progeny of eastern cottonwood with excellent form habit, which was established by controlled crossing. The exact origin of the parent trees could not be identified. They originated from one or more of the following states: Kansas, N. Dakota, and Ontario. In a six-year old clonal trial, one clone of this progeny had no mortality and showed a D.B.H. growth vigour, which was 198% of the mean of the standard clones 'Gelrica', 'Grandis', 'Harff', and 'Löns' (MOHRDIEK 1978). When compared with 'Gelrica' only, its D.B.H. was 246%.

For breeding of eastern cottonwood, the selection within open pollinated progenies seems to be less promising than selection within controlled crossings of parent trees from different provenances. In such crossings trees from fast growing provenances like Illinois or Ohio should be used; it is therefore necessary to test also the combining ability of trees of good suited and fast growing provenances. Parent trees with desired character performances should be selected for crossings in factorial and polycross designs. Using this approach, parent trees with a superior combining ability might be selected like e.g. mother tree "D60", which already has proven its high heritability in growth vigour and form habit (MOHRDIEK 1979). Furthermore, the crossing with other species like e.g. *Populus nigra* L. (MOHRDIEK 1979) and *Populus trichocarpa* TORR. et GRAY are promising as well (KOSTER 1976b, MOHRDIEK *et al.* 1979, STETTLER *et al.* 1980).

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Seventeen-year performance of Pinus flexilis and P. strobiformis progenies in eastern Nebraska

By D. F. VAN HAVERBEKE[1])

(Received 4th May 1982)

Summary

First and 17-year survival percentages were 32 and 15 for *Pinus flexilis* and 85 and 72 for *P. strobiformis* trees. Thirteen *P. flexilis* and 1 *P. strobiformis* progenies died during the test period. Surviving *P. flexilis* trees attained a mean height of 2.5 m; surviving *P. strobiformis* trees attained a mean height of 7.1 m. Differences in survival and heights were significant between species, but not among progenies within species. *Pinus flexilis,* except for low elevation, easternmost sources, is of little value in Great Plains plantings because of low survival and slow growth. *P. strobiformis* shows good potential for Great Plains use, if seed is collected at elevations of 2,300 m or higher in central Arizona and New Mexico. Genetic age-age correlations indicate that early selection is reliable.

Key words: Pinus flexilis, P. strobiformis, progeny testing, survival, height growth, genetic correlations.

Zusammenfassung

In einem Anbauversuch von *Pinus flexilis* und *Pinus strobiformis* in Nebraska wurden im Jahre 1964 49 Nachkommenschaften, darunter 28 aus Einzelbaumbeerntung, ausgepflanzt, nachdem diese im Jahre 1961 in einer Baumschule in East Lansing, Michigan, ausgesät worden waren. Bei *Pinus flexilis* überlebten im Alter 1 32% und im Alter 17 15%, bei *Pinus strobiformis* dagegen 85% im Alter 1 und 72% im Alter 17. Weitere 13 *P. flexilis* Nachkommenschaften und eine von *P. strobiformis* starben während der Untersuchungsperiode ab. Überlebende *Pinus flexilis* erreichten im Durchschnitt eine Höhe von 2,5 m; überlebende *P. strobiformis* eine Höhe von 7,1 m. Die Überlebens- und Größenunterschiede zwischen den beiden Arten waren also bedeutsam, nicht jedoch unter den einzelnen Nachkommen der Arten. Bei *P. flexilis* eignen sich östliche Herkünfte aufgrund geringer Überlebensprozente und langsamen Wachstums wenig für den Anbau in den Great Plains (Prärie). *P. strobiformis* kann für den Anbau in der Prärie gut verwendet werden, wenn die Herkünfte aus Höhen über 2300 m in Zentral-Arizona und New Mexico stammen.

