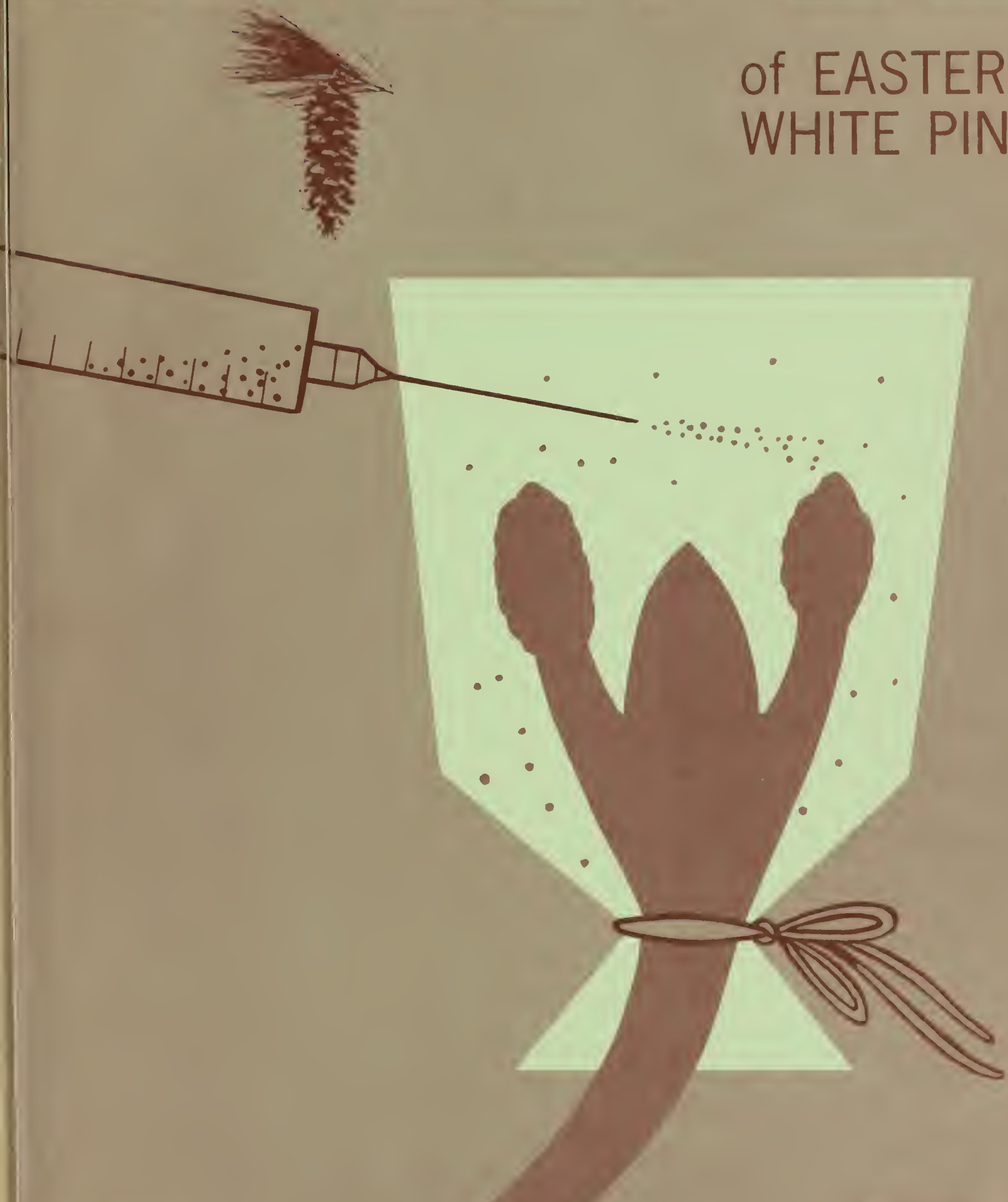
GENETICS of EASTERN WHITE PINE



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Genetics of Eastern White Pine

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INTRODUCTION

Eastern white pine (*Pinus strobus* L.) is one of the most widely ranging conifers of Eastern United States and Eastern Canada. It grows naturally from the Maritime Provinces of Canada west to Manitoba and Minnesota and south along the southern Appalachians to northern Georgia. There are several isolated distribution areas in the Central States.

A subtropical Mexican species has been described as *Pinus strobus* var. *chiapensis* Martinez or as *P. chiapensis* (Martinez) Andresen. It is morphologically similar to the more northern white pine, but is very different physiologically and is therefore not considered in this paper.

In the original forests, eastern white pine attained large sizes and was an extremely valuable timber tree. In modern forests, it is more often an old field tree which has grown to a diameter of 2 or 3 feet. Some of the most extensive stands are in the southern Appalachians, but originally they were most common in the Northeastern United States.

This species has been used successfully as an exotic tree in many temperate regions such as northern Italy, Romania, Great Britain, Japan, and New Zealand. In the United States it is planted commonly south of its natural range in parts of Indiana and Ohio, and grows well in parts of the Inland Empire where western white pine (*Pinus monticola* Dougl.) is native.

It grows naturally on a much wider range of site conditions (from swamps to well-drained sandy soils) than do other eastern American conifers. Considering this wide tolerance, one might expect the species to contain a large reservoir of local genetic variability (not indicated by experiment) and relatively slight development of site-adapted local races.

Despite interest by silviculturists in the species, genetic experimentation is recent. As of 1955, there had been good experiments on hybridization with other species and on clonal differences in blister rust resistance. Nearly all provenance and inheritance data are from more recent experiments.

SEXUAL REPRODUCTION

Flowering

For a general reference on this subject see Wright (1953). Female flowers are confined normally to the upper third of the live crown, and male flowers are borne on lower branches. In good years, many branches contain as many as 20 female flower buds which can be enclosed in a single pollination bag. Abundant female flowering may occur for 10 to 20 years before pollen production starts. That fact is important when planning seed orchards.

