a	25.5a	266.4a	115.1a	261.3a	576.5a	11.6a

Table 5. — Phenotypic (above diagonal) and genetic correlations (below diagonal) between traits.

	SW	CW	COT	HT90	BS90	BB91	BS91	HT91	DM91
SW	-	0.46	0.34	0.25	-0.05	-0.04	0.02	0.16	0.20
CW	0.46	-	0.11	0.13	-0.05	0.04	0.03	0.11	0.14
COT	0.68	0.29	-	0.10	0.04	0.001	0.03	0.08	0.11
HT90	0.52	0.23	0.41	-	-0.05	0.03	-0.23	0.70	0.81
BS90	-0.12	0.02	-0.07	-0.04	-	-0.05	0.18	-0.03	-0.02
BB91	-0.14	0.10	-0.11	0.08	0.25	-	-0.03	0.12	0.07
BS91	-0.04	0.09	-0.02	-0.14	0.37	-0.54	-	-0.22	-0.19
HT91	0.34	0.18	0.06	0.90	0.27	0.24	-0.30	-	0.79
DM91	0.45	0.27	0.12	1.00	0.26	0.22	-0.27	0.84	-

Note: 281 open pollinated families involved in estimation of phenotypic and genetic correlations. Phenotypic correlations >0.16 statistically significant at $p<0.05$.

Table 6. — Correlation coefficients between seedling traits and topographical variables.

	Topographical variables		
Traits	ASP	ALT	SLP
SW	0.02	0.11	0.07
CW	-0.08	0.14	0.04
COT	0.06	-0.06	0.01
BS90	0.06	-0.06	0.02
HT90	0.08	0.04	0.04
BB91	-0.07	0.03	-0.03
BS91	0.02	-0.02	0.06
HT91	0.09	-0.04	0.04
DM91	0.08	-0.01	0.07

correlations >0.16 are statistically significant at $p<0.05$

traits and topographic variables (ASP, ALT, SLP) were very weak and not statistically significant (*Table 6*).

Discussion

The results of the present study showed that although marginal populations of Anatolian black pine were genetically variable, a large amount of the total genetic variation in seedling traits was between families within populations. The topographical variables seem to have very little, if any, effect on genetic differentiation of marginal populations. The low marginal variance theory suggests that a particular species will have lower within-population genetic variance near the margins of its ecological range. Previous studies on marginal populations of white spruce (Tremblay and Simon, 1989) and ponderosa pine (Hamrick et al., 1989) reported that a certain degree of inbreeding occurs in marginal populations. However, the marginal populations of these species maintain a high genetic diversity. In Anatolian black pine, marginal populations in central Turkey appear to maintain a large amount of genetic variation within populations. This was also supported by the absence of topographical effects on genetic differentiation of populations. It is not unusual to observe that marginal populations of species have a large genetic variation within populations. Wilson et al. (1991) tested the hypothesis that marginal populations of *Leptospermum scoparium* exhibit lower genetic variance. They concluded that there is no general tendency for marginal populations to exhibit low genetic variation.

The magnitude of genetic variation observed within populations in this study compared with the results of other similar studies in conifers (Campbell, 1979; Rehfeldt, 1990) was considerably higher. Rehfeldt (1991) reported that conifer species differ in the manner by which they adapt to heterogeneous environments. For example, adaptive clines tend to be steep in Douglas-fir, while in ponderosa pine, and western larch it is gentle and in western white pine it is flat. The pattern of adaptation in European black pine follows a trend similar to western white pine based on the results of this two year-old seedling experiment. When the natural range of Anatolian black pine in Turkey is examined in detail, the environment is composed of a mosaics of micro-environments (Işık, 1990; Kaya and Temerit, 1993). There is sizable micro-environmental heterogeneity between localities of Anatolian black pine populations sampled in this study. In order to adapt to the mosaics of these micro-environments, the species has to maintain large amount of genetic variation between families within populations. Based the results of this study, it is genetically safe to use marginal populations of Anatolian black pine in central Turkey as a seed source for reforestation programs or by regenerating existing Anatolian black pine stands. Marginal populations should be well represented by including as many distantly related families as possible. Nevertheless, to obtain better picture of pattern of genetic adaptation of species there is a need for new study which will include more populations representing the entire species range in Turkey. Large within population genetic variation is also reflected by the estimated family heritabilities. Family heritabilities for growth traits were high. High heritabilities for seedling traits suggest that selection within populations will yield rapid genetic improvement. It is likely that gain by selection within population will be much more effective than selection between populations. The presence of a weak genetic correlation between timing of bud set and height growth in the same growing season will also increase the efficiency selection of within population for height increment.

