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Provenance and Progeny Variation in Pitch Pine from the Atlantic Coastal Plain

John E. Kuser and F. Thomas Ledig

ABSTRACT. A test of open-pollinated pitch pine families from 17 different locations on the Atlantic Coastal Plain was evaluated at 12 years of age. Genetic variation for growth was almost totally on the provenance level and was detectable among families within provenances in only a few cases. Mean volume decreased with latitude and also with distance of the seed origin from the test site. Provenances with the largest mean volume per tree came from locations 5.3 and 24.8 km distant from the test site and those with the smallest, from 349 and 388 km distant. The frequency of trees with serotinous cones varied from 2% to 48% and followed closely the pattern observed at the provenance origin. The frequency of epicormic sprouts was generally high, but differed significantly among provenances. FOR. SCI. 33(2):558–564.

ADDITIONAL KEY WORDS. Clines, adaptation, selection, cone serotiny, epicormic sprouts, *Pinus rigida*.

PITCH PINE (*Pinus rigida* Mill.) is the most northerly member of the important group known as the "southern yellow pines," but it is not as commercially desirable as other yellow pines. In the center of its range along the Atlantic coastal plain, most pitch pines are crooked, heavy-limbed, and slow-growing. Nevertheless, pitch pine has three advantages over its more important relative, loblolly pine (*P. taeda* L.): (1) it is more tolerant of ice, snow, and low temperature, (2) it is resistant to fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*), and it is capable of growing on sandier, poorer, more droughty soils than loblolly (Ledig and Fryer 1974). The hybrid of pitch pine and loblolly pine has been used in Korea for years (Hyun and Ahn 1959) and is now in demand in the northeastern United States.

A breeding program is now underway to improve the growth and form of pitch pine (Kuser 1985). The gains from breeding loblolly pine are well known (Zobel 1971). However, in pitch pine little has been published on genetic variation in economic traits, such as volume growth, that can be used to guide selection and breeding.

A pitch pine breeding orchard established in 1964 by Silas Little at New Lisbon, New Jersey, showed striking differences among clones in height, form, cone type, and presence or absence of epicormic shoots (Kuser and Knezick 1985). Open-pollinated pitch pine progeny of the orchard clones and their control-pollinated hybrids with loblolly pine have shown great variation in height growth at age 10 on test sites in New Jersey. The tallest of the pitch pine, and some of the tallest pitch × loblolly hybrids, are progeny of the tallest orchard clone, the ortet of which grows along the Great Egg Harbor River near Weymouth, New Jersey (Kuser, Garrett, and Knezick,

The authors are Associate Professor, Department of Horticulture and Forestry, Cook College, New Jersey Agricultural Experiment Station, Rutgers University, New Brunswick, New Jersey 08903 and Project Leader, Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, 1960 Addison Street, Berkeley, California 94704.

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in press). One open-pollinated pitch pine family from this clone averaged taller than 80 percent of the pitch × loblolly families in the same test plantation, while showing no incidence of the sweetfern rust (*Cronartium comptoniae* Arth.) cankers that afflicted many of the hybrids. However, the clones originated in stands scattered over the northeastern United States, and it is not certain how much of the variation among their progeny is due to provenance effects and how much to variation within provenances.

In 1971, one of us (FTL) established combined provenance and family tests to estimate the levels of genetic variation among and within stands of pitch pine and to determine whether performance was related to latitude of origin. This paper reports on 12-year results and relates them to earlier performance in the nursery and to observations on the parents.

Materials and Methods

Cones were collected in 1969 and 1970 from 156 trees in 17 natural stands of pitch pine, distributed over the Atlantic coastal plain (Figure 1). Seed was extracted, dried, and refrigerated until sown. Each provenance was represented by 8 to 10 open-pollinated families, except Batsto and Great Egg Harbor River, which had only 6 and 3, respectively (see Table 1). Further details on the sampling procedure were given by Ledig and Fryer (1972).