Mergen (1963a) reported female flowers on some 2-year-old hybrid (*P. strobus* X *P. griffithii*) seedlings brought indoors in midwinter and watered with a strong, complete fertilizer solution.

Buckingham (1963) reported exceptionally early flowering in the offspring of a particularly vigorous Maryland tree. One young tree produced 14 conelets in its fourth year; 19 trees produced a total of 92 conelets in the fifth year; and 28 trees produced a total of 257 conelets in the sixth year. The flowering trees were 4 to 10 feet tall.

Female flowering started at age 7 in Forest Service provenance test plantations. It was heaviest in central Pennsylvania and less heavy in southern

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Michigan and in Ohio. Northern origins produced the most flowers. In 1967 large cone crops were common on 10- to 15-foot trees in the Lake States.

Papers by Ahlgren (1956, 1962) and by Patton and Riker (1966) supply information about flowering of grafted trees. In northern Minnesota flowers were found on 4-year-old grafts, and flowering increased steadily (ages unstated) from 1954 until 1961. From 1959 to 1961 each flowering tree produced an average of seven cones. Light flowering occurred on 5- and 6-year-old grafts planted in Wisconsin.

Earliness of flowering was affected by age but not by species of understock. Scions placed on 16-year-old rootstocks flowered more heavily than did those grafted on 4-year-old rootstocks. Male flowers were produced earlier than female flowers on grafted trees, perhaps because the scionwood was collected from lower branches.

Seed Yields

In a series of cone collections made over the entire natural range in 1955, seed yields varied from 20 to 70 filled seeds per cone. For 200 southern Michigan trees sampled in 1967, the range was from 5 to 142 filled seeds per cone, and the range in seed weight was from 10 to 25 milligrams.

Climate or site can have a large effect on seed yield. In Philadelphia eastern white pine grows well, but it is not native. Cones mature 3 weeks earlier than in native stands in the nearby Pocono Mountains, and they are 10 to 20 percent shorter than in any native stands. In the city the average open-pollinated yield during a 10-year period was 1.1 filled seeds per cone; the average and maximum control-pollinated yields were 2.3 and 5 seeds per cone, respectively. Similar techniques yielded 20 to 40 filled seeds per cone in native stands. A low yield of 8 filled seeds per 200 cones was also recorded from an isolated native stand in Indiana.

Controlled Pollination Techniques

More details may be found in papers by Wright (1959) and by Wright and Gabriel (1957). Synthetic sausage casings have been used for most controlled pollinations. They are normally applied around clusters of current year's branchlets when the new growth is 4 to 6 inches long. At that time the female buds, borne terminally, are about one-fourth inch long and are enclosed in scales. This is done in late May or early June in the central part of the range.

Female strobili are ready for pollination 1 to 2 weeks later, when they are about one-half inch long. They are apparently at maximum receptivity when scales and bracts of the conelets are of equal length and there are noticeable spaces between conelet scales. This stage occurs 3 weeks later in northern Michigan than in southern Michigan, but it is reached within a 2- or 3-day period by all trees of the same stand. On a single tree most female strobili become receptive within a 2-day period and remain receptive for 3 or 4 days.

Pollen is shed at the same time female strobili on the same tree are receptive. It is easiest to collect nearly open catkins and let them dry inside for 1 or 2 days. The only sure way to force pollen by several days is to graft a few months ahead of time and maintain the grafts in a greenhouse; it can be forced by 1 day by placing cut branches in water a few days ahead of time.

Synthetic sausage casings become very hot and often cause damage to enclosed needles, but not to developing strobili (unless they touch the bag). Both the cone and seed set may be increased if such bags are left in place 15 months from pollination until cone maturity.

Pollen stored in a refrigerator at 25- to 50-percent relative humidity remains viable for several weeks. It will germinate *in vitro* but will not induce good seed set after a year's storage. However, 1-year-old pollen stored at 0° F. resulted in 50 to 80 percent as much sound seed as fresh pollen.

Immediately after pollination, the pollen germinates and the pollen tube grows slightly. Fertilization is delayed approximately 12 months (until June 17 to 23 as Wooster, Ohio, in 1965 and 1966). Seed coat formation starts before fertilization, apparently as the result of a stimulus supplied by germinating pollen. Thus, large, empty seeds may develop without fertilization, and the total number of seeds is not a good index of success in hybridization.

Cone insects are especially damaging to eastern white pine and cause greater variations in cone production than do physiological disturbances within a tree. Many trees flower heavily year after year but develop cones only when insect damage is low. Thor of Tennessee, Kriebel of Ohio, and the author of this review have all experienced 99-percent mortality from flower to cone.

A beetle, *Conophthorus coniperda* (Schw.), causes most damage (Henson 1966). Presumably oviposition occurs during the first year. Young second-year conelets contain adult beetles and soon drop. Moths (*Dioryctria* sp.) attack late enough during the second growing season to permit cones to reach 75 to 100 percent of normal length, but not to produce filled seeds. Moth damage is usually obvious but not serious.

Cones ripen from mid-August in the South to mid-September in the North. The date may vary as much as 2 weeks from year to year. Once mature, cones change color and open quickly, making it necessary to collect them early or to bag them prior to maturity. A many-year phenological record and squirrel activity are good guides to the proper collection time. Specific-gravity recommendations have not been formulated.

Empty and full seeds differ in specific gravity but not in color. They can be separated by flotation in absolute alcohol and air sorters. Separation is more difficult than in most hard pines because the differences in specific gravity are small.

