Genetic Variation in Longleaf Pine

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ABSTRACT

This paper provides an overview of genetic variation in longleaf pine (*Pinus palustris*). To that end, the distribution and magnitude of genetic variation in quantitative genetic traits are reviewed. Measures of the heritability of quantitative traits are summarized and the distribution of quantitative genetic variation within and among populations is described. Data from a study of 19 allozyme loci in 24 populations of longleaf pine are reanalyzed to provide estimates of genetic diversity within and among populations. All available evidence indicates that longleaf pine has the high levels of genetic diversity typical of other widespread conifer species. Also, like most wind-pollinated conifers, the majority of the genetic variation resides within rather than among populations. Study of the fine-scale genetic structure of an old-growth stand of longleaf pine (the Wade Tract) indicated that significant temporal and spatial genetic heterogeneity occurs throughout the site. Spatial genetic structure present in younger cohorts disappears in larger size classes as a result of natural demographic processes. Heterozygosity increased in the larger size classes, indicating that more homozygous individuals are selected against. Results of the Wade Tract study indicate that the genetic structure of this old-growth population is influenced by complex interactions between pollen and seed dispersal patterns, the spatial distribution of suitable recruitment sites, and, subsequently, by natural selection acting within recruitment sites.

INTRODUCTION

Genetic variation has a profound effect on a species' ability to adapt to changing environmental conditions. Species or populations with limited genetic variation are at relatively greater risk concerning their ability to adapt to changes in the environment. However, the amount of genetic variation available to the species is not the only factor that influences potential adaptation. The distribution of genetic variation within and among populations also can have a significant impact on the evolutionary potential of species and individual populations. Reviews of the plant genetics literature (Brown 1979; Hamrick and Godt 1989) have demonstrated that the level and distribution of genetic variation are associated with the life history characteristics of species. Long-lived perennial plant species with large geographic ranges, an outcrossing mode of reproduction and wind-dispersed seeds tend to have more genetic variation than species with other combinations of traits. In addition, for these species, most of the genetic variation occurs within rather than among populations. We predict, therefore, that longleaf pine (*Pinus palustris*) will have large amounts of genetic variation, the majority of which occurs within individual populations.

The expression of most traits of interest to evolutionary biologists, as well as forest geneticists, usually is controlled by a large number of genes. Detailed genetic analyses of such traits are difficult, however, because the expression of individual genes can not be identified or quantified. Analyses of quantitative traits are further complicated since phenotypic variation in such traits often are influenced by both genetic and environmental variation. Experimental protocols (e.g. common gardens or reciprocal transplant studies) have been

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Proceedings of the Tall Timbers Fire Ecology Conference, No. 18, The Longleaf Pine Ecosystem: ecology, restoration and management, edited by Sharon M. Hermann, Tall Timbers Research Station, Tallahassee, FL, 1993

developed that remove the majority of the environmental variation, allowing the amount and distribution of genetic variation to be described. The polygenic nature of quantitative traits does not, however, allow exact estimates of genetic diversity.

The development of biochemical and molecular techniques to identify variation at specific genes now allows more exact estimates of several population genetic parameters. By utilizing procedures, that can identify variation at several genetic loci, such as electrophoresis, quantitative estimates can be obtained for the percentage of polymorphic loci, the number of alleles per polymorphic locus, and the proportion of loci heterozygous per individual. Furthermore, variation in these parameters is easily partitioned into within and among population components.

In the following sections, we describe what is known about the distribution of genetic variation in longleaf pine. Several studies that describe levels and patterns of quantitative genetic variation across longleaf pine's range are reviewed. Data from a study of several isozyme genes are reanalyzed, and the distribution of genetic diversity within and among populations is described. Finally, we report preliminary results of an analysis of fine-scale genetic structure of an old-growth longleaf pine stand.