Seed were sown May 28–29, 1971, in 1.5 in. diameter by 3.875 in. long kraft paper tubes filled with a 1:1:1 sand:peat:topsoil mix. Germination was well under way by June 3. Seedlings were grown in a greenhouse at New Haven, Connecticut, for one month and then transplanted into the Washington's Crossing Nursery, Titusville, New Jersey. Seedlings were lifted in April and planted between April 28 and May 10, 1973, on the Lebanon State Forest.

The planting site is a level Lakehurst sand on the outer coastal plain of southern New Jersey. Large trees were felled and the brush was chopped. Rows were plowed at 2.4 m intervals and trees were dibble-planted at 1.8 m spacing within the plow line. To reduce competition from scrub oak (*Quercus ilicifolia* Wangenh.) sprouts, a mix of 2, 4-D and 2, 4, 5-T was applied with a mist blower in July 1976. Some herbicide damage was noted on the trees.

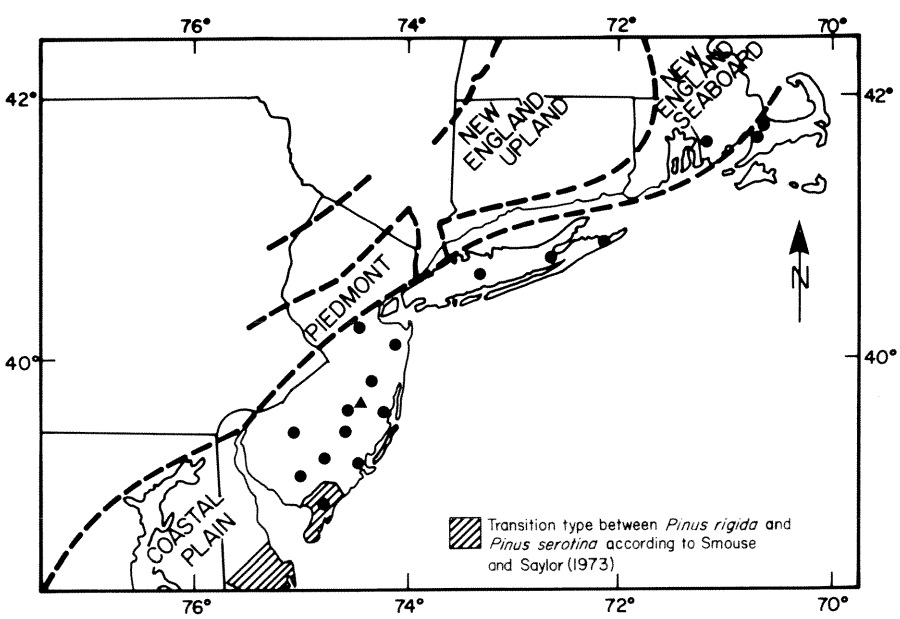

FIGURE 1. Map of the Atlantic coast in the Northeastern United States showing provenance locations (●) and location of the test site (▲).

TABLE 1. Provenance location data for coastal plain pitch pine provenances.

Provenance	County and state	Latitude (°N)	Longitude (°W)	Elevation (m)	Families (no.)
Sagamore	Barnstable, MA	41°46′	70°32′	61	10
Bourne	Barnstable, MA	41°43′	70°35′	30	10
Fall River	Bristol, MA	41°39′	71°01′	27	8
Beach Hampton	Suffolk, NY	40°59′	72°06′	3	10
Hampton Bays	Suffolk, NY	40°53′	72°33′	6	10
Commack	Suffolk, NY	40°48′	73°16′	46	10
Helmetta	Middlesex, NJ	40°23′	74°26′	15	10
Green Cove	Monmouth, NJ	40°15′	74°05′	30	10
Lakehurst	Ocean, NJ	40°01′	74°18′	18	10
Lebanon Lakes	Burlington, NJ	39°53′	74°34′	34	10
Waretown	Ocean, NJ	39°48′	74°12′	6	10
Fries Mills	Gloucester, NJ	30°40′	75°02′	40	9
Batsto	Burlington, NJ	39°39′	74°39′	6	6
Great Egg Harbor River	Atlantic, NJ	39°30′	74°46′	9	3
Oceanville	Atlantic, NJ	39°28′	74°28′	12	10
Cumberland	Cumberland, NJ	39°23′	74°57′	12	10
Clermont	Cape May, NJ	39°10′	75°46′	3	10