VEGETATIVE PROPAGATION

Rooting experiments started more than 30 years ago. Despite trials at various times of the year, with and without hormones, and in various rooting media, eastern white pine remains difficult to root. Deuber's (1942) paper remains a good source of information.

The age effect is pronounced. Cuttings made from young seedlings can be rooted relatively easily, but few experiments with trees more than 15 years old have been successful. There are also pronounced differences among trees; some root much better than others.

Single needle fascicles, even from older trees, can often be rooted. Generally they fail to develop terminal buds, and the method remains of academic importance.

Most early grafting experiments were made in a greenhouse on potted understocks, with good success. Patton and Riker (1966) reported that such grafts suffered heavy mortality and abnormal growth (crooked leaders, thin crowns, etc.) in later years. They prefer field grafts made just prior to the growing season on understocks which have been grown in place for several years. They used conventional tongue or cleft grafts and protected their scions with polyethylene and brown paper bags. Most such field grafts have grown straight but have thinner crowns than seedlings. Their differences in form may have been topophytic rather than due to the grafting method used.

In northern Minnesota, eastern white pine has been used as a scion on rootstocks of *Pinus resinosa*, *P. banksiana*, *P. sylvestris*, *P. mugo*, and *Abies balsamea* (Ahlgren 1966). The *strobus*-on-*mugo* grafts remained healthy longer than 5 years. The other combinations survived 1 to 5 years.

Eastern white pine was used successfully as a rootstock for scions of *Pinus peuce*, *P. koraiensis*, *P. cembra*, and *P. griffithii*, but not for scions of *P. resinosa*.

GENETICS AND BREEDING

Geographic Variation Pattern

Experimentation.—There are several records of eastern white pine plantations established with nonlocal seed. Lake States trees were used in the famous Biltmore plantations in North Carolina; North Carolina seed was used in a West Virginia plantation; out-of-State seed was used in some New York plantations. These examples, up to 80 years old, have grown well.

P. R. Gast's replicated provenance test at the Harvard Forest (described by Pauley *et al.* 1955) was the first to compare different seed sources. It included trees from several parts of New England. Heavy weevil injury precluded exact assessment of growth differences.

The *Forest Service rangewide provenance test* is the present source of most provenance information. Most of the seed was collected in 1956 and sown in 1957. Each seedlot was from several average trees in each of 26 natural stands. The nursery trials were conducted in New York, New Jersey, Maryland, North Carolina, and Wisconsin. Most were replicated but only the New Jersey data have been published. A large series of permanent test plantations were established from 1959 to 1962 by the Forest Service and cooperators. Most plantations contain only 15 or 16 of the 26 seedlots and were established with 2–0 stock. All plantations followed a randomized-block design with 4 to 25 replications and 1-, 4-, 25-, or 81-tree plots. Weed control varied from none to complete elimination of grass competition for 3 years, and post planting care varied from none to very intensive. Results of this experiment have been published by Santamour (1960), Wright *et al.* (1963), Sluder (1963), Fowler and Dwight (1964) and Funk (1965). In preparing this review, the author relied on those papers and on more recent unpublished data from many sources.

This Forest Service provenance test provides much valuable information on experimental procedure. The small-plot plantations have provided 95 percent of the information. The most reliable

TABLE 1.—*Origin of* Pinus strobus *seed for the Forest Service provenance study*

Number, State or Province, and county of origin	North lat.	East long.	Elevation	Average temperature		Length frostfree season	Annual precipitation
				Jan.	July		
	°	°	*Feet*	° *F.*	° *F.*	*Days*	*Inches*
1–GEOrgia [2], Union	34. 8	84. 0	2, 450	40	73	190	71
2–N CArolina, Transylvania	35. 2	82. 6	2, 120	39	72	170	61
3–TENNessee, Greene	36. 0	82. 8	2, 250	39	76	190	42
5–W VirginiA, Greenbrier	38. 0	78. 8	2, 600	32	72	150	39
6–PENNsylvania, Monroe	41. 1	75. 4	1, 800	24	66	130	49
9–PENNsylvania, Clearfield	40. 8	78. 5	--------	28	72	140	44
10–N York, Ulster	42. 0	74. 0	--------	25	72	160	39
12–N York, Franklin	44. 4	74. 2	1, 600	16	65	120	37
13–MASSachusetts, Worcester	42. 3	72. 4	1, 250	22	69	150	43
14–MAINe, Penobscot	44. 9	68. 6	150	18	68	130	40
15–IOWA, Allamakee	43. 3	93. 0	1, 000	21	73	140	33
16–OHIO, Ashland	40. 8	82. 2	1, 000	28	73	160	36
18–WISconsin, Forest	45. 7	88. 5	1, 500	11	67	120	29
19–MINNesota, Cass	49. 4	94. 7	1, 300	7	69	120	22
20–N Scotia, Lunenberg	44. 6	64. 6	150	20	65	--------	55
21–N Brunswick, Sunbury	45. 9	66. 8	200	18	66	140	40
22–QUEbec, Quebec	46. 8	71. 0	550	10	67	--------	42
23–QUEbec, Pontiac	47. 5	77. 0	1, 000	1	--------	--------	--------
24–ONTario, Norfolk	42. 7	80. 5	750	24	70	170	32
25–ONTario, Algoma	46. 2	82. 6	650	10	64	130	30
28–MINNesota, Lake	48. 1	91. 3	1, 300	13	64	140	26
29–MICHigan, Houghton	44. 3	84. 8	600	15	65	140	28
30–VirginiA, Pulaski	36. 9	81. 0	2, 400	35	73	170	43
31–WISconsin, Suak	43. 0	89. 5	1, 000	18	74	170	28
32–MICHigan, Newaygo	47. 1	88. 7	--------	22	71	140	31
35–MINNesota, Washington	45. 2	92. 8	--------	12	72	140	30

data (that is, the lowest error variance) were supplied by a plantation established with 2–1 seedlings and given intensive weed control. Replication was not continued from nursery to field plantation; it should have been because size differences due to nursery treatment are still evident at age 11. Replacement of first-year mortality was not successful; if anything it has clouded some of the growth data.