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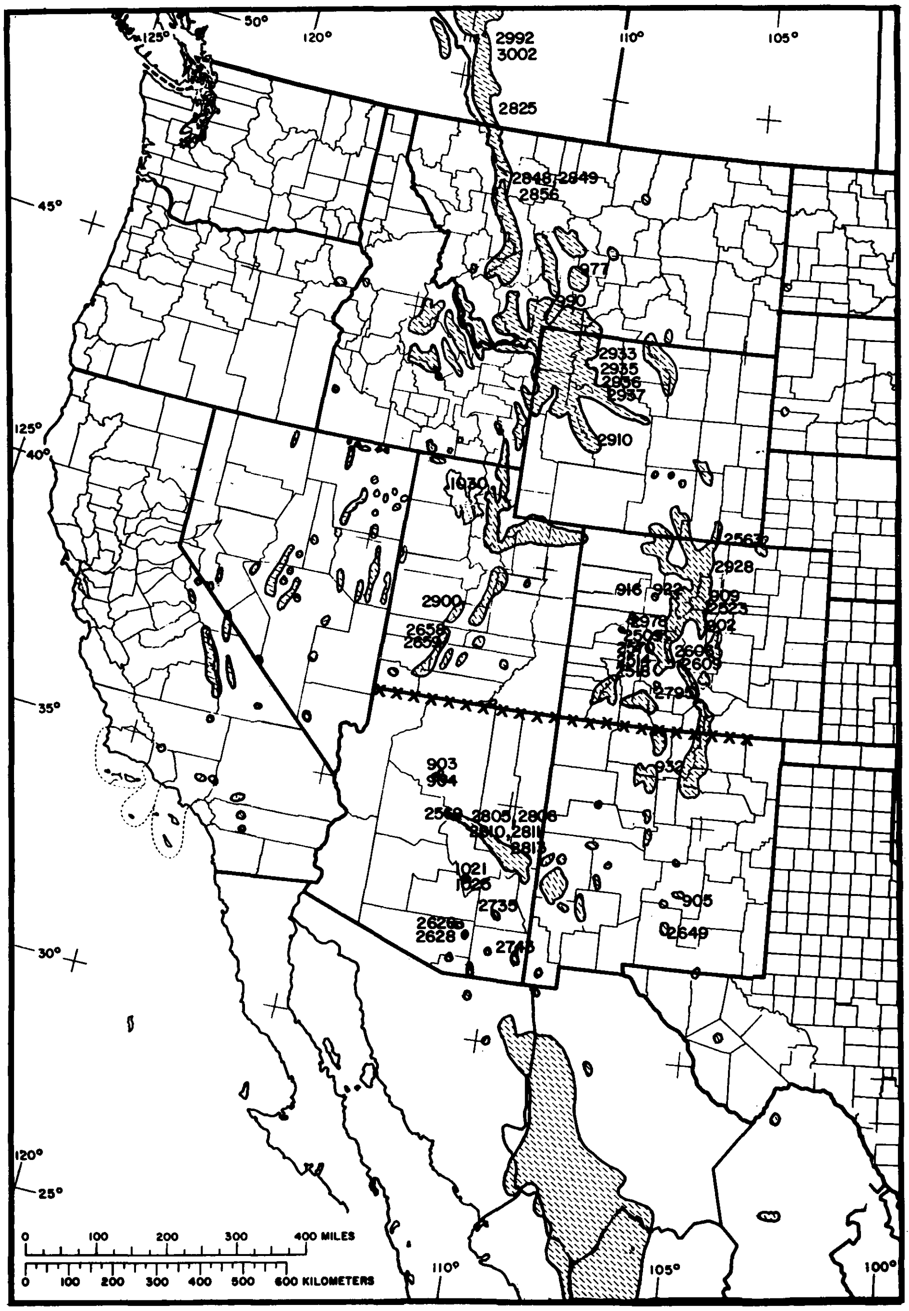

Figure 1. — Distribution of *Pinus flexilis* James (above hatched line) and *P. strobiformis* Engelm. (below hatched line).

Introduction

P. flexilis (limber pine) is native in the higher elevations of the Rocky Mountains of southeastern British Columbia and southwestern Alberta, Canada, southward to northern Arizona and New Mexico (Critchfield and Little 1966, Little 1971, 1979) *(Figure 1)*. Elevations vary from 1,525 m in Canada to 3,350 m in southern Colorado and northern New Mexico. *P. flexilis* also occurs through Nevada into southern California and in restricted areas of northeast Oregon (Peck 1947), southwest North Dakota (Potter and Green 1964), the Black Hills of South Dakota (Thilenius 1970), and southwest Nebraska (Gooding 1923). It is a slow growing species, usually less than 16 m tall at maturity.