The planting design was a compact family block (Panse and Sukhatme 1961). Provenances were randomized within each of three blocks, and families were randomized within their provenance. For each of the 156 families there were one to three 3-tree plots within each provenance × block combination. The number varied because family plots were arranged to permit the exterior rows of their provenance plot to be thinned or omitted from analysis without destroying the experimental design (i.e., without eliminating any families from the basic provenance-progeny test design).

In June 1985, we counted and measured the 1,759 surviving trees. The number of surviving trees per family ranged from 6 to 27, with a harmonic mean of 10.56. Data included survival, height (to the end of the 1984 growth), diameter breast high (dbh), cone occurrence (presence or absence), type of cone (serotinous or open) if present, and presence or absence of epicormic shoots. We computed bole volumes, using the formula $V = 0.002182D^2H\ (H/H\text{-}4.5)^{1/2}$ (Green et al. 1986), and converted volume to cubic meters. For growth traits, we performed analyses of variance on provenance means for height, diameter, and volume, and then conducted 17 separate analyses on family means within each provenance. We performed chi-square analyses on data for provenance variation in cone occurrence, cone type, and presence or absence of epicormic shoots (Sall and Stanish 1982).

Results

Overall survival was high (87%) but there were differences among provenances (Table 2). However, we could detect no geographic trend. Differences among provenances in height, dbh, and volume were also significant ($P < 0.0001$). Chi-square frequency analyses revealed significant differences among provenances ($P < 0.0001$) in cone occurrence and type (serotinous vs. open) and in occurrence of epicormic shoots. Major differences occurred in the incidence of serotinous cones. Only 2% of the trees from Bourne bore closed cones while 50% of the trees from Great Egg Harbor River did. The incidence of epicormic shoots was high, but varied from 78% for the Helmetta provenance to 98% for the Sagamore provenance.

Regressions of bole volume, height, or dbh against latitude of origin shows that in general, trees of southern origin tended to grow larger than those of northern origin (for volume, $r^2 = 0.65$; Figure 2). However, an alternative interpretation is possible (Figure 3). A simple linear relationship between volume and distance of the seed

TABLE 2. Percent survival, heights and dbhs of tallest and shortest families and provenance means (in boldface), percent of trees bearing cones, trees bearing closed cones (as a percent of all trees bearing cones), and percent with epicormic shoots.

