Nine-Year Performance of Pinus flexilis and P. strobiformis Progenies in Michigan and Nebraska

By J. W. WRIGHT, F. H. KUNG, R. A. READ, R. J. STEINHOFF, and J. W. ANDRESEN[1])

Limber pine (Pinus flexilis JAMES) is a high-elevation 5-needled white pine species of the central and northern Rocky Mountains and of isolated mountains in the Great Basin. The main portion of its natural range extends from southern Utah and Colorado northward to southern Alberta *(Figure 1)*. There are isolated occurrences in Nevada, California, and northern New Mexico. It is slow growing and usually less than 16 meters tall.

Southwestern white pine, also known as Mexican white pine (P. strobiformis ENGELM. = P. flexilis var. reflexa ENGELM.) is a closely related species of Arizona, New Mexico, a small part of western Texas and parts of Mexico. It grows at medium elevations and reaches larger sizes, up to 35 meters tall. It is probably distinct from the Mexican species P. *ayacahuite* EHRENB.

The taxonomy of these species has been confused, but was clarified by the work of **STEINHOFF** and **ANDRESEN**[2]). They concluded that these taxa are distinct and are entitled to specific status. Results of the present experiment confirm the separation but leave open the question of specific versus varietal status.

Trees labeled P. flexilis but which should be classified as P. strobiformis on the basis of growth rate have been planted commonly as ornamentals in northeastern United States. Several have grown more rapidly in diameter and almost as fast in height as native conifers. They hold promise as Christmas trees because of their soft, dark blue-green foliage. They have been crossed successfully with Himalayan white pine (P. griffithii MCCLEL.) and the hybrids have grown rapidly. Thus, there is also the possibility that P. strobijormis can be involved in the development of fast growing timber types of trees.

The present experiment is a continuation of the work started by **STEINHOFF** and ANDRESEN, for the purpose of studying Christmas tree, ornamental, and timber possibilities of these species.

Materials and Methods

STEINHOFF and **ANDRESEN** assembled seed from many natural stands of both species (Figure 1). The stands were scattered from southern United States to southern Canada. The seed was sown in an East Lansing nursery in 1961 and the seedlings were grown there for 2 years. A detailed description of the methods and results of that experiment is contained in a publication by **STEINHOFF** and **ANDRESEN**[2]). The seedlings were transplanted to nurseries in southern Michigan and eastern Nebraska in 1963.

Two permanent plantations were established in southwestern Michigan and one in eastern Nebraska with 2-1 stock in April 1964. These plantations contain trees from 51 localities. All follow a randomized complete block design with 1-tree plots and a 2.2 X 2.2 meter spacing. Each plantation is surrounded by a single row of trees of a fast-growing Arizona origin. Details of the plantations are as follow.

W. K. Kellogg *Forest* near Augusta, *Kalamazoo* County, *Michigan:* — 20 replicates. Steep south and east slopes with a gravelly loam soil derived from glacial till. Trees planted in plowed furrows and sprayed immediately with simazine; furrows resprayed in 1965 and 1966 with directed sprays of amino-triazole and simazine.

Fred Russ Forest near Dowagiac, Cass County, Michigan: — 60 miles southwest of Kellogg. 10 replicates. Level ground with a sandy loam soil. Trees planted in 2-foot strips which had been sprayed with amino-triazole the autumn before planting and which were sprayed with simazine immediately after planting.

Horning State Farm near Plattsmouth, eastern Nebraska: — 5 replicates. Gently sloping north aspect site with a site-loam soil derived from loess. Trees planted in cultivated strips sprayed annually with simazine.

