

GENETIC VARIATION IN THE SOUTHERN PINES: EVOLUTION, MIGRATION, AND ADAPTATION FOLLOWING THE PLEISTOCENE

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ABSTRACT.—Climate has certainly changed over time, requiring genetic change or migration of forest tree species. Little is known about the location of the southern pines during the Pleistocene glaciation, which ended around 14,000 years ago. Macrofossils of spruce (*Picea* spp.) dating from the late Pleistocene, which are typical of climates much cooler than presently occupied by the southern pines, have been found within the current range of the southern pines, indicating that the climate was considerably colder at that time. From this discovery it is reasonable to assume that the southern pines were situated south of their present range during the Pleistocene and migrated to their current location after the glaciers receded. Variation in adaptive and non-adaptive traits of the southern pines suggests that loblolly pine (*Pinus taeda*) existed in two refugia, one in south Texas/north Mexico, and one in south Florida. Longleaf pine (*P. palustris*) probably existed only in the western refugium. Slash pine (*P. elliottii*), on the other hand, presumably resided only in the Florida refugium, whereas shortleaf pine (*P. echinata*) is cold-hardy enough to have existed in a continuous distribution across the Gulf Coast. Implications of climate warming on the future of southern pines are discussed.

INTRODUCTION

There has been a great deal of discussion about “global climate change”. An increase in CO₂ in the atmosphere since industrialization has been well documented and is apparently causing an increase in average temperatures. A consensus is developing that global temperatures are on the increase. Changes in climate, however, are not new, but have occurred many times in geological history.

The most drastic climatic changes during the long history of the pines have been relatively recent, during the Pleistocene Ice Ages. During the 1.6 million years of the Pleistocene, large fluctuations in temperature resulted in the advance and retreat of glaciers with a periodicity of a little more than 100,000 years. The interglacial periods were short compared to the glaciated periods. The current interglacial period, the Holocene, began from 10,000 to 14,000 years before present (BP); the last interglacial, the Eemian, from 130,000 to 107,000 years BP (Critchfield 1984). The large fluctuations in climate, which resulted in lengthy migrations, undoubtedly affected the population structure of temperate forest tree species.

Climate during the height of the last of these glaciations, the Wisconsin (c. 18,000 years BP), was colder than at present in the southeastern United States. The glaciation extended as far south as southern Ohio (40°N), overlapping the

current northern distribution of the most temperate of the southern pines (Fig. 1). The southern pines were certainly situated south of their current location. The postulated palaeovegetation maps of Delcourt and Delcourt (1981) show oak, hickory, southern pine as far north as Tennessee (36°N). The maps of Webb et al. (1987), on the other hand, show southern pines absent at this time, and appearing in south Florida only at 12,000 years BP. Palynological evidence is difficult to interpret. Not only can pine pollen travel large distances, but it may be impossible to identify to the species level.

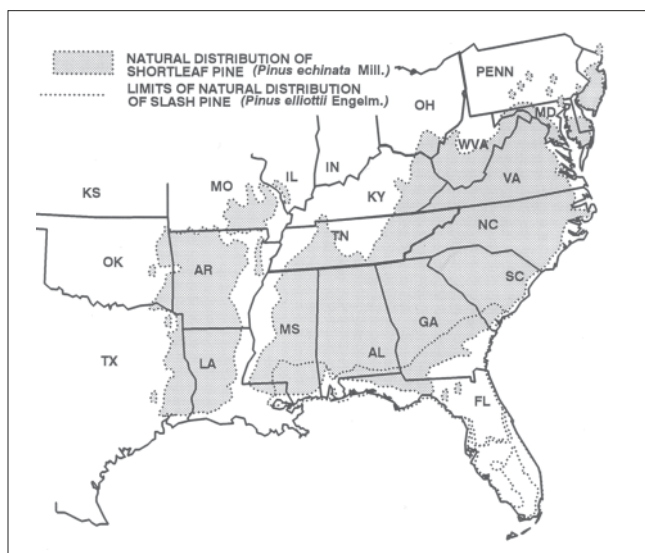


Figure 1.—Map of the Southeastern United States showing the current natural distribution of shortleaf and slash pines.