	Survival (%)	Height (m)	DBH (cm)	Cones	Sero-tiny	Epicor-mics
				..... %		
Sagamore, MA	95	4.3–**4.5**–4.9	7.9–**7.7**–9.9	37	7	98
Bourne, MA	92	4.0–**4.5**–4.7	7.1–**7.6**–8.6	42	2	95
Fall River, MA	90	4.2–**4.4**–5.0	7.4–**7.6**–8.1	48	4	92
Beach Hampton, NY	83	4.1–**4.4**–4.9	7.4–**7.9**–9.4	36	5	88
Hampton Bays, NY	90	4.7–**4.9**–5.3	7.9–**8.4**–8.6	26	17	94
Commack, NY	87	4.2–**4.5**–4.9	6.9–**8.4**–10.0	43	17	93
Helmetta, NJ	86	4.4–**4.7**–5.0	7.9–**8.7**–9.4	41	25	78
Green Cove, NJ	91	4.4–**4.7**–5.2	8.1–**8.7**–9.1	40	20	94
Lakehurst, NJ	80	4.5–**4.6**–4.9	8.1–**8.4**–9.4	42	36	94
Lebanon Lakes, NJ	80	4.7–**5.0**–5.3	8.4–**8.8**–9.4	40	45	93
Waretown, NJ	90	4.7–**4.9**–5.1	7.1–**8.9**–10.2	27	48	87
Fries Mills, NJ	86	4.5–**4.6**–4.9	7.6–**8.3**–10.7	47	18	96
Batso, NJ	81	4.6–**4.9**–5.6	7.9–**8.7**–10.0	53	19	91
Great Egg Harbor R., NJ	76	4.6–**4.7**–4.8	7.8–**8.5**–9.0	26	50	88
Oceanville, NJ	90	4.3–**4.6**–5.2	7.4–**8.6**–10.4	53	28	88
Cumberland, NJ	86	4.5–**4.9**–5.3	7.4–**8.6**–9.4	42	18	94
Clermont, NJ	90	4.1–**4.5**–4.9	7.1–**7.7**–8.6	46	12	93
Mean	87	4.7	8.3	41	20	92

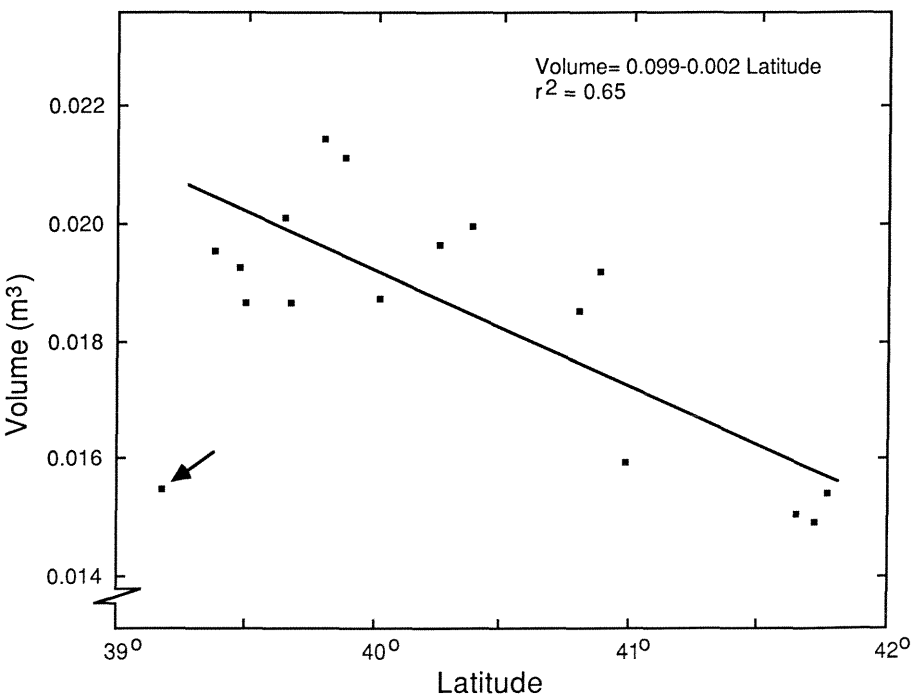

FIGURE 2. Relationship between mean bole volume and latitude of origin for pitch pine provenances from the Atlantic coast. Arrow indicates Clermont, a statistical outlier.

