ation we have observed are based on fifth year heights of white ash provenances on good sites and that we have only accounted for variation among provenances with respect to latitude. CLAUSEN (1984) reported that there is also a smaller longitudinal component to the variation among white ash provenances both for fifth year height and survival. While we have accounted for most of the geographical variation among the provenances, our analysis is incomplete and additional analyses involving parameters of multidimensional nonlinear response functions are needed. The optimal provenance prescriptions and their planting zones were described primarily to illustrate use of the value function and distribution of planting environments for determination of appropriate seed sources and zones for their use. These solutions are applicable for fifth-year height on good, and well-managed white ash sites provided the assumptions pertaining to parameters of the environmental distribution are reasonable, and the number of provenances used in the illustrations are an acceptable base for a regeneration program. Whether these allocations are appropriate for growth at later stages or for different site conditions depends on whether growth response functions and their variation patterns are substantially changed from those that we observed.

Acknowledgement

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Population Genetic Structure of Baldcypress (Taxodium distichum) in a Thermally Affected Swamp Forest

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Summary

Genetic structure of a mature baldcypress (Taxodium distichum) population in a swamp forest affected by thermal effluents from nuclear production reactors was measured by differences in allele frequencies at three loci. Tree mortality that resulted from discharge of hot water into the swamp was not selective on the basis of genotype. Allele frequencies were heterogeneous over space. Spatial autocorrelation indicated that the radii of genetically interacting groups of baldcypress do not extend across the entire swamp. The levels of gene flow detected among baldcypress samples were sufficiently high to prevent the differentiation of subpopulations due to drift in a population at equilibrium. However, a few trees breeding during unpredictable periods of low water and leaving large numbers of progeny may be responsible for the spatial hetrogeneity in allele frequencies. Population processes can amplify small differences due to drift even in the presence of gene flow.

Key words: baldcypress, gene flow, genetic differentiation, heterozygosity, population, population structure, spatial autocorrelation, Taxodium distichum.

Zusammenfassung

Genetische Struktur einer maturen Taxodium distichum Population wurde an den unterschiedlichen Allelfrequenzen dreier Loci gemessen. Die Population war Teil eines Sumpfwaldes, der von den Kühlwassern einiger Nuklearreaktoren beeinflußt war. Baummortalität, bedingt durch das Ablassen heißer Kühlwasser, war nicht korreliert mit dem Genotyp. Die gefundenen Allelfrequenzen waren heterogen im Raum verteilt. Räumliche Autokorrelation deutete an, daß die Radien genetisch interagierender Gruppen von Taxodium distichum sich nicht über das gesamte Sumpfgebiet erstreckten. Genfluß zwischen den untersuchten Taxodium distichum Proben war groß genug, um innerhalb einer sich im Gleichgewicht befindenden Popu-

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lation die Bildung von Subpopulationen durch Drift zu verhindern. Dennoch könnten einige wenige Bäume, die während unvorhersagbarer Niedrigwasser-Perioden eine große Zahl Nachkommen hatten, die räumlich heterogene Verteilung der Allelfrequenzen hervorgerufen haben. Populationsprozesse können geringe, durch Drift hervorgerufene Unterschiede, sogar bei auftretendem Genfluß verstärken.

Introduction

Baldcypress (*Taxodium distichum*) is one of the dominant canopy species of floodplain forests of the southeastern United States (LANGDON, 1958). Physiological and life-history characteristics of this species are strongly influenced by changing waters levels. Floodwaters disperse cypress seeds over long distances (LANGDON, 1958; SCHNEIDER and SHARITZ, 1988). Baldcypress seedling establishment is successful in periodically flooded environments but depends upon moist exposed substrates for germination and early seedling growth (MATOON, 1915, 1916; DEMAREE, 1932). Thus, the genetic structure of baldcypress is influenced not only by wind pollination as in other conifers, but also by water flow which disperses seeds and limits periods of seedling establishment.