VARIATION IN QUANTITATIVE TRAITS

Geographic Variation

Longleaf pine has been the subject of several studies designed to determine patterns of genetic variation in polygenic traits. The basic design of these studies was to collect open-pollinated seeds from representative trees from several geographic locations. Seedlings were then planted in one to several experimental plantations. At some subsequent time the surviving trees were measured for specific traits of interest. An excellent example is the work of Wells and Wakeley (1970). Seeds collected from at least 20 trees on each of 15 sites, representing much of longleaf pine's natural range were grown in 11 nurseries and transplanted into 18 plantations located throughout the native range of longleaf pine. Survival was recorded at the end of the first year following planting and after five and ten years. Height and damage by insects and disease were recorded in each plantation after the 3rd, 5th and 10th growing seasons. Diameter at breast height was measured on ten year-old individuals. The results presented below were averaged over all plantations.

Although survival after 10 years ranged from 75% for individuals from a northeast Alabama site to approximately 50% for individuals from a central Georgia site, no geographic trend was found. Infection due to fusiform rust (*Cronartium fusiforme*) was generally low, but trees from locations west of the Mississippi River had significantly lower rates of infection (mean = 2.9%) than trees from more eastern sites (mean = 8.0%). After ten years, fewer trees from southern Florida had initiated height growth (11.2%) compared to the other sources (47.4%). Height at ten years was significantly related to the geographic origin of the populations and to prevailing environmental conditions at the collection sites (Figs. 1 and 2). Trees from cool and dry environments (i.e. Virginia) were shorter than trees from warmer, more moist environments (i.e. southern Mississippi and southern Alabama). Exceptions to this pattern were the two Louisiana sites. Wells and Wakeley (1970) felt, based on anecdotal information concerning the low number of individuals that founded these populations, that the relatively poor performance of the Louisiana trees was due to inbreeding.

Other studies have focused on a single trait. Snyder (1961) collected seeds from 24 sites ranging from eastern Georgia to Louisiana and measured variation in root form in one-year old seedlings grown in a Mississippi nursery. Seedlings from sites located in eastern Georgia averaged 37 roots per plant while progenies from more western sites averaged 29 roots per plant. Snyder (1961) hypothesized that the more fibrous-rooted populations evolved under the wetter summers and falls that characterize eastern locations.

Henry and Wells (1967) analyzed genetic variation in brown-spot infection (*Scirrhia acicola*) on five-year old plants obtained from 15 geographic sources and grown in southern Mississippi. Seedlings from west of the Mississippi River were generally more heavily infected (>60%) than seedlings from the central part of the range (<60%). These results were supported by a subsequent study by Derr (1971).

Not all traits show a significant relationship with geographic origin. In a study of wood density, Saucier and Taras (1966) found no significant differences among five seed sources planted in Virginia.

In conclusion, a majority of the studies demonstrate that considerable genetic variation for quantitative traits occurs among populations from different geographic origins. This conclusion is consistent with similar studies of other forest tree species (Libby et al 1969). Also, the variation patterns described are consistent with the conclusion that trees from different geographic locations are adapted to local environmental conditions.

Genetic Variation Within Populations

To estimate the amount of genetic variation within populations it is necessary to grow individuals of known genetic relationships (i.e. half-sibs, full-sibs, or parents and their offspring) in a common environment. From the covariance of trait values among related individuals, estimates of narrow-sense heritability can be made. The narrow sense heritability of a trait is the ratio of the additive genetic variation to the total phenotypic variation (Falconer 1981). This statistic is of particular interest to forest geneticists and evolutionary biologists since additive genetic variation responds in a predictable fashion to natural and artificial selection pressures.