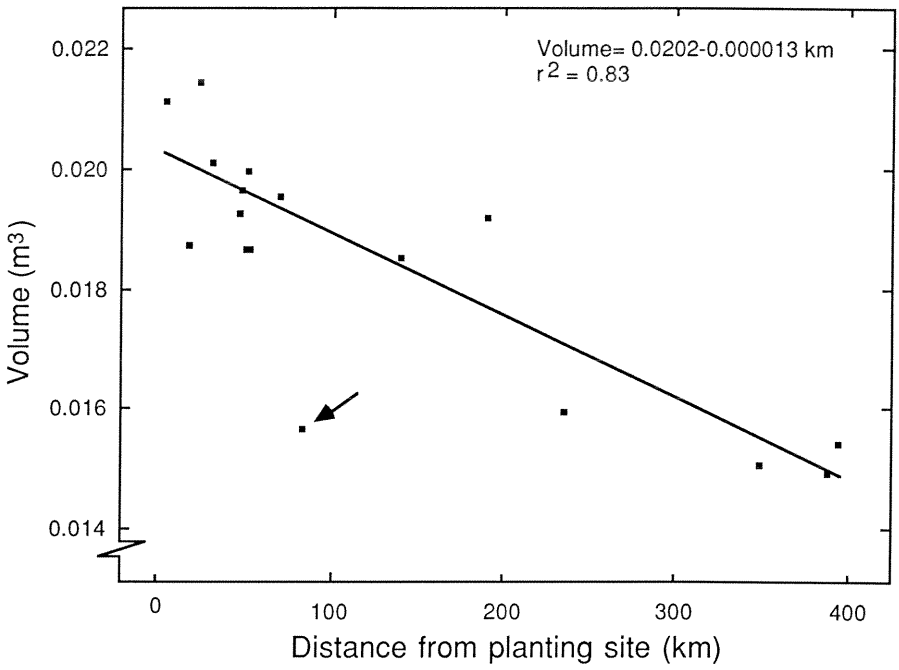

FIGURE 3. Relationship between mean bole volume and distance from the planting site for pitch pine provenances from the Atlantic coast. Arrow indicates Clermont, a statistical outlier.

source from the plantation has an $r^2 = 0.72$. Clermont deviates from the regression. Using Bliss's (1967) test it can be rejected as a statistical outlier, and the resulting linear regression has an $r^2 = 0.83$. Clermont pitch pine may differ from the other populations because of intergradation with pond pine (*Pinus serotina* Michx.). Smouse and Saylor (1973) considered pines on the Cape May Peninsula, the location of Clermont, to be a transition form between pitch and pond pines.

Variation within provenances was significantly different from zero in only a few cases. For volume, differences among families were significant at the 2.5% probability level for Commack, at the 5% level for Beach Hampton, and at the 10% level for both Batsto and Sagamore. This many cases of significance are almost equivalent to expectations due to chance alone for 17 separate tests. Fewer cases of significance were found for height and diameter.

Discussion

The correlation between bole volume on the one hand and latitude of provenance origin on the other follows a pattern common among pines of eastern North America; trees from southern seed sources tend to grow faster than those from northern seed sources (Ledig et al. 1976, Wells and Wakeley 1966, Williams and Funk 1978). The bole volume vs. latitude regression in this test confirms the conclusions drawn from a smaller data base at the New Lisbon breeding orchard (Kuser and Knezick 1985). It also provides confirmation for the results of a small 1966 provenance test at Green Bank, New Jersey in which trees of two southern New Jersey (Burlington County) seedlots outgrew those from Cape Cod, Massachusetts, and Cornwall, New York (Ledig and Fryer 1974). One of us (JEK) visited the Green Bank plantation in early 1985, and noted that the Burlington County trees had overtopped those from the other two sources. We also noted that the results at the test site in southern New Jersey are similar to those for the same provenances at two years of age in a Connecticut nursery (Ledig et al. 1976). In that test, the southern

provenances did best even though they were far from local, and the coefficient of determination for the regression of height on latitude was 83%.

Rather than a latitudinal cline, the data could be interpreted as a reflection of local superiority and an increasing lack of adaptation with increasing distance of the seed sources from the test site (Figure 3). This implies extremely fine adaptation, especially to climate. But, given the relatively weak climatic gradients within the New Jersey Pine Barrens, such a relationship would seem unlikely. In fact, little relationship is evident when the New Jersey provenances are compared in Figure 3; they all clump together except for Clermont. Correlation between volume and distance from the planting site for the New Jersey provenances alone (excluding Clermont) was not quite statistically significant ($r = -0.52$). Whether pitch pine provenances are closely adapted to climate at their origin or not, there is considerable overlap along the gradient sampled here.