The Savannah River Plant (SRP), a nuclear production site of the U.S. Department of Energy, is located along the Savannah River in South Carolina. The river floodplain contains a mixed deciduous swamp forest dominated by baldcypress and water tupelo (*Nyssa aquatica*) over 50% of its area (J-NSEN et al., 1984). Tributary streams have received cooling water discharges from SRP reactors for varying lengths of time since the early 1950s. Before start-up of the first reactor in 1953, baldcypress was distributed over large areas of the floodplain. Hot water effluents released at over 70° C from SRP nuclear reactors resulted in areas of total tree mortality in the floodplain swamp at the mouths of Four Mile Creek, Pen Branch, and Steel Creek (*Figure 1*). However, some trees continue to survive at the borders of tree-kill areas where water temperatures are elevated (thermal sites). Beyond the areas of partial tree kill, large portions of the SRP swamp have normal water temperatures and no reactor caused tree mortality (ambient sites).

Our purpose was to determine whether mortality caused by hot water effluents is associated with differences in the genetic structure of primary breeding population of baldcypress in the SRP swamp. We used enzyme variation at three loci to describe the substructure of baldcypress in this forest. These data were used to estimate relative gene flow and to correlate allele frequencies with geographical distance among locations in the swamp.

Materials and Methods

Mature leaves were collected from baldcypress trees at 12 locations in the SRP floodplain in 1983 (*Figure 1*). Pairs of locations, representing thermal sites and ambient sites, were chosen upstream and downstream of the mouths of each of three tributary creeks, Four Mile Creek, Pen Branch, and Steel Creek. Four Mile Creek and Pen Branch had continuously carried heated waters to the SRP swamp (3,000 ha) since the mid 1950's, resulting in extensive forest mortality. Steel Creek also had a major area of tree kill but at the time of collection had not received thermal effluents since 1968.

At each of the 12 locations, 26 to 40 trees with trunk diameters of 40 cm or greater were chosen within a radius of 100 m (*Table 1*). Because of their size they were assumed to have become established in the swamp forest before the initiation of reactor operations. Mature leaf samples were obtained, placed on ice and returned to the laboratory.

Leaf samples were prepared for electrophoresis by grinding in liquid nitrogen and extracting the homogenate w th a buffer containing compounds that complexed with phenols, enzyme inhibitors, and reducing agents (MITTON et al., 1979). Starch gel electrophores's of leaf extracts was performed as in MITTON et al. (1979). The electrophoretic variat on of glucose phosphate isomerase (GPI) and phosphoglucomutase (PGM) was scored on a lithium hydroxide discontinuous gel system. Occas onally, because of low enzyme activity, the sample size for a locus was slightly less than the total number of trees.

The BIOSYS-1 program was used to calculate allele frequencies and levels of genetic variability (SWOFFORD and SELANDER, 1981). G_{ST} values were estimated according to NEI (1973). Spatial autocorrelations of allele frequencies were calculated from a Gabriel distance matrix for the 12 baldcypress locations (SOKAL and ODEN, 1978). Estimates of relative gene flows were made from average allele frequencies as a function of the percent occurrence of the alleles in the 12 locations and also from the frequencies of private alleles, those alleles that were found only at a single location (SLATKIN, 1981, 1985). Statistical significance was indicated for all tests by $P \leq 0.05$.

Results

Allele frequencies and single locus heterozygosities differed among the 12 samples of baldcypress (*Table 1*). Six
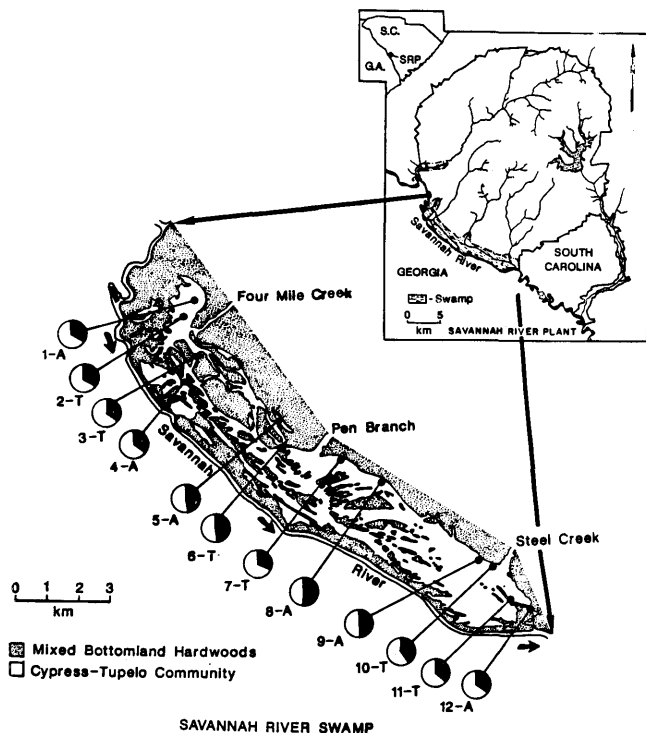