P. strobiformis occurs in the mountains from southwestern Colorado, through New Mexico, the Trans Pecos of Texas, and east central Arizona then southward into Mexico. (Critchfield and Little 1966, Little 1971, 1979) *(Figure 1)*. Elevations vary from nearly 3,000 m in Arizona to approximately 3,500 m in Mexico. *P. strobiformis* trees are usually open-grown and attain heights of approximately 35 m.

The distributions of these two species are reported to overlap in southern Colorado, northern New Mexico, and northern Arizona (Steinhoff and Andresen 1971); and both ranges parallel the western edge of the Great Plains region of North America.

The native environments of these taxa are characterized by shallow and rocky soils, limited precipitation, high winds, evaporation stress, and temperature extremes. These species could be of value for environmental and landscape plantings and for Christmas trees in the Great Plains--a region with few indigenous conifer species (Wright *et al.*

Table 1. — Survival of 49 *Pinus flexilis* and *P. strobiformis* progenies in a 17-year eastern Nebraska test.

Species	Progeny[1] (no.)	Location	Trees planted[2] (no.)	Survival[2] (%)
P. flexilis	922	W. Cen. Colo.	8	0.0
	1030	N. Cen. Utah	7	0.0
	2509[d]	W. Cen. Colo.	6	0.0
	2510[d]	W. Cen. Colo.	5	0.0
	2514[d]	W. Cen. Colo.	4	0.0
	2518[d]	W. Cen. Colo.	4	0.0
	2825	S. Alberta	7	0.0
	2856[b]	N. W. Mont.	5	0.0
	2910	Cen. Wyo.	7	0.0
	2928	N. E. Colo.	7	0.0
	2937[c]	N. W. Wyo.	6	0.0
	2992[a]	S. Alberta	6	0.0
	3002[a]	S. Alberta	4	0.0
	916	N. W. Colo.	10	10.0
	2978	W. Cen. Colo.	9	11.1
	977	S. Cen. Mont.	8	12.5
	2900	W. Cen. Utah	8	12.5
	2523	N. E. Colo.	7	14.3
	2606[e]	E. Cen. Colo.	7	14.3
	2609[e]	E. Cen. Colo.	7	14.3
	2659[f]	W. Cen. Utah	7	14.3
	2658[f]	W. Cen. Utah	5	20.0
	2848[b]	N. W. Mont.	4	25.0
	2849[b]	N. W. Mont.	4	25.0
	2933[c]	N. W. Wyo.	4	25.0
	2795	S. Cen. Colo.	10	30.0
	990	S. Mont.	3	33.3
	2936[c]	N. W. Wyo.	6	33.3
	902	E. Cen. Colo.	8	37.5
	909	E. Cen. Colo.	6	50.0
	2563	S. E. Wyo.	8	62.5
	2935[c]	N. W. Wyo.	1	100.0
Sub-total and $\bar{x}$ %			198	15.1

Species	Progeny[1] (no.)	Location	Trees planted[2] (no.)	Survival (%)
P. strobiformis	2743	S. E. Ariz.	5	0.0
	2628[j]	S. E. Ariz.	8	37.5
	2735	S. E. Ariz.	8	37.5
	903[g]	N. Cen. Ariz.	5	60.0
	905	S. E. N. Mex.	8	62.5
	2810[h]	Cen. Ariz.	10	70.0
	2569	N. Cen. Ariz.	11	72.7
	2813[h]	Cen. Ariz.	9	77.8
	1021[i]	S. E. Ariz.	5	80.0
	2626[j]	S. E. Ariz.	5	80.0
	932	N. Cen. N. Mex.	46	80.4
	2811[h]	Cen. Ariz.	9	88.9
	904[g]	N. Cen. Ariz.	5	100.0
	1025[i]	S. E. Ariz.	5	100.0
	2649	S. E. N. Mex.	5	100.0
	2805[h]	Cen. Ariz.	5	100.0
	2806[h]	Cen. Ariz.	10	100.0
Sub-total and $\bar{x}$ %			159	71.7
Total and $\bar{x}$ %			357	40.3

[1]) a-j = like letters identify single-tree progenies collected at same site.
[2]) includes replacement seedlings.

1970, Heit 1973). The plantation reported on here is part of a test of these two species, for which seedling and 9-year performances were reported previously (Steinhoff and Andresen 1971, Wright *et al.* 1971).