Genys (1968) started the *University of Maryland rangewide provenance test* in autumm 1962. He intensified the range sampling, using seeds from 99 natural stands. His seed was shared with two other States and two foreign countries. The permanent plantations, following randomized block designs with small plots, were established in 1965 and 1966. To date only nursery data are available.

The *Yale physiological experiments* (Mergen 1963b) used eight provenances from North Carolina to New Brunswick. The seedlings were grown outdoors for 3 years, potted, and subjected to varying temperature or day-length conditions for a few months. The trees were not replicated in the nursery, and some results may reflect nursery conditions as much as experimental treatment.

The *Michigan State University half-sib progeny tests* were started in 1960. These include seed collected from 123 native Michigan trees and eight permanent plantations established in 1965 or 1966. To date these have supplied more provenance than inheritance data.

Four other experiments deserve brief mention. Pellati (1967) reported on a 6-year study of progenies grown from seed collected in nine unknown-origin Italian plantations. The NC–51 Southern Appalachian provenance study, including 177 stand- or single-tree progenies collected from Maryland south, was started in 1965 and includes permanent test plantations in several Central States and a few foreign countries. INCEF, the forest experiment station in Romania, started a rangewide provenance test in 1967. At Yamabe, Hokkaido, the University of Tokyo has single plots of several northern provenances.

Phenotypic variation in cone and seed traits.—Many measurements were made on the cones and seeds collected for the Forest Service provenance test. There were statistically significant differences

[2] Two sets of abbreviations are used in this manuscript: 1. All capital letters for abbreviations of States for the seedlots as used in the computer study; and 2. Standard GPO abbreviations for States for the plantation numbers.

between trees from the same stand but not between stands in cone length, seed weight, and seed color.

Stratification requirements.—Mergen (1963b) tested seed from three localities. He stratified the seed at 35° to 40° F. and varied:

Length of stratification period—0 to 84 days;

Germination temperature—55°, 72°, and 90° F. Germination was very poor at 55° F. and most complete at 72° F. At the 72° F. temperature New Hampshire seed needed little stratification, 80-percent germinating after any length stratification period. North Carolina and New Brunswick seed, however, germinated well only if stratified more than 28 days.

Mergen also found that the North Carolina seed germinated very poorly at 90° F., with or without stratification. At the higher temperature there was a positive correlation between length of stratification (up to 42 days) and germination percentage.

Fowler and Dwight (1964) used 11 Forest Service seedlots. They stratified the seed for varying periods and germinated it at 65° to 75° F. All seedlots benefited by stratification, but to varying extents. The all-seedlot averages were:

Length of stratification, *days*	0	10	20	30	40	50	60
Germination, *percent*	13	31	48	52	61	68	75

Four northern origins (14–MAIN, 18 WIS, 20–N S, 25–ONT) germinated 11 to 43 percent with no stratification and 85 to 95 percent after 60 days' stratification. On the other hand, four southern origins (1-GEO, 3-TENN, 6-PENN, 16—OHIO) germinated only 1 to 5 percent with no stratification and 40 to 78 percent if stratified 60 days.

In the North, selection probably favored types with low stratification requirements because temperatures are just above freezing for a relatively short time in late autumn and early spring. Northern winters are much too cold to permit after-ripening. In the South, seed which ripens in August is subjected to several alternating short periods of near-freezing temperatures and warmer weather. If seed had too short a stratification requirement, it could germinate too early and be killed by later frosts.

Mortality after transplanting.—In the Forest Service experiment, mortality was negligible in all nurseries and in all plantations after the first year. However, some first-year losses in plantations were serious. They varied from 5 to 43 percent among plantations and from 0 to 70 percent among seedlots within a plantation.

Such losses could be traced to variations in nursery practice and weed control in the case of two Michigan plantations. That was true also of a Wooster, Ohio, plantation containing trees shipped from a Maryland nursery (average mortality 4 percent) and from a North Carolina nursery (average mortality 44 percent). Where replacement with 2–1 stock was practiced, replacement mortality was only 11 to 50 percent as high as mortality of the original 2–0 stock.

Probably it is best to say that no genetic differences in survival ability were proven and that better care could have minimized losses.

Effect of nursery culture on subsequent growth.—Published 2- and 3-year provenance data for eastern white pine are based upon replicated nursery tests and therefore provide valid genetic data. (Seed-size corrections were made when necessary.)

All test plantations in the Forest Service experiment are replicated, but in each case planting stock for a single provenance was lifted from *one* part of a seedbed. This means that, even with replication, first-year mortality and early growth of all trees of a seedlot in a plantation were influenced by common environmental factors. We commonly assume that nursery effects disappear quickly, but that may be wrong. Kriebel used stock from two different nurseries at Wooster, Ohio. The large difference seen at planting time was still evident at age 10. Lemmien planted the largest tree in the first position in every plot in his Augusta, Michigan, plantation. Eight years later the first tree remained largest in 34 percent of the plots, compared with 25 percent if initial-size effects had disappeared (the difference is significant).

This affects interpretation of the provenance data. Within any given plantation, statistically significant differences between origins may not have a genetic basis. Between-provenance comparisons are most valid when they involve data from several plantations and different nurseries. Fortunately, most data in tables 2, 3, and 5 are of this type.

Changes in relative growth rate with age.—At the time of this writing, the Forest Service provenance study is 11 years old from seed. Eleven plantations were measured frequently enough to provide data on changes in relative growth rate. At most central-southern test sites, height measurements taken in different years are significantly correlated (table 2). Most origins did not change rank by more than one or two positions since outplanting. The few large (by more than 3 positions) changes in rank are as follows:

Plantation 2, North Carolina. Between ages 7 and 10, seedlot 16-OHIO changed from average to tallest.