The climates are nearly similar at the two Michigan forests but the Kellogg site is more protected from wind

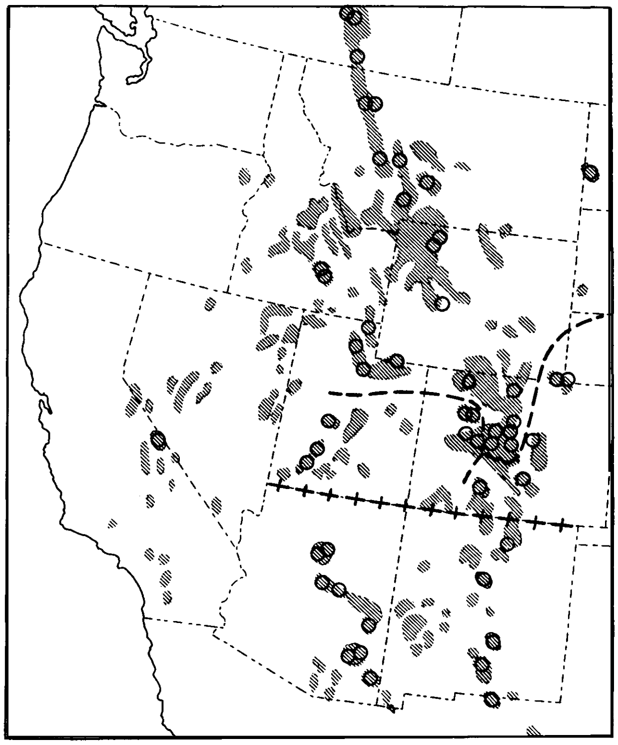

Figure 1. — Natural range (shaded) of Pinus flexilis (Colorado, Utah and northward) and P. strobiformis (Arizona, New Mexico, Texas) and location of seed collections used in the present experiment (circles). Dashes indicate approximate racial boundaries in P. flexilis; plusses indicate approximate boundary between species.

---

[1]) The authors are respectively Professor of Forestry, Michigan State University, East Lansing; Forester, Wyoming State Forestry Division, Cheyenne; Project Leader, Rocky Mountain Forest and Range Experiment Station, Lincoln, Nebraska; Research Geneticist, Forestry Sciences Laboratory of the U.S. Forest Service, Moscow, Idaho; and Chairman, Dept. of Forestry, Southern Illinois University, Carbondale. This study is part of the NC-51 project "Improvement of Forest Trees through Selection and Breeding" supported in part by regional research funds from the U.S. Dept. of Agriculture. We are indebted to W. A. LEMMIEN and J. N. BRICHT of the W. K. Kellogg and Fred Russ Forests for plantation measurements and maintenance. The original nursery experiment was supported in part by National Science Foundation Grant G-15879 and a grant from the American Museum of Natural History. Approved for publication as Journal Article No. 5110 of the Michigan Agricultural Experiment Station. — **KUNG** tranferred to Southerii Illinois University since the manuscript was submitted.

[2]) **STEINHOFF**, R. J. and J. W. ANDRESEN: Geographic variation in Pinus flexilis and Pinus strobiformis. Silvae Genetica 20, 1971. Additional information is contained in STEINHOPF's Ph. D. thesis submitted in 1964 to Michigan State University.

and received more effective weed control. The soils in the Nebraska plantation are apparently much more fertile than in Michigan. The growing season is of about the same length at all three sites but the precipitation/evaporation ratio is considerably lower in Nebraska than in Michigan.

In their nursery experiment, Steinhoff and Andresen maintained the separate identity of all single-tree progenies from the same stand. Their within-stand variances were low. Also the numbers of seedlings per half-sib progeny were very low in many cases. Therefore, in establishing the plantations, most stands were represented by bulked progenies. However, in the Kellogg, Russ and Horning plantations 14, 6 and 9 stands respectively are represented by single-tree progenies whose separate identity has been maintained. The number of separately identified single-tree progenies per stand varies from two to nine.

Height was measured at the end of the 1969 growing season at age 9 from seed. Foliage color was measured at age 7 at the Kellogg Forest in terms of grades 1 (yellow-green) to 8 (dark blue-green); the grades were defined in terms of live-tree standards. Winter injury was estimated as the percent (to the nearest 5 percent) of foliage which had turned brown before the start of new growth.