Figure 1. — Locations of 12 baldcypress subpopulations in the Savannah River Plant swamp forest (Table 1 for location identification). The thermal conditions of each location is indicated by the latter A (ambient) or T (thermal) after each location number. Mean heterozygosities (H) for three variables loci are presented by shaded portions of the pie diagrams for each sample. Arrows indicate the direction of water flow in the Savannah River floodplain swamp.

Table 1. — Allele frequencies for glucose phosphate isomerase (GPI) and phosphoglucomutase (PGM) loci in baldcypress. Location numbers are from *Figure 1;* the designation A or T after each number indicates ambient (A) or thermal (T) site. Heterozygosities (h) were obtained by direct count for each locus.

Locus[a]	Alleles	Four Mile Creek Upstream 1-A	2-T	Downstream 3-T	4-A	Pen Branch Upstream 5-A	6-T	Downstream 7-T	8-A	Steel Creek Upstream 9-A	10-T	Downstream 11-T	12-A
Number of trees		40	31	40	39	38	40	26	37	36	35	31	38
GPI-2	100	0.837	0.806	0.868	0.850	0.813	0.762	0.894	0.800	0.775	0.743	0.718	0.762
	80	0.100	0.161	0.105	0.125	0.125	0.188	0.106	0.150	0.175	0.216	0.244	0.188
	60	0.025	0.016	0.026	0.013	0.025	0.038	0	0.025	0.025	0.027	0	0.025
	Other	0.038	0.016	0	0.013	0.038	0.013	0	0.025	0.025	0.014	0.048	0.025
h		0.225	0.258	0.237	0.300	0.275	0.400	0.152	0.325	0.450	0.514	0.487	0.400
PGM-1	100	0.550	0.625	0.575	0.600	0.512	0.463	0.667	0.622	0.622	0.731	0.782	0.600
	80	0.425	0.359	0.375	0.287	0.450	0.463	0.321	0.284	0.311	0.192	0.179	0.400
	60	0.025	0.016	0.050	0.087	0.013	0.075	0.013	0.081	0.068	0.077	0.038	0
	Other	0	0	0	0.026	0.025	0	0	0.014	0	0	0	0
h		0.375	0.500	0.500	0.475	0.575	0.525	0.410	0.622	0.486	0.359	0.308	0.300
PGM-2	100	0.625	0.613	0.688	0.821	0.553	0.512	0.654	0.553	0.583	0.657	0.645	0.592
	80	0.350	0.371	0.300	0.154	0.382	0.463	0.250	0.382	0.389	0.329	0.306	0.408
	60	0.025	0.016	0.013	0.026	0	0.025	0.058	0	0.028	0.014	0.016	0
	Other	0	0	0	0	0.066	0	0.038	0.066	0	0	0.032	0
h		0.400	0.258	0.300	0.282	0.500	0.475	0.346	0.579	0.556	0.343	0.323	0.342

[a]) GPI = glucose phosphate isomarase and PGM = phosphoglucomutase.

alleles were identified for GPI-2, six for PGM-1 and four PGM-2. The loci were designated according to the relative electrophoretic mobility of their products, with the most anodal as 1. GPI-1 was monomorphic and was not used in any of the analyses. When data for all but the common allele were pooled and comparisons made across the 12 samples, there was significant spatial heterogeneity for PGM-1 (X^2 = 27.9) and PGM-2 (X^2 = 22.7) but not for GPI-2 (X^2 = 14.5) with 11 d.f. for each comparison. Hierarchical G_{ST} analysis indicated most of the variation in genotypic proportions was within populations (96.4%); the proportion of genetic variability between samples from different temperature environments (1.3%) or between creeks (0.4%) and within creeks (1.5%) was low and non-significant (*Table 2*). Thus, samples had significantly different allele frequencies for two of the three loci, but temperature and creek accounted for trivial and nonsignificant amounts of variation.