Plantation 4, Pennsylvania. Between ages 6 and 10 there was an increase in relative growth rate for seedlots 9–PENN, 10–N Y, 13–MASS; a decrease for 2–N C, 5–W VA, 22–QUE, 24–ONT and 30–VA.

Plantation 5, Kentucky. Between ages 3 and 8 there was an increase in relative growth rate for seedlot 25–ONT; a decrease for 23–QUE and 30–VA.

Plantation 13, southern Michigan. Between ages 3 and 10 there was an increase in growth rate for seedlots 6–PENN and 24–ONT; a decrease for 3–TENN, 13–MASS, and 28–MINN.

Plantation 14, southern Michigan. Between ages 6 and 10 there was an increase in growth rate for seedlots 14–MAIN and 24–ONT; and a decrease for 1–GEO, 13–MASS, and 28–MINN.

Five of the decreases in relative growth rate with increasing age involved southern Appalachian origins grown at North-Central test sites. But seven decreases involve northern origins grown at North-Central test sites; therefore, the pattern is not clearcut.

TABLE 2.—*Rank correlation coefficients, based on provenance means, showing the relations between relative heights measured at different ages*

Correlation is for ages (from seed)	Plantation number and State										
	1 Ga.	2 N.C.	3 Va.	4 Pa.	5 Ky.	6 Ohio	7 Ohio	8 Ohio	11 Ill.	13 Mich.	14 Mich.
2 and 3						.73					
8						.49			.58		
10									.60		
3 and 4					.97		.87	.69			
6								.61		.85	.85
7	.94		1.00		.90	.91	.85	.78			
8					.86	.87	.78	.79			
10										.70	.74
4 and 7					.94		.93	.77			
8					.91		.87	.79			
5 and 7	1.00	.99	.83								
10										.86	.77
6 and 8				.94				.80			
10				.90						.95	.86
7 and 8					.98	.90	.95	.96	.99		
8 and 10				.95							

TABLE 3.—*Changes in relative height, expressed as percent of plantation mean, with increasing age at the Fred Russ and W. K. Kellogg Forests (Plantations 13 and 14) in Southwestern Michigan.* [1]

Seedlot number	Relative height							
	Nursery, Age 3	Fred Russ Forest				Kellogg Forest		
		Age 4	Age 5	Age 6	Age 10	Age 5	Age 6	Age 10
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
1–GEO	114	128	123	113	111	118	117	102
3–TENN	130	112	113	116	110	133	132	114
6–PENN	111	101	117	134	138	108	115	109
24–ONT	106	117	115	113	117	103	106	110
9–PENN	121	115	120	122	112	114	109	107
10–N Y	106	106	105	105	106	104	107	108
13–MASS	122	124	115	108	99	118	107	104
20–N S	67	71	62	71	78	70	73	89
12–N Y	88	85	78	95	98	91	96	99
25–ONT	101	95	103	101	97	105	104	105
28–MINN	104	83	92	84	88	96	93	91
21–N B	76	78	82	90	97	75	80	92
14–MAIN	79	92	82	80	81	89	93	93
29–MICH	100	74	89	91	89	77	83	89
19–MINN	66					76	76	87
Mean height, feet	0.7	0.9	1.4	1.9	6.2	1.6	2.5	10.5

Ages shown are from seed. Seedlots are arranged in decreasing order of average height growth in Plantations 1 to 16.

Detailed data on changes in relative growth rate with time are presented for two Michigan test plantations (table 3). At Fred Russ Forest, seedlot 6–PENN changed from average at age 4 to nearly 40 percent above average at age 10, but most other differences diminished. At the W. K. Kellogg Forest, 60 miles northeast, there was a marked diminution in the range of variation. In 1961, seedlot 3–TENN was about 90 percent taller than 20–N S; in 1966 it was only 28 percent taller. Again, interpretation is not clear. The Kellogg Forest plantation differs from most others in its northern location, rapid growth, and low error variance. The diminution in superiority of Tennessee trees may be owing to the northern test location. Or as other plantations reach a period of rapid height growth, growth differences may become smaller.

The situation is very different for four plantations in the northern Lake States and Ontario (Nos. 17 to 20). They were established with stock grown in northern nurseries; however, southern Appalachian origins were largest at outplanting time. They soon lost this superiority, presumably as a result of winter cold. Consequently, there is little relation between nursery and later performance (King and Nienstaedt 1968).

Height growth in central and southern plantations.—The growth-rate pattern was similar in 16 central and southern plantations of the Forest Service provenance test (table 4). Absolute height varied considerably among plantations because of differences in site and age of measurement. But the same origins tended to grow fastest or slowest at all 16 sites. The high between-plantation correlations, most of them between r = .70 and .90 (table 5), makes this apparent.

The author calculated an "index of similarity" for each central or southern plantation by averaging its correlations with the other 15 plantations. Contrary to expectation, plantation 16 (southern Ontario) had the highest similarity index (.84) and seemed to give the most representative data. At the other extreme, plantations 1, 2, 3, 4, and 7 (Ga., N.C., Va., Pa., and Ohio) produced the least representative data (similarity indexes of .63 to .73).

In the Forest Service study the tendency for certain origins to grow either fast or slow at all sites was much stronger than the tendency for a local origin to surpass others. Among the several examples which could be quoted, one is particularly striking. In the Iowa plantation, the Iowa source grew the least.

Genys' (1968) 2-year height data for 99 origins grown in Maryland confirm geographic trends evident from the Forest Service data (table 6). By inference the same may be said of his material tested for 1 year in Pennsylvania, Germany, and Australia because internursery correlations were significant at the 1-percent level.