Results

After 6 years in the field, the trees varied from 10 cm to 2 m in height in the Michigan plantations, and from 15 cm to 2.5 m in Nebraska. The taller trees were well established and of good form. Many of the smaller in Michigan trees were almost hidden by weeds in spite of the weed control.

The differences between species were obvious, and almost every tree could be identified easily as belonging to one or the other on the basis of growth rate. Two progenies from northern New Mexico represented a zone of overlap; one from 2,100 m elevation was typical *P. strobiformis* and the other from 3,200 m elevation was typical *P. flexilis*. If introgression occurs, it has not been sufficient to make the northern New Mexico population intermediate.

In a single plantation there were differences of 10 to 20 percent in growth rate of single-tree progenies from the same stand, and larger differences among progenies of different stands from the same region. There were such differences in foliage color and hardiness, also. However, the error variances were so high that in no case were such differences significant statistically.

Pinus strobiformis was the faster growing species. It was essentially uniform from throughout Arizona and New Mexico although there was a hint (not significant statistically) of a cline in winter hardiness, southern Arizona trees suffering the most damage. The one Texas origin was enough faster growing to warrant special mention.

For convenience, *P. flexilis* was divided into three races. The northern race, extending from central Colorado and northern Utah northward to southern Alberta, was essentially uniform. It was impossible to detect any significant differences among stands or north-south trends. The single California origin was classified with the northern race. The southwestern race (western Colorado and southern Utah) was somewhat faster growing on the average, but the distinction was not clearcut. That race might equally well be considered as a portion of a cline extending from central Colorado westward through southern Utah. Or, the dividing line between northern and southwestern races might equally well be drawn to include more of the central Colorado sources with the southwestern population.

The southeastern race of *P. flexilis* is a more natural subdivision. It included six origins from the Wyoming-Nebraska border, eastern and southern Colorado, and northern New Mexico. These grew more rapidly and had bluer foliage than almost any other origins from farther north or west.

Mortality. — Mortality was much higher in northern than in southern origins (*Table 1*). This was probably related to the small size of northern seedlings, which were only 5 to 8 cm tall when planted and had very small root systems. They were unable to compete if there was slight weed competition.

Mortality was lower at Kellogg Forest that at Russ Forest 60 miles distant. The difference was probably due to the more effective weed control and greater protection from wind at the Kellogg Forest. The death rate was lower at both Michigan plantations than in Nebraska, in spite of the fact that complete weed control was practiced in the latter state. This difference is probably due to climate. Michigan, which is naturally forested, is much more humid and cooler than Nebraska.

In most pine and spruce experiments conducted at the same forests, most deaths occurred the first year or two after planting. However, both *P. strobiformis* and *P. flexilis* continued to succumb for 6 years after planting, and further mortality can be expected. Most delayed deaths involved trees which were not growing vigorously and were crowded by weeds. However, some seemingly vigorous trees died suddenly for no visible reason. Such late mortality was most pronounced in one seedlot of *P. strobiformis* from Cochise County in extreme southern Arizona. Those trees were no different from others in the species until three years after planting. Then, seemingly well established

Table 1. — Mortality by region of origin and plantation of *P. flexilis* and *P. strobiformis* planted as 2-1 stock in 1964.

Species and region of origin	Trees planted at			Cummulative mortality at					
	Kell. Mich.	Russ Mich.	Horn. Neb.	Kellogg Mich.		Russ Mich.		Horning Neb.	
				'64	'69	'66	'69	'68	'69
	number			*percent*					
P. flexilis									
Northern	143	113	132	20	38	67	72	71	81
Southwestern	297	80	36	20	31	40	48	44	66
Southeastern	260	50	26	17	27	30	30	36	53
P. strobiformis									
All except Cochise Co.	455	192	124	7	14	16	21	18	19
Cochise Co., Ariz.	20	10	5	20	45	30	80	60	80

Table 2. — Parental growth rate and progeny characteristics at age 9 of *P. flexilis* and *P. strobiformis* grown in Michigan and Nebraska.