The samples were in HARDY-WEINBERG equilibrium. Only three of 36 locus-sample calculations showed significant departures from expected frequencies; these included two instances of departure of PGM-1 and one instance for

Table 2. — The percentage of the variance of genotypic proportions accounted for in G_{ST} analyses by different hierarchical levels for the data from 12 collecting sites for baldcypress (NEI, 1973).

Locus[a]	Within Locations	Between Temperature Locations	Between Creeks	Within Creeks
GPI-2	98.93	1.06	0.00	0.00
PGM-1	96.02	0.76	0.23	2.98
PGM-2	95.57	1.99	0.98	1.46

[a]) Abbreviations are in *Table 1*.

PGM-2 (FISHER's exact test). This variation barely exceeds the number of significant departures expected by chance alone (three vs two).

Multilocus heterozygosities (H) were arcsin-square root transformed but did not differ among creeks or temperature categories (ANOVA; *Figure 1*). Significant positive spatial autocorrelations occurred for GPI-2 and PGM-1 allele frequencies over short distances (1 to 2 km). Correlations for PGM-2 were also positive but not significant over short distances (*Figure 2*). Significant negative correlations occurred at longer distances for GPI-2 and PGM-1. The pattern of spatial autocorrelation was less consistent for PGM-2, with significant negative and positive correlations occurring at unexpected distance intervals. The correlations for PGM-2 were probably due to the chance location of very similar or dissimilar samples in the SRP swamp and did not represent a general spatial trend.

Conditional average allele frequencies were calculated for each of the 16 alleles from the three loci as the sum of the location specific frequencies divided by the number of locations and plotted as a function of occupancy (i.e., the proportion of the locations at which an allele occurs; *Figure 3*). The number of locations at which alleles occur should increase rapidly as a function of their frequencies if gene flow is high (SLATKIN, 1985). The concave shape of the allele frequency vs occupancy curve suggests high levels of gene flow. The same rare alleles were often found in a large proportion of the locations. Gene flow (Nm = number of migrants per generation with N as the number of breeders and m as the migration rate) was quantitatively estimated from the frequencies of those alleles found at only one location (SLATKIN, 1985). For the SRP baldcypress population, Nm = 8.72; this value indicates that gene flow is sufficiently high to maintain the presence of rarer alleles within the subpopulations and prevent loss of alleles due to drift.
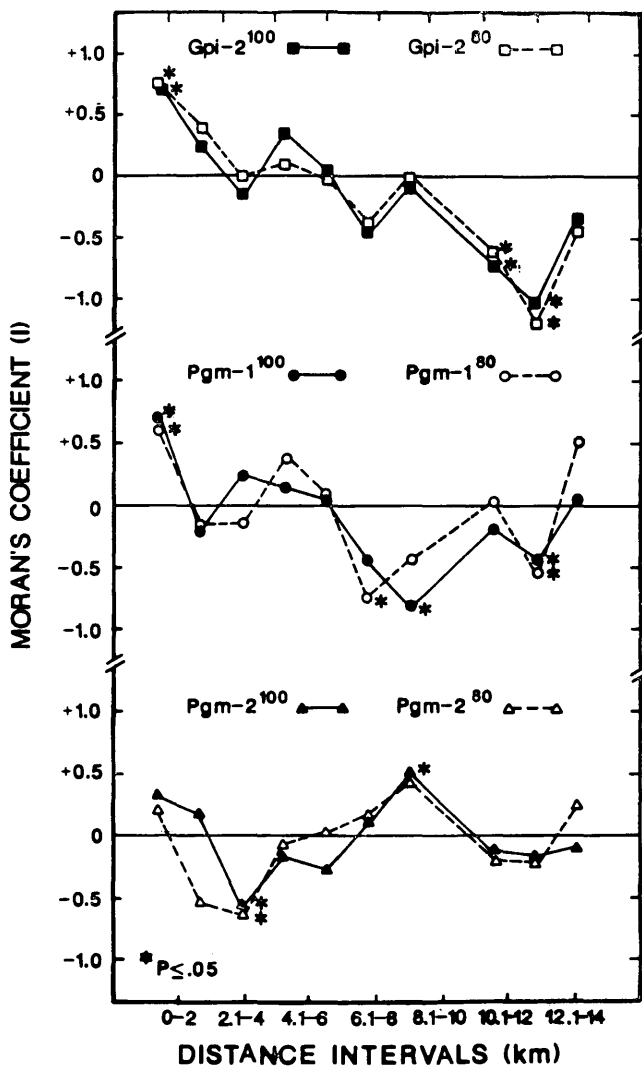
Figure 2. — Spatial autocorrelations as indicated by MORAN's I (SOKAL and ODEN, 1978) for the two most common alleles of glucose phosphate isomerase (GPI-2) and phosphoglucomutase (PGM-1 and PGM-2) plotted as a function of distance intervals between locations depicted in *Figure 1*. Asterisks indicate I values significantly different from zero.