The relation between growth and climate at the place of origin was obvious. Trees from the southern Appalachians grew fastest; there the winters are warm and the growing seasons are long. Emphasis on such correlations obscures an interesting part of the variation pattern, however. Trees from four stands in southern Virginia, with its mild climate, grew at average or below-average rates. Trees from three stands in southern Ontario were among the leaders in growth rate. That particular section of Ontario, a peninsula projecting into Lake Erie, has a mild climate although not so mild as found in West Virginia or Virginia.

The northern Illinois progenies did not grow as expected in the Maryland experiment. They are from an area climatically similar to parts of southern Michigan, but they grew much slower than did trees from southern Michigan. Perhaps the slower growth is the result of inbreeding in an isolated population, or perhaps it indicates that the Illinois stands were derived relatively recently from slow-growing Wisconsin or Minnesota populations immediatley to the north.

In the Forest Service experiment there were several large plantation X origin interactions. Most were not significant statistically because of the high error variances. It is not certain whether the remainder represent *bona fide* differences in reaction of particular origins to particular sites. Some can be explained in terms of persistent nusery effects.

Height growth in northern plantations.—Four test plantations in the northern Lake States and northern Ontario (Nos. 17 to 20 in table 4) yielded very different results (King and Nienstaedt 1968). In general, growth was slower than farther to the south and different origins performed best. The results from these four plantations were not well correlated with each other (table 5). In fact there was a negative correlation between results at Ganaraska, Ontario, and results in the northern Lake States.

A few generalizations can be made, however. Seedlots 31 and 32 from southern Wisconsin and southern Michigan generally grew well, and seedlots 1–GEO, 3–TENN, 14–MAIN, and 23–QUE grew poorly. As in the southern plantations, some seedlots performed exceptionally well at a variety of places. Most of the best origins were from south of the planting site.

Diameter and height/diameter ratio.—In October 1967, when the trees were 11 years old from seed, height and diameter at the 1-foot level were

Table 4.—*Relative height growth, expressed as percentage of plantation mean, of 25 eastern white pine origins grown in 20 test plantations* [1]

Seedlot number	Relative height in Plantation No.																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Ga.	N.C.	Va.	Pa.	Ky.	Ohio			Ind.	Ill.		Iowa	Mich.			Ont.	Mich.	Wis.	Minn.	Ont.
						Athens	Wooster			Cass	Kaskaskia		Russ	Kellogg	Pine River	Turkey Point	Manistique			Ganaraska
	Per-cent	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*	*Per-cent*
1-GEO	133	141	114	129	128	160	144	123	121	121	129	132	111	102	110	129	100	75	76	116
2 N C	—	132	—	119	137	130	116	119	145	113	119	100	—	—	—	—	—	—	—	—
3 TENN	—	129	—	127	130	145	120	119	130	108	138	136	110	114	125	111	89	77	75	103
6 PENN	105	115	117	111	110	122	140	119	130	116	108	127	138	109	117	111	98	94	96	119
24 ONT	—	—	—	112	—	—	—	130	—	—	—	—	117	110	—	—	—	—	—	—
16 OHIO	—	145	—	109	115	119	116	116	126	111	120	105	—	—	115	114	107	118	94	86
9 PENN	—	—	—	123	—	—	—	116	—	—	—	—	112	107	—	—	—	—	—	—
10 NY	—	—	—	114	—	—	—	109	—	—	—	—	106	108	—	—	—	—	—	—
5 W VA	117	106	117	91	120	95	104	127	102	108	104	109	—	—	—	—	—	—	—	—
13 MASS	—	—	—	106	—	—	—	109	—	—	—	—	99	104	—	—	—	—	—	—
18 WIS	—	101	—	78	108	102	104	105	102	108	102	95	—	—	100	93	97	114	105	94
32 MICH	—	95	—	—	99	107	60	91	98	81	100	109	—	—	110	—	114	106	114	—
31 WIS	—	—	—	95	—	—	—	—	—	—	—	—	—	—	102	—	112	124	119	—
30 VA	—	100	—	98	106	91	80	84	112	95	95	100	—	—	—	—	—	—	—	—
20 N S	98	82	106	89	86	95	104	91	79	103	105	95	78	89	98	108	87	76	73	115
12 N Y	—	78	—	100	81	75	104	98	79	95	93	100	98	99	102	103	102	111	85	106
25 ONT	74	78	74	100	81	95	108	98	79	95	89	100	97	105	89	96	106	101	118	90
28 MINN	—	—	—	96	—	—	—	91	—	—	—	—	88	91	85	—	98	102	105	—
21 N BR	—	—	—	97	—	—	—	70	—	—	—	—	97	92	—	—	—	—	—	—
15 IOWA	—	81	—	97	81	81	102	76	93	89	76	73	—	—	102	79	99	112	101	89
14-MAIN	—	69	—	91	69	68	80	95	70	81	70	77	81	93	90	92	96	79	88	97
29 MICH	—	73	—	91	—	—	—	88	—	—	—	—	89	89	80	—	102	93	88	—
19 MINN	73	—	74	83	66	75	84	81	74	95	81	73	—	87	90	89	97	96	107	90
23 QUE	—	71	—	74	74	65	68	106	70	81	73	77	—	—	88	78	90	96	115	94
35-MINN	—	77	—	—	—	—	—	—	—	—	—	—	—	—	111	—	112	105	106	—
Age, years	7	10	7	10	8	8	8	7	7	7	10	8	10	10	9	7	9	9	9	7
Mean height, feet	3. 1	11. 4	3. 7	5. 5	5. 4	3. 3	2. 5	2. 8	2. 2	2. 7	8. 1	2. 2	6. 2	10. 5	1. 7	4. 2	2. 8	1. 9	2. 3	3. 8
Coefficient of vairation, percent (=standard deviation of seedlot mean/plantation mean ×100)	8. 4	6. 2	9. 3	7. 6	5. 3	6. 9	13. 0	6. 2	6. 4	—	6. 1	6. 4	5. 7	3. 0	7. 1	—	6. 9	8. 0	8. 4	—

[1] Seedlots are arranged in decreasing order of average growth rate in plantation 1 to 16.