Materials and Methods

Seedling stock originated from 60 sources of *P. flexilis* and *P. strobiformis* seed assembled from native stands throughout the species ranges in 1959—60 by Steinhoff and Andresen (1971). The seed was sown in an East Lansing, Michigan nursery in 1961, transplanted after 2 years into nurseries in Michigan and Nebraska, and field-planted as 2 + 1 stock in April, 1964. Forty-nine progenies were represented in the Nebraska test; 28 of them consisted of single-tree collections *(Table 1)*.

The plantation is located 90 km east of Lincoln, in southeast Nebraska, near the Missouri River (41° 00' N. latitude, 95° 54' W. longitude) on a silty clay loam soil derived from loess, with a gently sloping north facing slope. The elevation is 335 m. The growing season averages 170 days, and the mean annual precipitation is 760 mm of which approximately 75% falls during the growing season.

Seedlings were machine-planted in a randomized complete block design, in 1-tree plots, with 5 replications. Seedlings were spaced 1.8 m apart within rows which were 3.4 m apart. Excess seedlings were potted and kept in a shadehouse for replacing failed seedlings in 1965 and 1966.

Survival and tree heights were evaluated by Chisquare and variance analyses, respectively; and genetic age-age correlations (ages 3 to 17) were computed.

Results

Survival

Analyses based on as few as three trees obtained survival estimates with poor resolution. That coupled with the confounding influence of extensive seedling replacement, discouraged a formal analysis of survival. Chi-square analysis, however, indicated significant differences (P = < 0.05) in survival between species, but not among progenies within species *(Table 2)*.

Survival was very low within the 32 *Pinus flexilis* progenies during the first (1964) growing season. Only 32% of the *P. flexilis* seedlings survived; 85% of the *P. strobiformis* seedlings survived.

Mortality of *P. flexilis* seedlings exceeded mortality of *P. strobiformis* seedlings by 51% (65.7 vs. 15.1) during the 1964—1966 establishment period. Seedling replacement of *P. flexilis* was 44% during this 3-year period. All seedlings of 13 *P. flexilis* progenies and the southernmost *P. strobiformis* progeny (2743) died during this early period.

During the next 9 years (1967—1975) the rate of tree mortality within both species decreased. However, the number of *P. flexilis* trees that died during this period was about 2 1/2 times (23 vs. 9) as great as the number of *P. strobiformis trees* that died. From the 13th through the 17th year (1976—1980), 12 apparently healthy *P. flexilis* and 3 *P. strobiformis* trees died without obvious cause. *Dothistroma* needle blight *(Dothistroma pini* Hulbary) had been present in the plantation since 1971 and may have been a weakening influence on *P. flexilis;* it was not the cause of mortality.

Survival at the end of 17 years was 15% for *P. flexilis* and 72% for *P. strobiformis* trees, respectively *(Table 1)*. Survival percentages were similar among single-tree progenies from the same collection site.

Height

In 1962, the 2-year-old *P. flexilis* and *P. strobiformis* seedlings in the Michigan nursery ranged in height from 41 to 74 mm and 99 to 150 mm, respectively (Steinhoff and Andresen 1971). In 1966, at the end of the third field season

Table 2. — Chi-square analysis of *Pinus flexilis* and *P. strobiformis* survival at age 17.

Source of Variation	Chi-square x^2	d.f.	Probability of Larger $\chi 2$
Among progenies	178.0	46	P < .01
Between Species	125.8	1	P < .01
Within P. flexilis	21.3	29	.25 < P
Within P. strobiformis	30.9[1]	16	.05 < P < .01

[1]) Significance due to one *P. strobiformis* progeny with 0.0 percent survival (# 2743).

