

# EFFECT OF LARGE-SCALE MOVEMENT OF LOBLOLLY PINE SEED ON GENETIC INTEGRITY OF THE SPECIES IN ITS NATURAL RANGE

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## INTRODUCTION

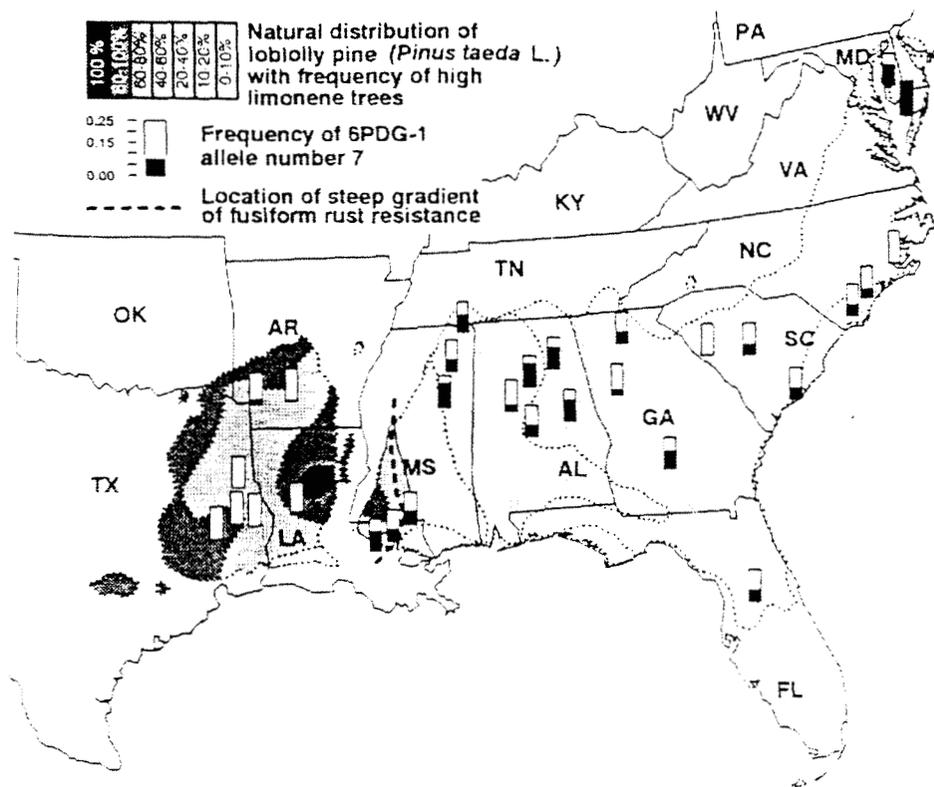
### Geographic variation

Geographic variation of the major southern pine species has been well studied. Seed collected from different geographic areas vary greatly in their potential for growth and survival depending on where they are planted. In seed source studies of forest tree species, it is often observed that sources from warmer climates grow faster than local sources as long as they are not moved to greatly differing climates. This is true in loblolly pine and is at least partially due to warm-climate sources growing longer in the fall than sources from colder climates (Jayawickrama et al. 1998). There is some advantage to moving loblolly pine seed sources northward to improve yield.

While north/south differences in adaptive traits in loblolly pine are significant, the east/west differences have been much more important economically. The most important early study of loblolly pine seed sources was Philip C. Wakeley's Bogalusa, LA, planting of 1927. There, loblolly pines (*Pinus taeda* L.) grown from local seeds (Livingston Parish, LA) produced about twice the wood volume through age 22 as did trees of the same species grown from Arkansas, Georgia, and Texas seeds (Wakeley and Bercaw 1965). More important, there was a very large difference among sources in susceptibility to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*). The sources from Arkansas and Texas were very resistant, the Livingston Parish source was moderately resistant, and the Georgia source was very susceptible. Because of the results of this study and other later studies, east Texas and Livingston Parish loblolly seedlings have been moved eastward to areas with severe fusiform rust infection. They have been planted over hundreds of thousands of acres in the southern Coastal Plain, where they have exhibited both substantial rust resistance and good growth rates (Wells 1985).