TABLE 5.—*Similarity between results at various plantations, as measured by rank correlation based on 7- to 10-year height*

Plantation number	1 Ga.	2 N.C.	3 Va.	4 Pa.	5 Ky.	6 Ohio Athens	7 Ohio	8 Ohio Wooster	9 Ind.	10 Ill. Cass	11 Ill. Kas-kaskia	12 Iowa	13 Iowa Russ	14 Mich. Kell-ogg	15 Mich. Pine River	16 Ont. Turkey Point	17 Mich. Mani-stique	18 Wis.	19 Minn.	20 Ont. Gan-araska
2-N.C.	.90																			
3-Va.	.90	.60																		
4-Pa.	.50	.74	.25																	
5-Ky.	.70	.88	.70	.71																
6-Ohio	.60	.77	.60	.71	.88															
7-Ohio	.25	.46	.25	.85	.70	.79														
8-Ohio	.65	.62	.65	.78	.83	.85	.87													
9-Ind.	.60	.83	.60	.74	.94	.83	.74	.74												
10-Ill.	.60	.59	.60	.69	.82	.92	.91	.85	.80											
11-Ill.	.35	.76	.35	.72	.91	.93	.78	.81	.86	.87										
12-Mich.	.70	.82	.70	.80	.82	.85	.67	.83	.76	.64	.80									
13-Mich.	.90	.82	.70	.91	.72	.76	.90	.94	.83	.74	.73	.88								
14-Mich.	.70	.78	.90	.86	.70	.70	.76	.84	.83	.59	.67	.89	.87							
15-Mich.	1.00	.78	1.00	.67	.84	.74	.61	.72	.94	.66	.76	.77	.76	.83						
16-Ont.	1.00	.64	.90	.83	.84	.90	.94	.92	.76	.92	.90	.89	.79	.62	.77					
17-Mich.	.10	.15	.10	.34	.08	.16	−.01	.20	.15	.05	.00	.22	.28	.19	.20	.35				
18-Wis.	−.60	−.11	−.60	−.30	−.14	−.26	−.31	−.16	−.24	−.16	−.22	−.26	−.22	−.15	.00	−.33	.59			
19-Minn.	−.50	−.26	−.50	−.39	−.47	−.40	−.43	−.41	−.30	−.41	−.56	−.33	−.16	−.11	−.26	−.61	.33	.57		
20-Ont.	.69	.24	.61	.31	.31	.39	.39	.39	.18	.37	.25	.42	.51	.23	.28	.43	−.36	−.71	−.65	
Average rank correlation in comparison with plantations 1 to 16	.69	.73	.63	.72	.80	.80	.70	.79	.80	.75	.75	.79	.82	.77	.80	.84	.15	−.28	−.36	−.36

measured on the 15 originals in the Kellog Forest plantation in southern Michigan. Then height/diameter ratios were calculated. The results are presented in table 7.

As expected, there was a strong relation between height and diameter. But there were also large differences in the height/diameter ratio. Those differences were almost as significant statistically as were the ones for height or diameter. The largest difference was between medium-height, large-diameter seedlot 1–GEO and tall, medium-diameter seedlot 24–ONT. There was also a large contrast in diameters between 3–TENN and 24–ONT which were similar in height.

These data indicate that height growth and diameter growth may be inherited separately. If so, both must be considered in choosing provenances for commercial planting.

Female flower production.—A few female flowers were produced in 1963 (age 7) in North Carolina Plantation 2. At five more northerly test sites flowering started in 1964 or 1965 in the Forest Service provenance study. Usually the first year's flowering was very light, confined to 1 or 2 percent of the trees.

Second-year flowering data are available for five plantations (table 8). Flowering was heaviest in Pennsylvania Plantation 4 although that was not the tallest.

Flowering data are always variable. Nevertheless genetic differences in earliness of flowering were evident. Three slow-growing northern origins (20–N S, 21–N B, and 28–MINN) produced the greatest number of female strobili, on more than twice as many trees as the average for the experiment. Flowering was very light on all five southern Appalachian seedlots, whether of medium or fast growth rate.

Foliar morphology.—Genys (1968) and Mergen (1963b) reported appreciable differences in leaf length of 2- or 3-year-old seedlings of different provenances. Evidently such variation becomes less with age. Leaf length, leaf width, serrations per millimeter, number of resin canals, and number of endodermal cells were measured at Kellogg Forest at age 6. Between-provenance differences were significant at the 5-percent level but were not large. The extreme differences were only about 10 percent of the experiment mean, and they followed no recognizable geographic pattern.

Between-provenance differences in foliage color of *Pinus strobus* are about as large as might be encountered among single trees in a healthy wild stand. Their genetic basis can be demonstrated statistically by careful observation, but the differences are unimportant from the practical standpoint.