Discussion

Elevated water temperatures in the Savannah River floodplain swamp forest on the SRP have caused changes in the spatial patterns of abundance of local plant and animal species and in their interrelationships within communities (DUNN and SHARITZ, 1987; GIBBONS and SHARITZ, 1981; JENSEN et al., 1984; SCOTT et al., 1985), The temperature increases also have had evolutionary consequences (HOLLAND et al., 1974; CHRISTY and SHARITZ, 1980). There are several instances where high environmental temperatures have been shown to influence the genetic structure of natural populations on the SRP. For example, allele frequencies have changed in a largemouth bass population as an apparent response to elevated temperatures over the last 25 years (SMITH, M. H., et al., 1983). Similarly, mosquitofish populations in the streams that carry heated reactor effluents into the swamp have allele frequencies that differ from those of populations occurring in ambient temperature waters (SMITH, M. W., et al., 1983.)

The distribution of genetic variability within and among the samples of baldcypress in the SRP swamp indicates

that the genetic structure of mature trees in this population has been negligibly affected by the hot water from reactor operations. Hierarchical G_{ST} calculations show that the genetic variation between the ambient and thermal locations is approximately 1 to 2% for three loci (*Table 2*). The genetic structure of the large, mature baldcypress population in the swamp is essentially the same at the different locations, even though hot water has killed a significant number of trees in portions of the swamp forest. Thus, mortality in the area of partial tree-kill appears to be random with respect to genotype and multilocus heterozygosity for the three loci.

In baldcypress and in other plant species, sensitivity to high temperature stress may depend on life-history stage. The trees chosen for this study dominated the swamp forest canopy: they were tall, probably nearing 100 years old, and most likely had well-developed root systems. Juvenile life stages of baldcypress, particularly seedlings, may be more sensitive to high temperature stress than are mature trees. In thermally affected areas of the SRP swamp, individuals younger than 25 years may have genetic characteristics that differ from those of mature baldcypress trees because of the selective influences of high water temperature during establishment and development. Further studies are needed to test this hypothesis.