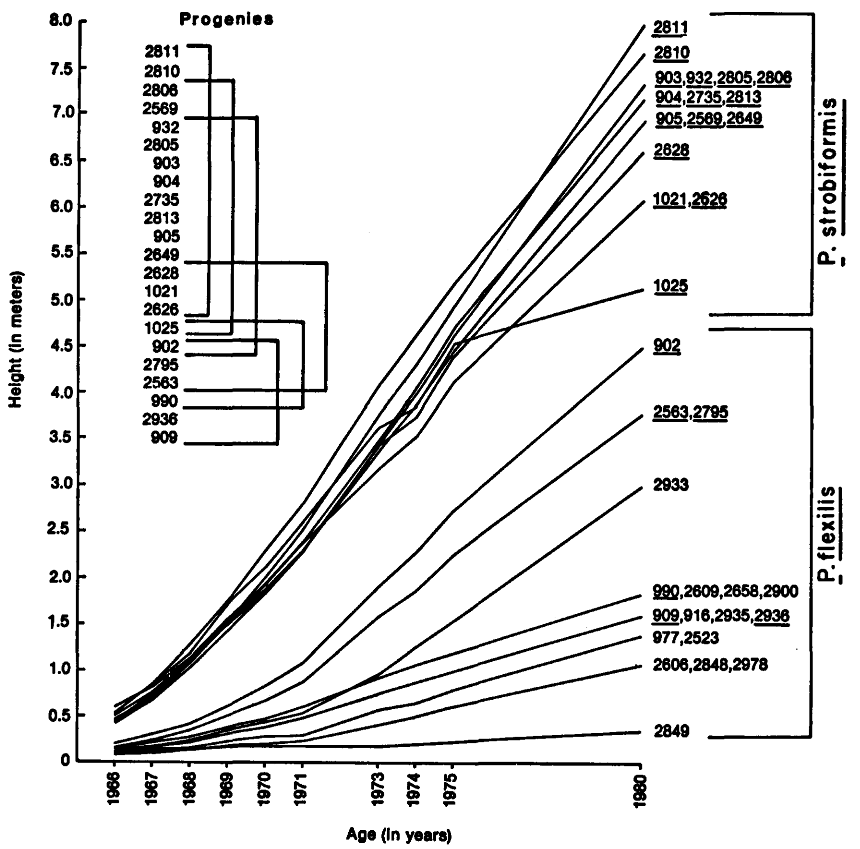

Figure 2. — Height growth of *P. flexilis* and *P. strobiformis* progenies during 17-year period in an eastern Nebraska plantation. (Tukey's multiple range test: means of progenies within same bracket do not differ at 5% level).

in Nebraska, *P. strobiformis* seedlings were more than three times as tall as *P. flexilis* seedlings (0.47 m) *(Figure 2)*. Throughout the test period, *P. strobiformis* trees maintained a growth rate advantage of more than 400% greater than *P. flexilis* trees. After 17 years in the field (age 20 from seed) *P. strobiformis* and *P. flexilis* trees averaged 7.1 and 2.5 m (118 and 46% of the plantation mean of 5.7 m), respectively. None of the 18 *P. flexilis* progenies exceeded the plantation mean height; 15 of 16 *P. strobiformis* progenies exceeded it *(Figure 2)*. There is significant separation among progenies for height growth; but distinctive differences are evident only between the best and the poorest performing ones *(Figure 2, Table 3)*. The principal separation is between species rather than among progenies within species.

Age-Age correlation

The consistency of progeny performances, as indicated in *Figure 2*, suggested a strong age-age relationship in progeny height growth. Analysis of the 34 progenies revealed a high and positive series of phenotypic and genotypic correlations for height, ages 3 to 17 *(Table 4)*.

Table 3. — Variance analysis of *P. flexilis* and *P. strobiformis* heights at age 17.

Source of Variation	df	Analysis of Variance M.S.	F	Significance of F
Progenies	21[1]	14683.557	11.729	.001
Replications	4	1485.932	1.187	.326
Residual	61	1251.950		
Total	86	4575.094		

[1]) Progenies with only one tree remaining alive at age 17 excluded from analysis.

Discussion and Interpretation

Survival

Pinus flexilis and *P. strobiformis* seedlings were the same age when planted in the field; however, *P. flexilis* seedlings were smaller and perhaps marginal for field planting on Plains sites. WRIGHT *et al.* (1971) reported that failure or low survival of northern *P. flexilis* progenies was probably related to small seedling size.

Progeny # 2563 from southeast Wyoming, with 5 of 8 trees surviving, shows the most promise among the *P. flexilis* progenies tested, and appears to be worthy of further consideration in the Great Plains on the basis of its survival *(Table 1)*.