### Gene flow

The Mississippi River Valley provides a barrier to gene flow in the southern pines because pines are not part of the natural vegetation in the moist, alluvial soil of the Valley. Now mostly agricultural, the Valley has historically been home to vast hardwood forests, undoubtedly because of the absence of fire. Of the three southern pine species that occur both east and west of the Mississippi River, loblolly (*Pinus taeda* L.), longleaf (*P. palustris* Mill.) and shortleaf (*P. echinata* Mill.), only in loblolly pine are there important differences between western and eastern seed sources (Schmidting 2001). This difference between loblolly pine and the other species is probably rooted in the Pleistocene geologic era. During the height of the Wisconsin Ice Age, 14,000 years before present, the South was occupied by a boreal forest. Patterns of genetic variation in allozymes indicate that longleaf resided in one refugium in south Texas / north Mexico and migrated northward and eastward when the ice retreated (Schmidting and Hipkins 1998). It is probable that loblolly pine originated from two isolated refugia, one in southwest Texas / northeast Mexico, and one in south Florida / Caribbean (Schmidting et al. 1999). The two populations converged at the Mississippi River Valley at the close of the Pleistocene era. The 100,000-year isolation of the two populations, in differing environments, resulted in the differences we see today.



**Figure 1.** Map of the southeastern United States showing the natural distribution of loblolly pine and the distribution of trees with high limonene content in cortical gum (redrawn from Squillace and Wells 1981). Also shown is the frequency of the slowest migrating allele of the enzyme 6PDG-1 in electrophoresis (from Schmidting et al. (1999)).

Squillace and Wells (1981) showed that extensive geographic variation exists in the highly heritable monoterpene composition of bud resin in loblolly pine. Especially notable was east-west variation. Variation was largely clinal, but all trees west of the Mississippi River Valley had high beta phellandrene. Limonene content showed the greatest east-west variation. In most of the populations west of the Valley, 100% of the trees had high limonene, whereas populations in many areas of the east coast had zero trees with high limonene (Fig. 1). A re-drawn version of Figure 3 of Squillace and Wells (1981) appears to show that gene flow is occurring eastward across the Mississippi River Valley, especially at the southern end of the distribution.

An eastward gene flow across the Valley would also account for the resistance to fusiform rust (inherent in western seed sources), which is possessed by loblolly pine from Livingston Parish, Louisiana, even though this source is east of the Valley. The distribution of resistance to fusiform rust in an intensive sampling of loblolly pine seed sources across the Valley, showed a pattern very similar to that of limonene in Figure 1, i.e. an indication of gene flow for resistance from west to east, especially at the southeastern end of the western population (Wells et al. 1991).

Allozyme data offers evidence that gene flow is largely one-way across the Mississippi River Valley in loblolly pine (Schmidting et al. 1999). In electrophoresis of the enzyme 6PGD-1, allele number seven, the slowest migrating allele, has an average frequency of 13% in loblolly pine populations across the south, and ranges from 0 to 25% in individual populations (Fig. 1). There is a striking difference in frequency across the Mississippi River Valley. This allele is absent or very rare west of the Valley, whereas just to the

east of the Valley the allele occurs in substantial frequencies (Fig. 1), suggesting that gene flow from east to west is very low. Prevailing winds during pollination as well as during seed fall are from west to east, which probably accounts for the directionality of gene flow.

## The problem

Several long-term tests have shown that loblolly pine from east of the Mississippi River has an inherently faster growth rate than western loblolly. Trees from some eastern sources have grown about 8 feet taller in 25 years than trees from western sources; a substantial difference (Wells and Lambeth 1983).

In the last few decades some forest products manufacturers have planted substantial numbers of loblolly seedlings from Atlantic Coastal Plain sources in southern Arkansas, southeastern Oklahoma, and the Ouachita Mountains of Arkansas and Oklahoma (Lambeth et al. 1984). The short-term economic value of these transfers, at least for a pulpwood rotation, is great. However, the lack of long-term adaptability in growing stock transferred in the westward direction may result in catastrophic losses late in the rotation (Lambeth et al. 1984).