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Macrofossils (including cones and needles) of boreal species, spruce (*Picea* sp.) and jack pine (*Pinus banksiana*) have been identified from several Wisconsin deposits (c. 14,000 years BP), one as far south as Louisiana (31°N) (Critchfield 1984). These locations are within the current natural ranges of even the more austral of the southern pines (Fig. 2). The current natural range of shortleaf pine (*Pinus echinata*) extends as far north as Ohio and New Jersey, but is several hundred kilometers south of the nearest jack pine in northern Michigan. Shortleaf pine overlaps the natural range of red spruce (*Picea rubens*) in the Appalachian Mountains, but shortleaf pine does not occur above 910 m, whereas red spruce does not occur below 1370 m (USDA 1990). Spruce and shortleaf pine do not currently grow on the same sites, but “disharmonious” associations could have existed during the Pleistocene (Wright 1989).

GENETIC VARIATION IN THE SOUTHERN PINES

Genetic variation in the more commercial southern pines is well known, especially for the adaptive traits of growth, survival, and pest resistance (summarized in Schmidting 2001). The results of common-garden experiments as well as allozyme studies are available for shortleaf, longleaf (*P. palustris*), loblolly (*P. taeda*) and slash (*P. elliottii*) pines. These four species exhibit four different patterns of variation. The first three occur on both sides of the Mississippi River, but the last occurs only to the east of the river. This is an important factor in the evolution of the species.

Longleaf Pine

Provenance tests have shown that substantial variation in growth, survival, and disease incidence exists in longleaf

pine (Wells and Wakeley 1970). Growth is generally related to latitude or temperature at the seed source (Schmidting and Sluder 1995). Geographic variation in longleaf pine parallels that of other forest tree species; seedlings from warmer climates grow faster than those from colder climates, if they are not transferred to greatly differing climates.

In longleaf pine there are no differences in adaptive traits among sources east of the river versus those west of the river, after the minimum temperature at the seed source is taken into consideration (Schmidting 1999). Given the lack of such differences in adaptive traits, it was surprising to find a linear decrease in variability from west to east in allozyme diversity (Schmidting and Hipkins 1998). Sixty percent of the variation in expected heterozygosity was explained by longitude of the seed source (Fig. 3).

The most attractive explanation for the observed trend in variation is that longleaf pine originated from a single, limited refugium in southeast Texas or northeast Mexico, resulting in a reduced level of genetic variability as the rapidly migrating population was affected by stochastic events (Fig. 2).

Loblolly Pine

Like longleaf pine, loblolly pine occurs on both sides of the Mississippi River Valley (Fig. 4). Provenance tests have shown that substantial geographic variation in growth, survival, and disease susceptibility exists in loblolly pine (Wells and Wakeley 1966). Growth is generally related to latitude or temperature at the seed source (Schmidting 1997). Geographic variation parallels that of longleaf pine; seedlings from warmer climates grow faster than those from colder climates, if they are not transferred to very different climates.