Species and race or region of origin	Annual height growth of parents	Progeny height			Progeny foliage color	Progeny with forks	Winter foliage damage at Russ Forest
		Kell. Mich.	Russ Mich.	Horn. Neb.			
	cm.	*cm.*	*cm.*	*cm.*	*grade*	*% of trees*	*% of foliage*
P. flexilis							
Northern	4—15	27	25	30	2.5	0	2
Soutwestern	9—22	50	40	42	2.1	0	7
Southeastern	7—18	62	61	55	5.4	0	3
P. strobiformis							
Ariz., N. Mex.	25—32	140	113	158	6.7	3	23
Texas (1 origin)	29	165	153	—	6.2	21	18

Explanation of color grades: 0 = yellow-green, 8 = blue-green.

trees became yellow, suffered reduced growth rate, and died. Of 35 trees planted, 24 survived the first year, 11 survived 6 years and only 1 had normal color and growth rate after 6 years.

Growth rate. — At age 2 *P. strobiformis* averaged three to four times as tall as northern *P. flexilis*. This difference was accentuated with age, probably because of encroachment of weeds on the small trees. By age 9, *P. strobiformis* trees were five to six times as tall as some *Pinus flexilis* origins *(Table 2)*.

One *P. strobiformis* seedlot, from a single tree on the Texas-New Mexico border, deserves special mention because it was 10 to 30 percent taller at age 9 than origins from Arizona or New Mexico. The difference between it and any other single-tree progeny was significant (5% level) in both Michigan plantations. Peculiarly, that seedlot was one of the slowest growing in the species while in the nursery.

At age 9 there was almost a 2-to-1 difference in height between the fastest growing (southeastern) and slowest growing (northern) races of *Pinus flexilis* although even the fastest growing origins compared unfavorably with *P. strobiformis*. The tallest single tree was less than 1 m in height.

The reason for the very great species difference in growth rate is probably to be found in the elevational zones occupied by the two taxa. The *P. strobiformis* seed was collected at elevations from 2,300 to 2,900 m in Arizona and New Mexico; the *P. flexilis* collections from southern Colorado and southern Utah were made at elevations of 2,500 to 3,400 m. At the same elevation, the climates are generally much warmer and the growing seasons longer in Arizona and New Mexico than in the states immediately to the north. These differences are accentuated when the trees grow at lower elevations south than north.

Data on parental growth rates were inexact, having been derived from stands of widely varying ages and site conditions. Thus, only the most general comparison — between species — is possible. The *P. strobiformis* parents grew appreciably faster than the *P. flexilis* parents *(Table 2)*.

In the plantations, the current height growth of well-established *P. strobiformis* trees varied from 30 to 50 cm in the year. That is higher than in older trees in native stands. It is 10 to 20 percent slower than is expected of eastern white pine *(P. strobus* L.) at the same age on similar sites. However, the diameters of the largest trees were greater than usual for eastern white pine of the same height. Thus the timber possibilities of *P. strobiformis* in eastern United States remain debatable. Both species are known to be susceptible to white pine blister rust *(Cronartium ribicola* Fisch.).

Foliage color. — Foliage color was measured once at Kellogg Forest during the winter of 1967—68. Later observations indicate that the ratings have not changed appreciably and are approximately the same at the Russ Forest.

All *P. strobiformis* except the one unhealthy seedlot from Cochise County Arizona (data for that one included in *Table 2)* had dark blue-green foliage. That color, combined with the density of the needles, makes the species promising for Christmas tree and ornamental use.

The southeastern race of *P. flexilis* was almost as blue-green. However, most origins from other parts of the range were yellow-green, almost as if suffering from a nutrient deficiency. These color differences were also noticeable in the nursery.

Forking. — The data on tree form are almost meaningless for the slow-growing northern origins. In a tree which grew only 4 cm per year it was difficult to distinguish between a leader and a lateral branch which might grow vertically the next eyar.