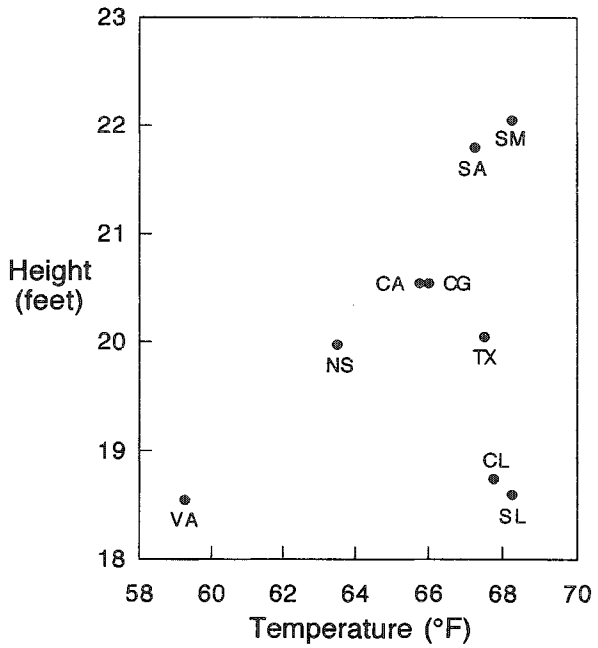

Figure 1. The relationship between tenth year height and mean annual temperature at the collection site. Letters indicate collection site: VA = Virginia; CL = central Louisiana; SL = southeastern Louisiana; NS = northeastern South Carolina; TX = Texas; CA = central Alabama; CG = central Georgia; AS = southern Alabama; SM = southern Mississippi. Data are from a composite of 18 plantations. Modified from Wells and Wakeley (1970).

Several studies of longleaf pine populations have estimated the narrow-sense heritabilities of a wide array of traits (Table 1). For most of the traits studied, estimates of narrow sense heritability are high, indicating that considerable genetic variation for these traits is maintained within populations. Several of the traits examined, including survival, duration of the grass stage, height growth, and disease resistance, have an important role in the life cycle of longleaf pine.

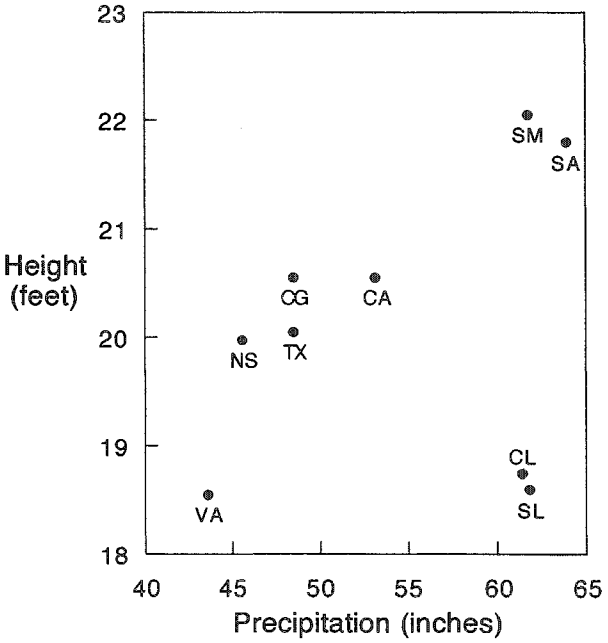

Figure 2. The relationship between tenth year height and mean annual precipitation at the collection site. Letters indicate collection sites (see Fig. 1). Modified from Wells and Wakely (1970).

Genetic Variation Within and Among Populations

From the studies described above, it is difficult to determine the proportion of the total genetic variation that resides within or among populations. This ratio is of interest to evolutionary biologists since it can be compared directly to similar ratios developed for single gene traits. Thus, it should be possible to determine whether genetic variation in these two types of traits have similar distribution patterns.

We found only one study of longleaf pine that allows such a comparison. Wells and Snyder (1976) collected seed from three seed parents in each of 24 populations located throughout the central portion of longleaf pine's range. By analyzing progeny from each tree they partitioned the total genetic variation into three components. Estimates of these

three genetic components were obtained for four quantitative traits from the mean squares of a nested Analysis of Variance (Table 2). The three variance components are: σ_P^2, variance due to differences among populations; σ_F^2, variance due to differences among the three open-pollinated families; and σ_w^2, variance within each open-pollinated family. This last variance component also includes some environmental variation resulting from microenvironmental differences in the experimental plantation. Since longleaf pine is predominantly outcrossing and pollen dispersal in wind-pollinated species is thought to be extensive, considerable genetic variation within open-pollinated progenies is to be expected. Nevertheless, the sum of the three components (V_g) may overestimate the total genetic variance. The ratio of σ_p^2 to V_g is the proportion of total genetic variation that occurs among populations and can be compared directly to similar ratios calculated for single gene traits (G_{ST}, see below).