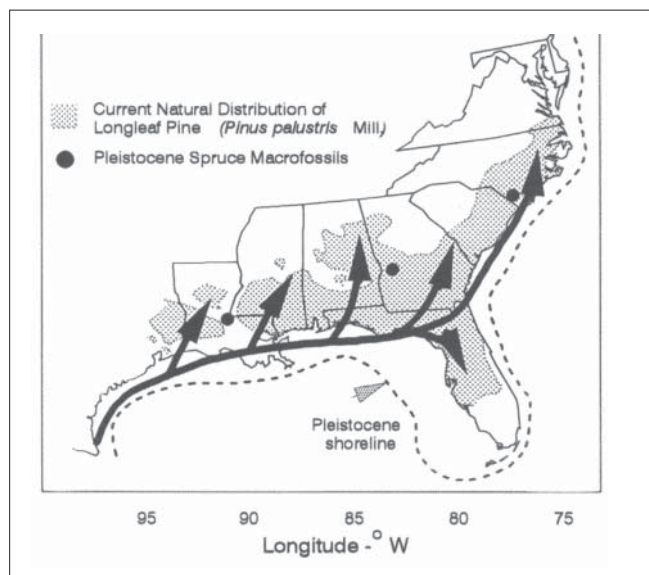


Figure 2.—Post-Pleistocene migration route accounting for the variation. Adapted from Schmidting and Hipkins (1998).

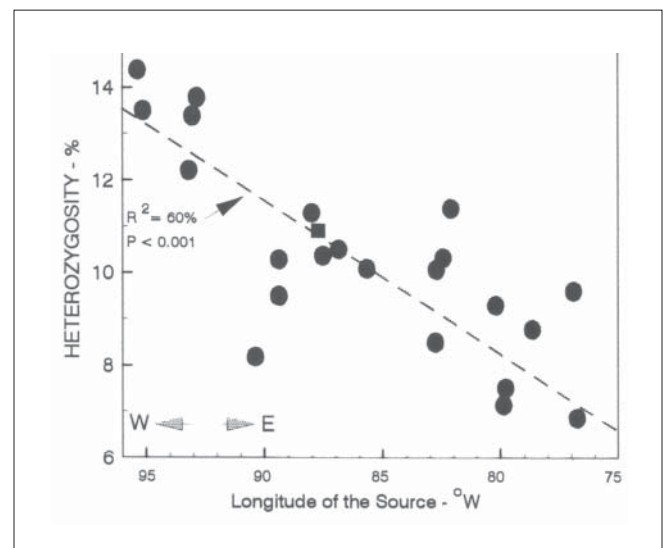


Figure 3.—Variation in expected heterozygosity by longitude in longleaf pine. Adapted from Schmidting and Hipkins (1998).

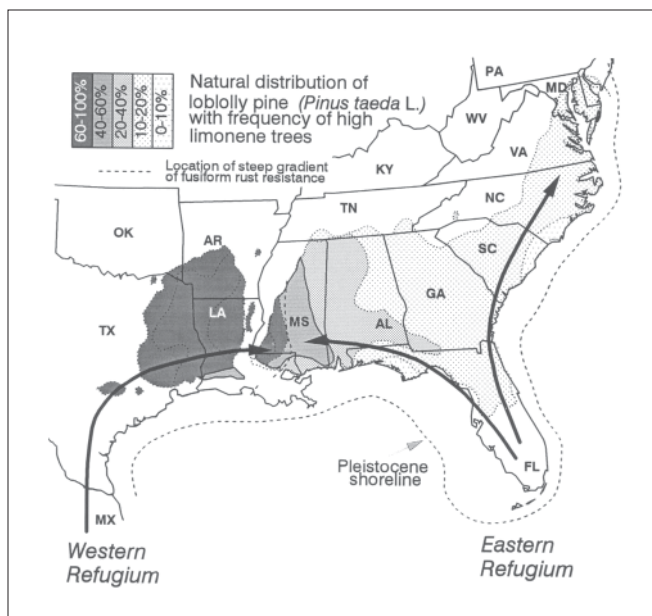


Figure 4.—Current natural distribution of loblolly pine showing the frequency of trees with high cortical limonene content. Also shown are the proposed Pleistocene refugia and migration routes.