The faster growing trees generally had one straight stem. The one exception was the Texas origin of *Pinus strobiformis* which had a tendency to produce forks as the result of simultaneous elongation of two nearly equal buds. In view of the small number of trees involved, the difference between the Texas and other origins in this respect was not significant statistically.

Winter hardiness. — After being grown for two years in protected seedbed, the seedlings were lined out for an additional year in a nursery which was fully exposed to strong winter winds. Winter burn was noted but not measured on several *Pinus strobiformis* origins after a winter in the transplant beds.

In the plantations, winter injury has been slight at the Kellogg Forest plantation which is on steep east and south slopes protected from the prevailing west winds during the winter. It was also slight in Nebraska. Conditions are more conducive to winter injury at the Russ Forest. The experimental plantation is on level land and is unprotected from winter winds. Damage was especially severe during the winters of 1966—67 and 1968—69. The northern and southern races of *P. flexilis* suffered little, possibly because the trees were so small as to be protected by the weeds. The southwestern race of *P. flexilis* suffered a slight amount of damage. Damage was appreciable only on *P. strobiformis* and in that species was worst on the origins from southern Arizona. Even on these, injury was limited to the needles; buds and cambium did not suffer.

Summary

Trees grown from seed collected in 51 natural stands of *Pinus flexilis* and *P. strobiformis* were grown in two Michigan and one Nebraska plantations. The species were distinctly different in growth rate. *P. strobiformis* from Arizona and New Mexico was uniformly rapidly growing, attaining average heights of 1.3 to 1.6 m at age 9 from seed; a single Texas origin grew faster. That species had dark blue-green foliage and suffered moderate winter injury at one site. For convenience, *P. flexilis* was divided into northern (n. Utah and N. Colorado northward), southwestern (sw. Colorado, s. Utah) and southeastern (Wyoming-Nebraska border, se. Colorado, n. New Mexico) races. The northern, southeastern and southwestern races grew about 20, 30 and 45 percent as tall respectively as *P. strobiformis*. Most *P. flexilis* origins were yellow-green and suffered no winter injury.

Wechselwirkung zwischen nicht allelen Genen bei Pappelhybriden

Von Gustav Vincent und † Miroslav Polnar[1])

Der Züchtungserfolg mittels Hybridisation setzt nicht nur eine sorgfältige Auswahl der Elternpaare, sondern auch eine gerichtete (direktionelle) Selektion der aus einzelnen Kreuzungen entstandenen Hybrid-Sämlingen voraus. In unserer früheren Studie (Vincent und Polnar 1970) haben wir der Auswahl von Elternpaaren Aufmerksamkeit gewidmet. Diese Studie soll einen Beitrag zur Bewertung der gerichteten Selektion von Hybrid-Sämlingen liefern.

Wir sind von der Heterogenität der Nachkommenschaften folgender Kreuzungen ausgegangen:

Populus generosa Kunovice × *P. 'serotina'* Praha 1,
Populus generosa Kunovice × *P. 'serotina'* Praha 2,
P. generosa Kunovice × *P. 'serotina'* Praha 3,
P. generosa Kunovice × *P. 'serotina'* Hradec Králové,
P. generosa Kunovice × *P. nigra* Stará Boleslav,
P. 'grandis' Kunovice × *P. 'serotina'* Praha 1,
P. 'grandis' Kunovice × *P. 'serotina'* Praha 2 und
P. 'grandis' Kunovice × *P. tacamahaca* Nemilkov.[2])