The ratios calculated for the four traits measured by Wells and Snyder (1976) indicate that the majority (>90%) of the genetic variation resides within populations. Although these values may be overestimates due to the inclusion of some environmental variation in σ_w^2, these results still indicate that the majority of the genetic variation resides within longleaf pine populations.

SINGLE GENE MARKERS

The most commonly used procedure available to analyze genetic variation in single gene traits is starch gel electrophoresis. Variation at specific loci can be identified by different rates of migration of alleles within a gel placed in an electric field. By adding specific stains, differences in migration rates can be visualized on the gel, and the genotypes of individuals can be scored directly. The majority of the loci identified by electrophoresis code for enzymes and typically are referred to as isozyme or allozyme loci. Presently, 20 or more allozyme loci can be resolved for a typical plant species.

Isozyme loci have several advantages (Hamrick 1989): (1) the genetic inheritance of isozyme loci can be demonstrated easily; most loci have simple Mendelian inheritance; (2) most isozyme loci are codominant, and allele frequencies can be estimated easily; (3) estimates of levels and distributions of genetic diversity can be compared directly among populations and species; (4) many isozyme loci can be assayed from a small amount of material; usually a single leaf or a seed will suffice; (5) most isozyme loci are expressed at all stages of the life cycle; and (6) isozyme loci can be resolved for most plant species regardless of habitat, size or longevity.

Variation Within and Among Populations

Duba (1985) used 19 allozyme loci to measure variation within and among 24 longleaf pine populations. The collections included 22 populations distributed throughout Alabama, southeastern Mississippi, southwestern Georgia and the panhandle of Florida, plus two more distant populations, one from central Florida and one from North Carolina.

Since Duba (1985) provided allele frequencies at each locus for each population, we could calculate several genetic parameters from his data. These included percent of loci polymorphic (P), number of alleles per polymorphic locus (A) and Hardy-Weinberg expectations of individual heterozygosity (H_e = genetic diversity). These three measures of genetic variation were calculated within species as a whole (each parameter designated with a 's' subscript) and within individual populations ('p' subscript). The ratio (G_{ST}) of genetic diversity among populations (H_{es}-H_{ep}) to the total genetic diversity (H_{es}) was calculated for each locus and summed across the 19 loci.

Significant differences ($P < 0.05$) in allele frequencies among populations were found for 17 of the 19 loci. There were no clear-cut differences between any two populations for the number of alleles per polymorphic locus, but populations differed in the presence of specific alleles and in the frequency of these alleles (Duba 1985). The proportion of loci polymorphic per population (P_p) ranged from 31.6% to 57.9% and was negatively correlated ($r = -0.63$, $P < 0.002$) with latitude (Duba 1985). Genetic diversity (H_{ep}) showed a similar trend. Finally, measures of genetic similarity (Nei 1972) calculated across all loci demonstrated no relationship with the geographic location of the populations, although the lowest genetic identity was between the North Carolina population and one of the Mississippi populations. The mean G_{ST} value across all loci was 0.062, indicating that the majority of allozyme variation occurred within populations.

Genetic diversity measures obtained for longleaf pine can be compared directly with values for other species or groups of species (Table 3).

Both *P. taeda* and *P. palustris*, which shares much of its range with longleaf pine, have higher percentages of polymorphic loci (P_s), average numbers of alleles per polymorphic locus (A_s), and average heterozygosities (H_{es}) than other *Pinus* species, other woody perennials, or all other seed plants.

There are also differences in the genetic diversity within populations of longleaf and loblolly pine. Within its populations (Table 4), longleaf pine has a lower percentage of polymorphic loci (P_p) than loblolly pine but more alleles per polymorphic locus (A_p). Genetic diversity (H_{ep}) within populations of longleaf pine is lower than that for *P. taeda*, indicating that allele frequencies at individual loci are more unequal in longleaf pine populations. The genetic parameters estimated for longleaf pine are similar to the values for other species in the genus *Pinus* and other woody perennials, but are higher than the means for all other seed plants.