Although east-west variation in adaptive traits such as growth, disease resistance and survival is minimal in longleaf pine, it is very important in loblolly pine (Wells and Wakeley 1966). In loblolly pine, western sources are slower growing, survive better, and have greater resistance to fusiform rust (*Cronartium quercuum* f.sp. *fusiforme*). The isolating effect of the Mississippi River Valley has often been cited to explain the east-west differences in loblolly pine. Pines do not exist in the Valley, because they cannot compete with broadleaved trees in the rich, moist alluvial soils where fire is infrequent. There is also an obvious difference in cortical monoterpenes between eastern and western populations (Fig. 4). Limonene is especially high in western populations (Squillace and Wells 1981). Although monoterpene composition is often considered a non-adaptive trait, it may function in insect resistance. The pattern of high limonene among populations on both sides of the Mississippi River appears to indicate there is gene exchange across the river, at least in the eastward direction. This possibility is supported by the existence of rust-resistant populations, common in the west, just east of the river (Fig. 4).

In loblolly pine, there was no east-west trend in allozyme variation (Schmidtling et al. 1999) and there appears to be a tendency for more variation in the central part of the natural range. There are some differences in the occurrence of rare alleles among populations. Twenty of the rare alleles were detected only in the eastern populations whereas only two were found exclusively in the western populations. Nearly all the alleles that are found in the western populations can be found in the eastern populations, but many of the alleles

found in the eastern populations were not found in the western populations.

One of the alleles of enzyme 6PGD-1 is relatively common in many populations of loblolly pine east of the river, having a frequency as high as 0.29 in one population in Maryland, but is very rare west of the river. The distribution of allozyme alleles suggests that gene flow in a westerly direction across the Mississippi River is restricted. On the other hand, the continuous clinal variation in limonene content (Squillace and Wells 1981) and fusiform rust resistance (Wells et al. 1991) across the Mississippi River (Fig. 4) suggests that there is no barrier to gene flow in the eastern direction across the valley. Prevailing winds since the beginning of the Holocene 14,000 years ago are primarily in the eastern direction, and are certainly a factor in this predominantly one-way gene flow.

Some interesting similarities exist between all populations of longleaf pine and western populations of loblolly pine. Like western populations of loblolly pine, longleaf pine is resistant to fusiform rust and much less susceptible to tip moth and southern pine beetle (Snyder et al. 1977), although the mechanisms probably differ. These similarities suggests that western loblolly populations and all longleaf populations shared an environment at some time in the past where selection for resistance to these pests was important. The proposal that longleaf pine and western sources of loblolly pine both originated in a common refugium in south Texas/northeast Mexico fits the circumstantial evidence. The present climate in south Texas is too dry for *Australes* pines, but was probably much wetter during the Pleistocene (Watts 1983). Other pines occur just south of the border in Mexico, at high elevations (Critchfield and Little 1966).

The lack of a trend in allozymes in loblolly pine, coupled with the distinct east versus west variation in fusiform rust resistance and other adaptive traits suggests that loblolly pine was located in two refugia during the Pleistocene (Fig. 4), in Texas/Mexico and Florida/Caribbean as proposed by Wells et al. (1991). Using the genetic distances from the allozyme data of Schmidtling et al. (1999), I have calculated a divergence time of 97,000 years between the western and eastern sources, which is a good approximation of the time since the last interglacial period, the Eemian, in this region.

Shortleaf Pine

Shortleaf pine has the most temperate distribution of the major commercial southern pines, extending into Ohio and New Jersey to the north, and barely reaching into north Florida in the south (Fig. 1). Like longleaf and loblolly pines, shortleaf pines occur on both sides of the Mississippi River.

Like longleaf pine, provenance tests have shown that substantial variation in growth, survival, and disease

incidence exists in shortleaf pine (Wells and Wakeley 1970). Growth is generally related to latitude or temperature at the seed source (Schmidting 1995). As with longleaf pine, there is no east/west variation in adaptive traits in shortleaf pine.

Unlike longleaf pine, there is no east/west trend in allozyme variability (Raja et al. 1997, Edwards and Hamrick 1995). There is no trend consistent with a relatively fast migration from a restricted refugium. The relative cold-hardiness of shortleaf pine may have made such a migration unnecessary. It is here proposed that shortleaf pine had a more-or-less continuous distribution across the Gulf of Mexico, on the exposed continental shelf (Fig. 5).