Da die Mutterbäume und die meisten Vaterbäume der aus diesen Kreuzungen entstandenen Hybrid-Sämlinge heterozygot waren, ging es bei ihrer ersten Nachkommenschaft um eine Generation, in welcher die Verteilung der ungleichen Phänotypen der üblichen Frequenz der einzelnen Phänotypen in der Generation F_2 der homozygoten Eltern entsprach. Die Aufspaltungen von Phänotypen ergeben — nach dem Mendel'schen Kombinationsgesetz — in den F_2-Populationen der homozygoten Eltern oder in den F_1-Populationen der heterozygoten Eltern bei dominanten Allelen und bei difaktorieller Veranlagung folgende Zahlenverhältnisse:

$$\mathrm{AaBb} \times \mathrm{AaBb} \rightarrow \left\{ \begin{array}{lll} 9\,\mathrm{A^-B^-} & /= 1\mathrm{AABB} & + 2\mathrm{AaBB} + 2\mathrm{AABb} + 4\mathrm{AaBb}/ \\ 3\,\mathrm{aaB^-} & /= 1\mathrm{aaBB} & + 2\mathrm{aaBb}/ \\ 3\,\mathrm{A^-bb} & /= 1\mathrm{AAbb} & + 2\mathrm{Aabb}/ \\ 1\,\mathrm{aabb} & & \end{array} \right.$$

Bald nach der Wiederentdeckung der Mendelschen Gesetze hat man Ausnahmen von diesen monogenischen Zahlenverhältnissen festgestellt. Eine freie Kombination der Elternmerkmale in der Nachkommenschaft kann dann erwartet werden, wenn Loci mit Genen, welche einzelne Merkmale bestimmen, in unterschiedlichen Chromosomenpaaren sich befinden. Die Koppelung der Gene (genes linkage) in einem Chromosomenpaar führt zu Abänderungen der erwähnten Zahlenverhältnisse. Man muß auch die Wechselwirkung zwischen Genen (genes interaction) von zwei oder mehreren Chromosomenpaaren in Betracht ziehen. Durch diese sog. nichtallele Wechselwirkung zwischen zwei Loci wird das Spaltungsverhältnis 9 : 3 : 3 : 1 dadurch geändert, daß zwei oder drei von vier spaltenden Typen einen gleichen Phänotypus besitzen. Wir können dann in der Nachkommenschaft nur zwei oder drei Typen unterscheiden, und wir addieren die Zahl der Individuen mit gleichem Phänotypus. Die nichtallele Wechselwirkung führt üblich zu folgenden Zahlenverhältnissen:

$$\begin{array}{r} 9 : 7 = 9 : /3 + 3 + 1/ \\ 13 : 3 = /9 + 3 + 1/ : 3 \\ 12 : 3 : 1 = /9 + 3/ : 3 : 1 \\ 15 : 1 = /9 + 3 + 3/ : 1 \end{array}$$

Bei der Kreuzung der ausgewählten und in der früheren Studie (Vincent und Polnar 1970) beschriebenen Pappelhybriden haben wir von allem die Wechselwirkung zwischen den nicht allelen Genen verfolgt. In jeder, durch die Kreuzung der gleichen Eltern erhaltenen Nachkommenschaft haben wir bei einzelnen Sämlingen folgende Merkmale charakterisiert:

die Farbe der Blätter bei ihrer Entfaltung,
die Farbe der Blätter nach abgeschlossener Entwicklung,
die Form der Blattspreite,
die Geradschaftigkeit des Stammes,
die Wuchsform.

In jeder Gruppe — Population von Sämlingen, welche dieselben Eltern besaßen, hat man die Verteilung der Phänotypen mit gleicher Blattfarbe, Blattform, Blattrand, Rindenfarbe, Stamm- oder Wuchsform festgestellt und dadurch die empirischen, nach diesen Merkmalen bestimmten Spaltungsverhältnisse ausgedrückt.

---

[1]) Die von Ing. Miroslav Polnar geleistete wissenschaftliche Arbeit in der Forschungsanstalt für Forstwirtschaft und Jagdwesen, Station Uherské Hradiště — Kostelany n/M. wurde am 14. August 1971 durch sein frühzeitiges Ableben unterbrochen.

Die Anschrift von Doc. Dr. Gustav Vincent DrSc.: Institut für experimentelle Botanik der Akademie der Wissenschaften, Brno, Poříčí 3b, Tschechoslovakei.

[2]) Nähere Angaben über die erwähnten Mutter- und Vaterbäume siehe G. Vincent und M. Polnar 1970.