The proportion of the total genetic diversity found among longleaf pine populations (G_{ST}, Table 4) is somewhat lower than the value for *P. taeda*, but is equivalent to the mean values for the genus *Pinus* and other woody perennials. Trees have less variation among their populations than non-woody plants (Hamrick et al 1992), an observation supported by comparing the G_{ST} value for longleaf pine with the mean G_{ST} value for other plant species.

Fine-Scale Genetic Structure

In 1987, we began a study of the fine-scale genetic structure of an old-growth stand of longleaf

Table 1. Estimates of within population variation for several quantitative traits of *P. palustris*. The data presented are the narrow-sense heritabilities of the traits indicated.

Traits	Heritability (h^2)	Source
Survival to 2nd year	0.35	Goddard and Bryant (1981)
Duration of grass stage	0.50	Layton and Goddard (1982)
Height at 15 years	0.53	Snyder (1973)
Height at 21 years	0.58	Sluder (1986)
Diameter at 21 years	0.72	"
Volume/tree at 21 years	0.82	"
Rust free at 21 years	0.78	"
Brown spot infection	0.44	Snyder and Derr (1972)
Cortical monoterpene composition	0.45	Franklin and Snyder (1971)
Branch angle	0.43	Snyder and Namkoong (1978)
Branches (number)	0.21	" "
Needle length	0.34	" "
Needles/tree	0.15	" "
Forking percentage	0.06	" "
Dorsal stomata	0.39	" "
Rows of dorsal stomata	0.47	" "
Bud diameter	0.27	" "
January bud length	0.62	" "

Table 2. The distribution of quantitative genetic variation within and among 24 populations of *P. palustris*. Where: σ_W^2= an estimate of the variance among open-pollinated progeny of a single tree (this measure consists of genetic differences among individuals plus variation due to any local microenvironmental effects in the plantation); σ_F^2 = an estimate of the genetic variance among open-pollinated families from the same population; σ_P^2 = an estimate of the genetic variance among the 24 populations. V_G = total genetic variance ($V_G = \sigma_W^2 + \sigma_F^2 + \sigma_P^2$). Data are modified from Wells and Snyder (1976).

	Variance estimates				
Trait	σ_W^2	σ_F^2	σ_P^2	V_G	σ_P^2/V_G
Height	1.21	0.30	0.19	1.70	0.112
Dbh	4.26	1.14	0.40	5.80	0.068
Survival	449.9	59.0	52.2	561.1	0.093
Plot volume	0.0032	0.0012	0.0004	0.0048	0.083

Table 3. Levels of genetic diversity for *P. palustris* compared to other taxonomic groupings.

Species/Group	Number of populations or entries (N)	Percent polymorphic loci (P_S)	Number of alleles per polymorphic locus (A_S)	Genetic diversity (H_{es})	Source
P. palustris	24	100.0	2.79	0.163	Duba (1985)
P. taeda	22	90.2	2.86	0.221	Hamrick unpubl.
Pinus spp.	93	69.6	2.86	0.157	Hamrick et al (1991)
Woody perennials	191	65.0	2.88	0.177	Hamrick et al (1991)
All plant species	655	51.3	2.89	0.150	Hamrick et al (1991)

Table 4. Levels of genetic diversity within and among populations of *P. palustris* compared to values from other taxonomic groupings.

Species/Group	Number of populations or entries (N)	Percent polymorphic loci (P_P)	Number of alleles per polymorphic locus (A_P)	Genetic diversity: within populations (H_{ep})	Genetic diversity: proportion among populations (G_{ST})	Source
P. palustris	24	53.5	2.92	0.150	0.062	Duba (1985)
P. taeda	22	72.7	2.28	0.198	0.114	Hamrick unpubl.
Pinus spp.	93	50.1	2.57	0.136	0.065	Hamrick et al (1991)
Woody perennials	196	49.3	2.55	0.148	0.084	Hamrick et al (1991)
All plant species	669	34.6	2.43	0.113	0.228	Hamrick et al (1991)

Table 5. Levels of genetic diversity in six plots established in the Wade Tract longleaf pine population. See the text for a definition of the symbols used.