More importantly, even if these trees are harvested completely in a pulpwood rotation, their pollen will affect the seed produced in surrounding native stands. It is not known how the non-local genotypes will affect the native gene pool. In this paper, published allozyme data are used to infer changes in the gene pool that could be attributed to seed transfers.

## The data

The loblolly pine populations sampled in Schmidting et al. (1999) were established during three different time periods. The youngest population was comprised of bulk seed collected around 1980 in 10 natural stands scattered across the natural range of loblolly pine. Three of the natural stands were west of the Mississippi River Valley and seven were east of the Valley. Allozyme data were collected from embryos, giving a genetic snapshot of the populations being established naturally around 1980.

The second youngest population was comprised of seed collected from plantings of the Southwide Southern Pine Seed Source Study (SSPSSS) (Wells and Wakeley 1966). The SSPSSS plantings were established using seed collected around 1950 from 14 natural stands, two from west of the River and 12 from east of the River. Allozyme data were collected from megagametophytes, giving a genetic sampling of the populations being established around 1950 when the original collections were made.

The oldest population was comprised of seed from orchard selections in U.S. Forest Service seed orchards. Only seed collected from clones whose ortets were in existence prior to 1930 were used in this study. Seed from orchard ramets whose donor ortets were established after 1930 were excluded due to the possibility that the donor trees were planted by the Civilian Conservation Corps, and therefore could be non-local in origin. In all, nine seed sources were sampled: two western and seven eastern. Allozyme data were collected from megagametophytes, giving a genetic sampling around 1920 when the original donor trees were established.

Table 1, adapted from Schmidting et al. (1999), shows east-west differences in various measures of allozyme variability for the three population ages. In general, the younger populations tend to have fewer polymorphic loci and lower expected heterozygosity than the older populations. Western populations also have a tendency to have fewer alleles per locus than eastern populations, which one might expect if gene flow between the populations only occurred from west to east. There is no obvious trend over time in the number of alleles per locus by time of establishment.

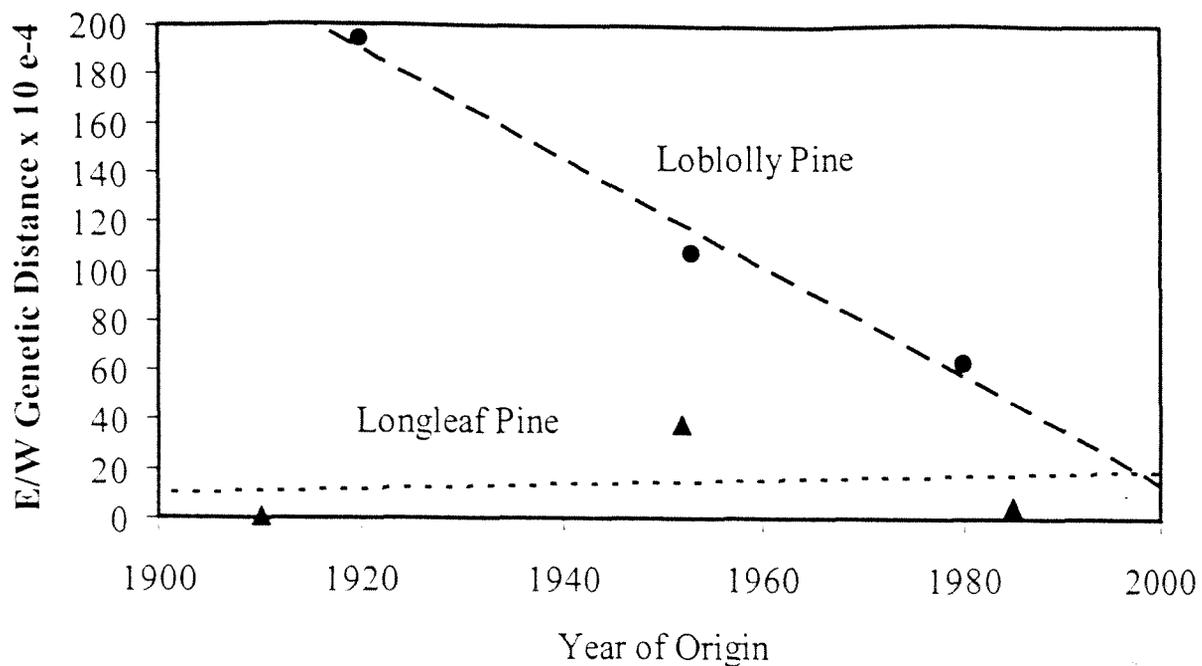
**Table 1.** Allozyme variability of eastern versus western loblolly pine populations from three different eras. Data extracted from Schimidtling et al. (1999).