Height

Extremely slow initial and subsequent growth characterized all progenies of *P. flexilis* from the high elevation sites in Colorado (909, 916, 2606, 2928, 2978), Utah (2658, 2900), Wyoming (2935, 2936) and Montana (977, 990, 2848, 2849). *P. flexilis* from low elevations in eastern and southern Colorado (902 and 2795) and from the high plains of southeast Wyoming (2563) had a slow growth rate initially, but growth increased to a moderately fast rate after approximately 8 field seasons.

At age 9, the northern, southwestern, and southeastern progenies included in the Nebraska test grew 19, 27 and 35 % as tall, respectively, as *P. strobiformis* (WRIGHT *et al.* 1971). This 17-year evaluation yielded percentages of 23,

Table 4. — Correlations among ages 3 to 17 for 34 progenies of *Pinus flexilis* and *P. strobiformis*.

Phenotypic/genotypic Age Correlations for Progenies

Age	3	4	5	6	7	8	10	11	12	17
3		1/1+	.99/1+	.98/1+	.98/1+	.98/1+	.96/.99	.96/.98	.95/.98	.92/.94
4			1/1+	.99/1+	.99/1+	.98/1+	.97/.99	.96/.98	.96/.98	.93/.94
5				1/1+	.99/1+	.99/1+	.98/.99	.97/.97	.97/.97	.94/.95
6					1/1	1/1+	.99/.99	.98/.98	.98/.98	.95/.96
7						.99/1+	.99/1	.98/.99	.98/.99	.95/.97
8							.99/1	.99/.99	.99/.99	.97/.97
10								1/1	1/1	.98/1+
11									1/.99	.99/1
12										.99/1

Age	Year	% Variation Due to progenies	C.V.	$\bar{x}$ Ht (m)
(3)	1966	56.8	.33	.38
(4)	1967	62.7	.32	.39
(5)	1968	68.2	.30	.88
(6)	1969	68.6	.30	1.21
(7)	1970	68.0	.30	1.51
(8)	1971	75.1	.25	1.89
(10)	1973	78.5	.22	2.80
(11)	1974	80.1	.20	3.22
(12)	1975	81.8	.19	3.72
(17)	1980	83.8	.17	5.72

24 and 57%, respectively; there was a 22 percent improvement in the performance of the southeastern racial progenies and no overall improvement within the northern and southwestern progenies.

Wright *et al.* (1971) reported the 9-year height growth pattern of *P. strobiformis* to be uniformly rapid; the current analysis confirms the continuance of this growth pattern but with no significant differences among *P. strobiformis* progenies. This suggests there is no height advantage in selecting one progeny over another for use in eastern Nebraska.

Separation of the *P. strobiformis* progenies into a northern series (903, 904, 932, 2805, 2806, 2810, 2811, and 2813) and a southern series (905, 1021, 1025, 2649, 2735, 2626, 2628), however, shows an average height advantage of 0.9 m (3 ft) in the northern series. Also, there was an average survival advantage of 14% in the northern series (*Table 1*). Neither the height advantage nor the increased survival percentage were significant, however.

Age-Age correlations

Analyses of height growth in other coniferous species indicate that early selection, on the basis of high phenotypic correlations of juvenile-mature height measurements, may not be reliable (Namkoong *et al.* 1972, Namkoong and Conkle 1976, and Franklin 1979). These researchers found periods of inconsistencies (low or negative correlations) in genetic age-age correlation displays. They attributed these periods of inconsistencies to changes in the internal environment of the trees (organizational and reproductive and other) and to external environmental factors (crown closure, stand competition and other). They suggest that selection in some of the species they analyzed should be delayed for as long as half the rotation age. Lambeth (1980), however, cites genetic tests in which genetic correlations remained high and positive, even through crown closure, with correlations as large and sometimes larger than their phenotypic counterparts. Although the data base in this evaluation is limited, the consistently high and positive phenotypic and genotypic correlations obtained from analyses of these data indicate that early selection within *P. flexilis* and *P. strobiformis* is feasible and can lead to greater efficiency in terms of genetic gain per year. It may be argued, however, that since there is no significant variance among progenies within species, the correlations cannot be interpreted.