Plot	N (adults)	P_p(%)	A_p	H_{ep}	H_o	F
High 1	222 (64)	100.0	2.55	0.201	0.184	0.085
High 2	388 (53)	100.0	2.41	0.187	0.168	0.102
High 3	175 (53)	90.9	2.65	0.185	0.165	0.108
Mean high density plots	262 (57)	97.0	2.54	0.191	0.172	0.098
Low 1	418 (26)	95.4	2.57	0.174	0.165	0.052
Low 2	301 (32)	100.0	2.55	0.189	0.165	0.127
Low 3	448 (26)	100.0	2.59	0.176	0.153	0.131
Mean low density plots	389 (28)	98.5	2.57	0.180	0.161	0.103
Mean all plots	326 (42)	97.7	2.55	0.185	0.167	0.101

pine in southern Georgia. The Wade Tract, located a few miles south of Thomasville, in Thomas County Ga., is an 80 hectare stand that is one of the largest remaining old-growth longleaf pine populations in the Southeast. This stand is the location of an extensive demographic study established by W. J. Platt and his colleagues in 1979 (Platt et al 1988).

Our objective was to describe the distribution of allozyme variation throughout this population to better understand interactions that exist between seed and pollen dispersal, seedling establishment and survival, and mortality associated with intraspecific competition. Specifically, we wanted to document the influence of natural demographic processes on the distribution of genetic diversity within this population. We also wanted to determine whether genetic structure of the population influences demographic processes. Although our ultimate goal was to document the interplay between ecological and genetic forces that impact this population, our first objective was to describe current patterns of genetic diversity within the Wade Tract. It is this aspect of our research that is discussed below.

During the fall of 1987 we established six one-hectare plots within the mapped plot of 60 ha. studied by Platt et al (1988). Three areas were randomly selected to represent locations with high adult densities (> 50 trees $\geq$ 30 cm dbh per hectare) while the other three were areas with lower adult densities (< 35 trees $\geq$ 30 cm dbh per hectare). During the subsequent year each of the six plots were systematically searched for every established individual. Grass stage juveniles less than 1.5 m tall which had not previously been tagged as part of the demographic study (Platt et al 1988) were assigned uniquely numbered tags and were mapped relative to surrounding tagged, mapped trees. Needle samples were collected from every individual and were kept cool until they were returned to the laboratory at the University of Georgia for enzyme extraction.

We used 22 polymorphic allozyme loci to analyze the level and distribution of genetic diversity within the Wade Tract. Since we only used loci known to be polymorphic it is not surprising that the proportion of polymorphic loci within each one hectare plot approached 100% (Table 5). There is some variation among the one hectare plots for the number of loci polymorphic (P_p) due to presence/absence of rare alleles, but these differences are not statistically ($P > 0.05$) or biologically significant. Values for the number of alleles per polymorphic locus (A_p) also are relatively uniform across the one hectare plots, with no apparent differences among the high and low density plots. The high density plots do appear to have higher expected heterozygosities (H_{ep}). This difference results from more even allele frequencies in the high density plots since consistent differences in P_p and A_p were not seen. Higher H_{ep} values may be a result of the higher density of adults in these plots.

Inbreeding coefficients ($F = 1 - \text{Obs } H/H_{ep}$) were calculated for each one hectare plot. In all six plots there is an overall deficiency of heterozygotes ($F > 0$). Two factors could produce an apparent deficiency of heterozygotes. First, although we do not have a direct estimate of the level of inbreeding in this stand, numerous studies of the mating systems of coniferous trees indicate that 5-15% of the viable progeny result from self-fertilization or bi-parental inbreeding (Mitton et al 1981; Guries and Ledig 1982; Gibson and Hamrick 1991). We suspect that longleaf pine is no exception; its low adult densities may lead to more selfing relative to conifer populations with higher adult densities (Smith et al 1988). The observation that the low density plots have somewhat higher inbreeding coefficients is consistent with this argument.