Slash Pine

A number of the Australes pines occur only east of the Mississippi River Valley, including slash pine, pond pine (*Pinus serotina*), table mountain pine (*P. pungens*), pitch pine (*P. rigida*) and spruce pine (*P. glabra*). Slash pine is the most austral of the major southern pines and occurs mainly in Florida (Fig. 1). Slash pine has obvious affinities to *P. caribaea* of the Bahamas and Cuba, and before 1954 they were considered the same species (Little and Dorman 1954, Farjon and Styles 1997). There is clinal variation in many adaptive traits in slash pine in a north-south direction (Squillace 1966). It seems logical to assume that slash pine existed in a refugium in south Florida, the Bahamas, or Cuba, and migrated north after the retreat of the glaciers, approaching but not able to cross the Mississippi River against the prevailing winds. The expected decrease in variability in allozymes from south to north along the putative migration route has been documented (Schmidting and Hipkins 2000).

The other southern pines with eastern distributions probably resided in refugia in north Florida to North Carolina (Fig. 5). Table mountain pine may be an exception. This pine exists at high elevations in the Appalachian Mountains and may simply have moved to a lower elevation.

THE FUTURE

Consensus is developing that global temperatures are on the rise, because of the human-induced increase in “greenhouse” gasses such as CO₂. During past climatic changes, forest trees, as well as other organisms, have been able to migrate to areas of favorable climate, or to change genetically through natural selection. Evolution is not static but is a constantly ongoing process.

Climate has been warmer in the past, such as during the Hypsithermal era, about 5,500 years BP. Climate has also been colder, e.g., “the Little Ice Age” in medieval times. The changes that have been projected by many climatic models, however, will be very fast, perhaps too fast for these natural processes to occur (Davis 1990).

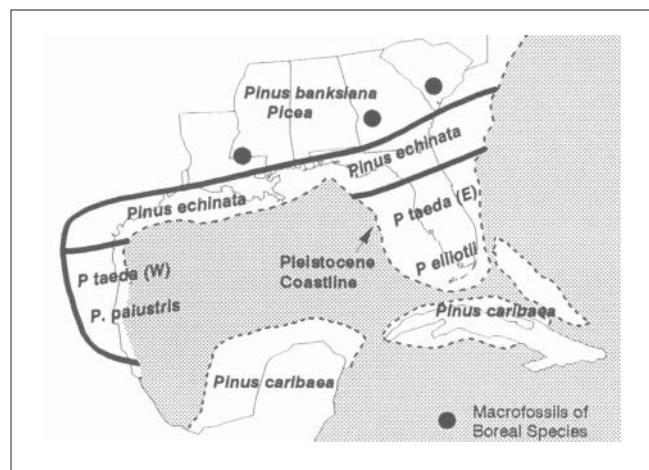


Figure 5.—Proposed location of the major southern pines during the Wisconsin Glaciation.

The southern pines have a great deal of genetic plasticity as is evident in the South Wide Southern Pine Seed Source Study (Schmidting 2001). In this study, it is common for even very poorly adapted sources to live past 35 years (and reproductive maturity) albeit growing very slowly. Even this great plasticity may not be enough.

At some point foresters and other biologists may have to intervene in the process to mitigate the effects of this human-induced change. In this case, gene conservation would become very important.

CONCLUSIONS

In spite of the relative uniformity of the Coastal Plain of the southeastern United States, important genetic differences exist among the southern pine species in response to the last glaciation. Longleaf pine resided in a southwestern refugium and slash pine in a Florida refugium. Loblolly pine resided in both refugia, the two populations being isolated genetically. Shortleaf pine probably resided in a continuous population across the exposed continental shelf. The many advances and retreats of glaciation during the Pleistocene undoubtedly had profound effects on variation and speciation in the southern pines.

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