Contrary to favorable experience with *P. strobiformis* in this test, commercial seed lots of unspecified Arizona origin previously grown in Nebraska, primarily for Christmas trees, have shown severe winter foliage injury in the nursery and have produced a high percentage of slow growing trees. These Arizona origins of *P. strobiformis* may have originated from low elevations in southern Arizona. *P. strobiformis* may be a very site specific species; therefore, for planting in Nebraska, it is recommended that: (1) *P. strobiformis* seed be collected from elevations of 2,300 m or higher in central Arizona and New Mexico to maximize height growth and to minimize the possibility of winter foliage injury; (2) *P. flexilis* seed be collected from low elevations in the easternmost part of its range; and (3) clonal seed orchards be established from plus trees selected at an early age from progeny plantations.

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Genetic Variation in Fruitfulness in a Loblolly Pine (Pinus taeda L.) Seed Orchard[1])

By R. C. SCHMIDTLING[2])

(Received 21st June 1982)

Abstract

In a loblolly pine seed orchard in South Mississippi, more than 50 percent of the variation in female flowering, cone production, and seed production, and about 40 percent of the variation in male flowering was attributable to genetic effects.

Although the more fruitful clones tended to produce an abundance of strobili every year, there were year × clone interactions for male and female flowering. This indicates that the genetic makeup of seeds collected from year to year may vary considerably, even if collected separately by clone.

Key words: Heritability, pollen, seed, *Pinus taeda* L., genotype × environment interactions.

Zusammenfassung

In einer *Pinus taeda* L. Samenplantage in Süd-Mississippi ließen sich bei der Variation im weiblichen Blühverhalten, der Zapfen- und Samenproduktion mehr als 50% und bei der Variation im männlichen Blühverhalten ca 40% auf genetische Effekte zurückführen. Obwohl die fruchtbaren Klone in jedem Jahr zu einer starken Blütenproduktion neigten, gab es bei den männlichen und den weiblichen Blüten eine Interaktion zwischen Jahr und Klon. Dies zeigt, daß die genetische Zusammensetzung gesammelter Samen trotz klonweise getrennter Ernte von Jahr zu Jahr beträchtlich variiert.

Introduction

Large differences often exist in fruitfulness between southern pine clones. This could be a serous problem in seed production if only a few clones in a orchard produce most of the seed. BERGMAN (1968) estimated that 2 of 15 clones produced over half of the seed in a loblolly pine *(Pinus taeda* L.) orchard. Others estimate that 20 percent of the clones produced 80 percent of the seed (North Carolina State University 1976). A less pessimistic estimate was provided by BEERS (1974) who found that the top 20 percent of clones in seed production produced 56 percent of the seed in a slash pine *(P. elliottii* ENGELM.) orchard. DANBURRY (1971) estimated that seed production could be increased by 50 percent and that seed cost could be reduced by one-third if only the most productive half of the clones available in a radiata pine *(P. radiata* D. DON) seed orchard in Australia were retained. He assumed that growth and fruitfulness were weakly correlated genetically. Inherent fruitfulness can be especially important, since as a general rule trees which are inherently unfruitful no not respond well to flower inducing treatments (BERGMAN 1968).

The inherent ability of the individual tree to flower is the most important factor influencing fruitfulness in southern pines (SCHMIDTLING 1974, SHOULDERS 1967). It is important to consider this variation in the experimental design of seed orchard studies. In several fertilizer experiments, from 33 percent (SCHMIDTLING 1974) to 56 percent (SCHMIDTLING 1975) of the total variation in fruitfulness was attributable to clonal effects, even though the treatment effects were large and significant. Broad-sense heritability estimates for fruitfulness of 0.50 for slash pine (VARNELL *et al.* 1967) and 0.40 to 0.70 for loblolly (SCHMIDTLING 1974) corroborate this observation.

Inherent variation in male flowering is also large, but the effects are seldom quantified. Male strobilus production is more difficult to assess than female strobilus production because catkins are numerous and do not persist after pollen is shed. BARNES and BENGSTON (1968) and SCHULTZ (1971) found strong clonal effects on male flowering in a slash pine fertilization and irrigation study. WEBSTER (1974) also observed strong clonal effects on male flowering in a loblolly pine orchard.

Most studies have shown that male and female flowering are not closely correlated. STERN and GREGORIUS (1972) found that the correlation between male and female flowering in Scots pine *(P. sylvestris* L.) is weak. SCHULTZ (1971) found a negative genetic correlation between male and female flowering in slash pine. This relationship between

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