A second factor that could produce an apparent deficiency of heterozygotes is the occurrence of different allele frequencies in subdivisions of each one hectare plot (i.e., a Wahlund effect). The patchy distribution of longleaf pine seedlings could produce a significant Wahlund effect. Hamrick et al (1989) demonstrated that a similar pattern of seedling recruitment produced a significant level of genetic structuring within several populations of ponderosa pine (*Pinus ponderosa*) in eastern Colorado. The low density plots on the Wade Tract might also be expected to have more pronounced Wahlund effects due to the higher incidence of younger individuals (the larger sample sizes in the low compared to high density plots reflect larger numbers of juveniles in the low density plots; Table 5).

Nei's (1973) genetic diversity statistic was relatively low ($G_p = 0.014$) among the six one hectare plots (Table 6). Nonetheless, because of the large sample sizes involved, this value represents a significant level of heterogeneity in allele frequencies among the plots ($\chi_5^2 = 54.66$; $P < 0.001$). We also subdivided each one hectare plot into four 1/4 hectare subdivisions and repeated the analyses. A significant level of heterogeneity was indicated at this spatial scale as well ($G_{SP} = 0.010$; $\chi_{23}^2 = 39.04$; $P < 0.025$). Thus, even on a scale of 50 meters or

so there is significant genetic heterogeneity. It is possible that the patchy recruitment ecology of longleaf pine plays a significant role in organizing genetic diversity within this old growth population.

By sampling every individual within the six one-hectare plots we obtained large enough sample sizes to compare levels of genetic diversity and inbreeding coefficients of the different size/age classes. First, we compared grass stage individuals in each plot with older individuals (saplings, subadults or adults). In four of the six plots there was a trend toward a higher level of heterozygosity in the larger/older age classes (Table 7). Comparisons of the inbreeding coefficient of the two groups also produced a consistent trend; grass-stage individuals have higher inbreeding coefficients than older individuals. A second analysis in which the larger/older individuals were divided into several DBH classes produced essentially the same pattern (Fig. 3). There is a gradual but significant ($t_4 = 9.2$; $P < 0.001$) increase in mean heterozygosity from the smaller size classes to the larger size classes. There also is a significant decrease ($P < 0.01$) in the inbreeding coefficient between the grass stage (0 DBH) and the 0-8 cm DBH class. A second decrease in the inbreeding coefficient occurs between the two largest DBH classes. The largest size class has a slight excess of heterozygotes among trees (Fig. 3).

Table 6. The distribution of genetic diversity within and among plots and subplots in the Wade Tract longleaf pine population.

H_T = total genetic diversity = 0.192

H_{SP} = genetic diversity within subplots = 0.186

G_P = proportion of total genetic diversity among plots = 0.014

G_{SP} = proportion of total genetic diversity among subplots = 0.010

Even though many of the differences described above are subtle (but statistically significant due to the large sample sizes) we feel that they represent biologically significant trends. Our interpretation of these results is somewhat complex, however. Two factors could produce a decrease in the inbreeding coefficient with increasing age/size. First, selection may act against inbred progeny during the early stages of the life cycle, and could have produced the significant decrease in the inbreeding coefficients between the two smallest size

Table 7. Comparison of genetic parameters between longleaf pine individuals in the grass stage (GS) versus those which have bolted (i.e. saplings, subadults, adults; SSA). See the text for a definition of the symbols used.

	N		H_e		F	
Plot	GS	SSA	GS	SSA	GS	SSA
High 1	114	108	0.189	0.213	0.085	0.085
High 2	116	272	0.180	0.194	0.137	0.067
High 3	46	129	0.185	0.185	0.113	0.103
Mean high density plots	92	170	0.185	0.197	0.112	0.085
Low 1	137	281	0.164	0.184	0.066	0.038
Low 2	45	256	0.182	0.196	0.132	0.122
Low 3	128	320	0.179	0.173	0.152	0.110
Mean low density plots	103	286	0.175	0.184	0.117	0.090
Mean all plots	98	228	0.180	0.191	0.114	0.088