		Old (Orchard)	Middle (SSPSS)	Young (Bulk)
Number of Alleles per Locus	E	2.55	2.01	2.33
	W	2.33	1.83	2.08
Percent Polymorphic Loci	E	63.4	53.9	44.4
	W	66.7	45.8	44.5
Expected Heterozygosity	E	0.195	0.180	0.170
	W	0.196	0.140	0.158

The most intriguing trend is in the genetic distance between eastern and western populations. Allozyme data can be used to establish a genetic distance, or index of dissimilarity, to infer relatedness, or genetic divergence. Using the raw data from Schimidtling et al. (1999), Nye's genetic distance was derived using BIOSYS (Swofford and Selander 1989) and plotted versus time of establishment (Fig. 2). Populations from the apparent transition zone, southeastern Louisiana and southwestern Mississippi, were not included in the analysis.

The allozyme data originating from trees established during three different periods, ca. 1920, 1950, and 1980, show a dramatic decrease in genetic distance between western and eastern sources over time (Fig. 2). This decrease appears to be too abrupt to be due to natural gene flow, which has undoubtedly been continuous from west to east since the end of the last glaciation more than 10,000 years ago, a very long time compared to the less than 100 years represented in this study.

An allozyme data set similar to the loblolly data is also available for longleaf pine (Schimidtling and Hipkins 1998). The longleaf populations represented in the data set are very similar to those for loblolly: older seed orchard selections circa 1910, SSPSS plantations derived in the early 1950s, and recent bulk collections from natural stands (Schimidtling and Hipkins 1998). Again, Nye's genetic distance was derived using BIOSYS (Swofford and Selander 1989). The results for the longleaf data are quite different than for the loblolly data, as one would expect since longleaf expresses little east/west variation and has not been widely planted (Fig. 2). The genetic distance between eastern and western sources is much less overall than for loblolly, and there is no obvious trend over time. Instead, the genetic distance appears to be more or less constant over time, unlike in loblolly pine.



**Figure 2.** Plot of genetic distance between eastern and western sources versus year of origin for loblolly pine (data from Schmidting et al. (1999)) and longleaf pine (data from Schmidting and Hipkins (1998)).

### Implications

It appears that the widespread movement of loblolly pine seed sources has a significant effect on native gene pools. Planting non-local sources can increase genetic diversity in local populations but may have important implications for growth and adaptability depending on the direction of seed movement.

Moving western seed sources east of the Mississippi River, which mimics natural gene flow, probably has a positive effect on adaptability since western seed sources tend to be hardier, more fusiform rust resistant, and tend to tolerate crowding better than eastern sources (Schmidting and Froelich 1993). Eastern sources tend to grow faster than western sources, so moving seed sources from west to east probably has a slightly negative effect on growth.

Moving seed sources from east of the Mississippi River west may be problematical in the long run. During drought, plantings of eastern sources are susceptible to catastrophic failure (Lambeth et al. 1984). Dendrochronological analyses of western plantings of the Southwide Southern Pine Seed Source Study (SSPSSS) have shown that eastern sources tend to keep growing at the onset of a drought, whereas western seed sources cease growth immediately (Grissom and Schmidting 1997). Since periods of severe drought are common in the western part of the loblolly pine distribution, mal-adapted genes from eastern sources could be incorporated into western populations through pollen shed and cause long-term decreases in adaptability.

This mal-adaptation may become even more important in the future. Most global climate change models predict that in the western part of the loblolly pine range, the climate will become drier than at present (Schwartz 1991). Thus, the incorporation of eastern genes into western populations does not bode well for the future.

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# Silviculture and the Conservation of Genetic Resources for Sustainable Forest Management



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