The existence of a strong genetic correlation between height growth and diameter growth and the weak or non-existent genetic relationship between height growth and phenological traits make height growth an excellent choice for further genetic studies in this species. In fact in the second year, the genetic correlations between height growth and timing of bud set was negative. This means that the later the seedlings set bud, the less total height increment they achieved. This could be very useful in breeding since selection based on height growth will not affect the adaptability of selected families. However, there were strong maternal effects on height growth of families in 1990. These maternal effects on growth traits were also carried over to the second growing season. If an early testing program is practiced in Anatolian black pine using height growth as a trait, tree breeders should be aware of the strong maternal effect on this trait.

To be certain of the results observed here in marginal populations, further similar studies, which will explore the genetic structure of centrally located populations of Anatolian black pine, should be conducted with a larger number of populations in order to be able to better understand the genetic structure of natural populations in Anatolian black pine.

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Variation in American Beech (Fagus grandifolia Ehrh.): Isozyme Analysis of Genetic Structure in Selected Stands[1])

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Summary

The genetic structure of *Fagus grandifolia* EHRH. stands in Massachusetts (MA) and West Virginia (WV) was studied by analysis of isozyme variation at nine loci. The stands were found to be substructured into mosaics of putative clones and trees of seedling origin. The level of genetic diversity was high: observed per locus heterozygosities averaged 0.382; number of alleles per locus averaged 2.9. Significant deviations from Hardy-Weinberg equilibrium were detected for up to five of the nine loci studied. Deviations resulted from an excess of heterozygotes at the 6PG-2, MDH-1, and CTO-1 (MA only) loci, and a deficiency of heterozygotes at the CTO-2 and PER-3 loci. Overall, positive mean F_{IS} values indicated slight deficits (2.3%) of heterozygotes within populations. Positive assortative mating, as a result of crossing within clonal and/or family patches in stands, may be responsible. A mean F_{ST} value of 0.064 provided evidence for moderate differentiation between the two populations. Clonal structure had a small effect on the computation of population genetic statistics for these two stands.

Key words: *Fagus grandifolia*, isozyme, clone, stand structure, population structure, F-statistics.

FDC: 165.3; 165.5; 176.1 *Fagus grandifolia*.

Introduction

American beech (*Fagus grandifolia* EHRH.) is a widespread, highly shade-tolerant species occurring in 20 forest types throughout its range (*Fig. 1*) (BURNS and HONKALA, 1990). It is one of relatively few tree species which reproduce both sexually by seed and vegetatively by production of root sprouts (BORMANN and LIKENS, 1979; WARD, 1961). Although seeding must be the mechanism for initial establishment, root sprouting appears to be the main mode of regeneration on specific sites and in certain areas of its range (BORMAN et al., 1970; FORCIER, 1975; HELD, 1980).

The role of root sprouting in hardwood trees as a successional mechanism has received some attention (FORCIER, 1975; HELD and WISTENDAHL, 1977). Sprouting ensures the continued development of stems in species such as beech where seed production may be low, erratic, subject to heavy predation by animals, or where embryos may be non-viable. Production of root sprouts appears also to be a process by which beech maintains its dominance in the community. Root sprouting is also an obvious means by which specific genomes are perpetuated and where conditions are favorable, increased and spread through the forest community. This characteristic undoubtedly has an effect on the genetic structure and composition of populations within a species, but has been little studied in this regard for woody species other than *Populus* (CHELIAK and PITEL, 1984; HYUN et al., 1987) and *Alnus* (HUENNEKE, 1985).

Beech bark disease is a major dieback-decline disease that causes significant mortality and defect in American beech. It results when bark, attacked and altered by the beach scale, *Cryptococcus fagisuga* LIND., is invaded and killed by the fungi, primarily *Nectria coccinea* var. faginata LOMAN, WATSON, and AYERS, and *N. galligena* BRES. (EHRLICH, 1934; LOHMAN and WATSON, 1943; COTTER, 1977). Some trees remain insect- and disease-free in stands long-affected by beech bark disease, and challenge trials have shown them to be resistant to *C. fagisuga* (HOUSTON, 1982, 1983). Resistant trees are found in relatively low numbers (ca. <1% of all beech trees in stands examined), and frequently occur in discrete groups.

As part of a study of the distribution of genotypes within stands of American beech relative to patterns of beech bark disease, a number of stands of this species located from Prince Edward Island, Canada, to West Virginia, U.S.A. were sampled, and beech trees within

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