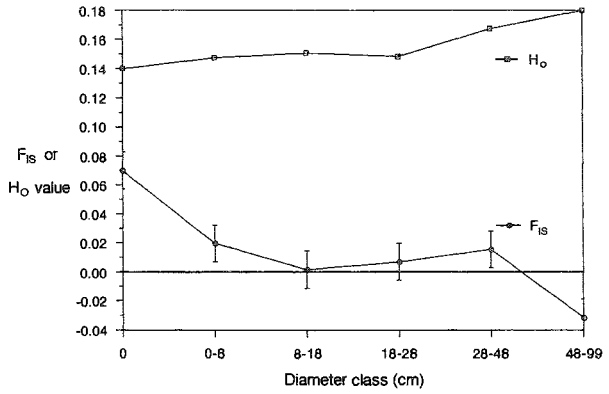

Figure 3. Changes in observed heterozygosity (H_o) and in the deviation from Hardy-Weinberg expectation (F_{IS}) as a function of the size class of trees located on the Wade Tract. Bars on F_{IS} values represent 95% confidence limits.

classes. Selection against inbred or highly homozygous individuals may continue throughout subsequent life cycle stages but may be less severe than in early life cycle stages. Second, natural demographic processes will reduce the number of established juveniles within each patch, making it more difficult to demonstrate the existence of patch structure and simultaneously reducing the Wahlund effect. The most apparent effect of this process will be on the oldest age/size classes, as the last remnants of the patch structure disappears. This scenario is the most likely cause of the apparent decrease in the inbreeding coefficient between the two largest size classes. In essence, we argue that the Wahlund effect acts to maintain an apparent deficiency of heterozygotes long after natural selection has acted against inbred individuals. Once the Wahlund effect is removed (i.e., with the decay of the patch structure in the largest size classes), the excess of heterozygosity that has resulted from selection acting on the smaller size classes is exposed.

CONCLUDING REMARKS

This review of genetic variation in longleaf pine has demonstrated that longleaf pine is similar to other conifers in terms of the amount of genetic diversity it maintains and in how this diversity is distributed within and among its populations. Regardless of whether quantitative or biochemical traits are being considered, longleaf pine has a large amount of genetic variation, most of which occurs within populations. Significant genetic differentiation also occurs among regional populations for the majority of the traits examined. Furthermore, at least for quantitative traits, variation patterns are closely associated with environmental variation among collection sites. Preliminary results from the genetic analysis of the Wade Tract indicate that genetic variation within this old-growth population is not distributed at random but is structured in space and time. It appears, that seed and pollen dispersal combine with demographic and ecological processes (eg, the distribution of sites suitable for recruitment, and seedling and sapling mortality within those sites) to produce the genetic structure that is observed. Natural selection acts in the context of this structure to reshape the genetic composition of the population as cohorts of trees grow and become reproductive.

Both the demographic and the genetic structure of second-growth stands are likely to be very different from those that occur on the Wade Tract. An example is provided by the results of Wells and Wakeley (1970) who state that the poor performance of the central Louisiana individuals (Figs. 1 and 2) almost certainly is due to inbreeding. Seeds from one location were obtained from approximately 30 trees that were the progeny of four parent trees that survived logging in 1905. The second Louisiana population was thought to have had a similar history (Wells and Wakeley 1970).

Our studies of the fine-scale genetic structure of the Wade Tract population gives us a basis with which to compare the characteristics of this population and other old-growth sites from different habitats. The Wade Tract also serves as a standard against which to compare the demographic and genetic characteristics of second-growth forests that may have experienced very different ecological and evolutionary histories.

ACKNOWLEDGMENTS

We wish to acknowledge the assistance of Susan Sherman-Broyles in the acquisition of many of the publications cited in this paper and for technical assistance in the laboratory. We also wish to thank Sue Langevin, Andy Schnabel, Mary Jo Godt, Roger Laushman, Sue Sherman-Broyles, Scot Surles, Karen Hamrick, and Maynard Hiss for assistance with various aspects of the research on the Wade Tract. The Tall Timbers Research Station has provided logistical support while work was being conducted on the Wade Tract. This research was supported by National Science Foundation grant BSR-8718803 and BSR-8718993.

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