Over 95% of the total genetic variability of the SRP baldcypress population can be found within each of the 12 samples analysed (*Table 2*). Wind pollinated, outcrossing tree species tend to have very high levels of genetic variability within each local population (HAMRICK et al., 1979). The apparent high number of alleles per locus in baldcypress is characteristic of other long-lived woody perennials (HAMRICK et al., 1979). Thus, the patterns of genetic variability in bald cypress are essentially the same as those of wind dispersed, outcrossing terrestrial conifers such as ponderosa and bristlecone pine (LINHART et al., 1981; HIEBERT and HAMRICK, 1983). These species probably maintain large effective population sizes because of interpopulation gene flow.
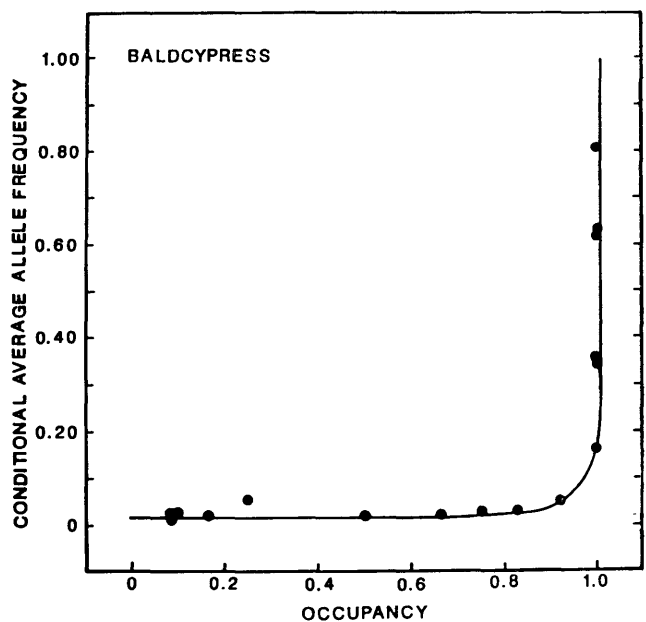

Figure 3. — Conditional average frequency of 16 alleles vs occupancy, as defined by the proportion of the 12 subpopulations of baldcypress in which each allele was found. The line was fitted by eye.

The SRP baldcypress population has high levels of gene flow as evidenced by the relatively homogeneous distribution of all alleles among locations (*Figure 3*). Our estimate of gene flow (Nm) suggests that more than eight individuals disperse among the sampled subpopulations per generation, a level that is high among plant and animal taxa previously evaluated (SLATKIN, 1985). The indirect measures of gene flow are consistent with the life-history properties of the species. Baldcypress is capable of long distance dispersal, either by wind pollination or by water mediated seed dispersal (SCHNEIDER and SHARITZ, 1988). Given the short distances between locations in this study, and their upstream-downstream positions relative to water flow in the Savannah River floodplain, a high number of migrants between the subpopulations is expected.

Baldcypress subpopulations are genetically heterogeneous across the SRP swamp forest, yet distances between them are short and gene flow is high. Gene flow should act to prevent genetic subdivision (MAYR, 1963). The number of effective migrants per baldcypress subpopulation exceeds the minimum required to ensure qualitative equivalence of the subpopulations relative to the occurrence of low frequency alleles (WRIGHT, 1931). The patterns of spatial autocorrelation with most of the significant positive values occurring at the shortest distance and negative ones at the longer distances further document the effects of gene flow in making allele frequencies of adjacent populations most similar (*Figure 2*). PGM-2 is an exception to this generalization and may reflect the effects of localized selection or drift. When gene flow is high, population subdivisions may be maintained by natural selection (ALLENDORF, 1983) acting directly on biochemical loci (DiMICHELE and POWERS, 1982; WATT et al., 1983). However, we have no evidence for selection on the three loci studied here.

Baldcypress seedlings are established only in years when water levels remain low enough to allow seed germination (DEMAREE, 1932) and promote early seedling growth. Cone production also varies greatly among trees and years (MATOON, 1915; DETWEILER, 1916; SCHNEIDER and SHARITZ, 1988). Although the soil seed bank may store baldcypress seeds from year to year (SCHNEIDER and SHARITZ, 1986), it is likely that most seedlings arise from a few parent trees that happen by chance to be bearing large numbers of cones during those years of low water levels. Opportunities for seedling establishment are limited and not predictable over years from conditions prior to times of low water. Highly successful reproduction by a few individuals within local areas may be responsible for the observed spatial structuring of the population even with high gene flow between subpopulations. Thus, the patterns of genetic structure in baldcypress suggest that despite the large number of trees in the swamp and high gene flow, population processes may amplify small genetic differences due to drift.

Acknowledgements

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