The variation in cone serotiny is especially interesting because it can be related to frequency of serotinous-coned trees in the parental population (from Ledig and Fryer 1972). Frequencies in the parental population are somewhat higher than those in the provenance test. However, the correlation was high and positive ($r = 0.85$; Figure 4), further evidence that the serotinous cone habit is under genetic control, and confirming the earlier evaluation of serotiny in the field.

The low level of replication makes it difficult to be precise about the level of family variation. Nevertheless, the results are in agreement with nursery trials (Ledig et al. 1976) in which variation among families within these provenances was negligible. Conversely, results of isozyme analyses indicated that 97% of the genetic variation in a rangewide sample of pitch pine was localized within provenances (Guries and Ledig 1982). It is not obvious how to reconcile the apparent contradiction between results for the quantitative traits and the enzyme loci. Red pines (*Pinus resinosa* Ait.) and Torrey pines (*P. torreyana* Parry ex Carr.) have almost no quantitative variation within populations, and the low level of quantitative variation is paralleled by a near lack of detectable variation for isozymes (Fowler and Morris 1977, Ledig and Conkle 1983). Furthermore, species like Douglas-fir (*Pseudotsuga menziesii*

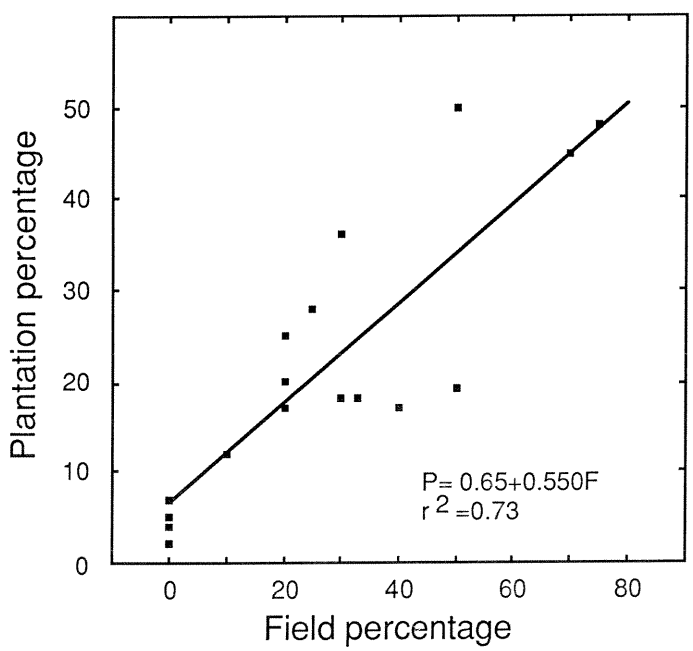

FIGURE 4. Relationship between frequency of cone-bearing trees with serotinous cones in a pitch pine provenance test and the frequency among parents at the site of origin.

[Mirb.] Franco) and loblolly pine that have high levels of variation for quantitative traits are also among the most variable on the isozyme level (Conkle 1981). In pitch pine, geographical patterns of variation for isozymes agree with those for seedling morphology and growth (Fryer 1987). Obviously, further study is needed to determine whether quantitative variation within populations of pitch pine is indeed low or whether the present samples are atypical. Sampled trees in all stands except Batsto and Great Egg Harbor River were in close proximity so their progenies may be related, resulting in an underestimate of the genetic variance.

The absence of variation for growth traits at the family level may suggest that a pitch pine improvement program should concentrate on selection among stands. However, in some provenances, the range in height and diameter was substantial; in Batsto, for example, the range among families was greater than that between provenance means.

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