TABLE 6.—*Two-year height and date of bud set of seedlings grown in Maryland as part of the University of Maryland rangewide provenance study*

State or Province of origin	Height age 2	Approximate date at which 50 percent of 2-year-old trees formed terminal buds
	Centimeters	
N C, S C, TENN	[1] 17–22	[2] Nov. 3
VA	15–16	Nov. 4
W VA and MD, below 2,300 feet	17–19	Nov. 2
W VA and MD, above 2,300 feet	15–16	Nov. 1
PENN, OHIO	17–20	Nov. 1
CONN	18–19	Oct. 28
N Y, MASS, VT, NH, MAIN	15–18	Oct. 26
N S, N B, PR EDWARD	10–13	
S ONT	18–20	Oct. 14
S MICH	17–18	Oct. 17
WIS	14–16	Oct. 8
N ILL	12–14	Oct. 28
MINN, NE IOWA	11–15	Oct. 3
S QUE	14–17	Oct. 12
N CENTRAL ONT	12–14	Oct. 6
MANITOBA, N ONT, N QUE	8–12	

[1] The figures given indicate the range in seedlot means. Differences between individual seedlots of 2.8 and 3.7 cm. were significant at the 5- and 1-percent levels, respectively.

[2] In most regions there was a range of 10 days among the means of individual seedlots. Differences between individual seedlots of 14 and 19 were significant at the 5- and 1-percent levels, respectively.

TABLE 7.—*Geographic variation in height, diameter, and height/diameter ratio, expressed as percent of plantation mean, at age 11 at Kellogg Forest, Mich.*

Seedlot	Relative height	Relative diameter	Height / Diameter ratio
	Percent	*Percent*	*Percent*
1–GEO	103	107	90
3–TENN	112	113	95
6–PENN	111	106	101
24–ONT	109	99	105
9–PENN	103	100	98
10–N Y	108	100	103
13–MASS	100	103	93
20–N S	91	84	103
12–N Y	100	92	102
25–ONT	104	98	101
28–MINN	92	86	101
21–N B	93	86	102
14–MAIN	96	92	99
29–MICH	94	86	100
19–MINN	83	85	94
Plantation mean	13. 5 feet	3. 5 inches	
F value	[1] 8. 53	[1] 8. 86	[1] 6. 67

[1] F values of 2.25 were needed for significance at 1-percent level with 14/121 degrees of freedom.

Table 8.—*Female flower production at ages 9 or 10 from seed in five centrally located plantations*

Seedlot	Mean height at 16 sites	Trees with female flowers at plantation number				
		4 Pa.	7 Ohio	8 Ohio	11 Ill.	14 Mich.
	Percent	*Percent of trees*	*Percent of trees*	*Percent of trees*	*Percent of trees*	*Percent of trees*
1-GEO	126	0	0	2	2	0
2-N C	125	6	2	8	2	-----
3-TENN	125	12	2	0	2	0
6-PENN	118	56	15	3	2	8
24-ONT	114	37	------	12	------	22
16-OHIO	114	25	9	10	0	-----
9-PENN	112	37	------	12	------	20
10-N Y	109	19	------	11	------	10
5-W VA	105	19	3	0	8	-----
13-MASS	105	25	------	24	------	17
18-WIS	100	31	5	0	0	-----
32-MICH	99	------	6	0	4	-----
31-WIS	99	62	------	------	------	------
30-VA	98	0	3	0	1	-----
20-N S	93	31	19	26	6	48
12-N Y	93	37	7	2	2	12
25-ONT	92	19	17	15	2	12
28-MINN	90	31	------	31	------	27
21-N B	90	56	------	11	------	26
15-IOWA	83	25	4	0	2	-----
14-MAIN	82	50	9	12	0	3
29-MICH	82	31	------	9	------	11
19-MINN	80	12	5	8	2	17
23-QUE	76	37	6	20	4	-----
Average percent		20	7	7	3	13
Average number of flowers per flowering tree		5	4	3	1	3
Year		1966	1965	1965	1966	1966

Foliar mineral composition.—In the winter of 1965-66, at the end of the 9th growing season, leaves were collected from the Fred Russ and Kellogg Forest plantations in southwestern Michigan. The needles were collected in a standard manner from all trees, bulked into two samples (first five or second five replicates) per origin per plantation, dried, ground and analyzed in a micro-Kjeldahl apparatus (nitrogen) or a direct-reading spectrometer (11 other elements) (Hilton 1968).

The concentration of N, Ca, Cu, and Zn varied significantly among provenances (table 9). Also, there was a significant amount of plantation X origin interaction in concentration of P, Fe, B, and Al. For a single origin, concentration of those elements was consistent between the two samples from the same plantation but was different between plantations.

Origins which were highest in nitrogen were low in copper (r = −0.80, significant at 1-percent level). Also, the fast-growing Georgia and Tennessee trees were noticeably low in foliar nitrogen. Those facts may or may not signify cause-and-effect relations.

Monoterpene composition of the cortex.—Mirov and others used terpene composition as an aid in pine identification and classification. Hilton (1968) similarly used material growing in the Forest Service rangewide provenance study, sampling the same provenances in each of four southern Michigan plantations. At each planting site he took two 10-tree samples (one from the first five replicates, the other from the second five replicates) per origin to estimate error variance. In all trees he sampled oleoresin obtained from the cortex of year-old branches.

The concentration of alpha-pinene, myrcene, and limonene varied significantly among origins, being consistent from plantation to plantation (table 9). There was, however, no recognizable geographic pattern. Nor did the monoterpenes furnish clues as to the reasons for differences in growth characters.

Previous investigators of other species have reported that environment has very little influence on monoterpene composition. Hilton, however, found considerable interaction between origin and plantation. Indeed, such interaction accounted for

Table 9.—*Geographic variation in foliar mineral and cortical monoterpene composition of* Pinus strobus [1]

Seedlot	Foliar concentration of				Cortical concentration of		
	N	Ca	Cu	Zn	Alpha-pinene	Myrcene	Limonene
	Percent p.p.m.	*Percent p.p.m.*	*Percent p.p.m.*	*Percent p.p.m.*	*Percent of monoterpenes*	*Percent of monoterpenes*	*Percent of monoterpenes*
1-GEO	1.71	.42	7.6	47	22	11	6
2-N C	------	------	------	------	17	14	5
3-TENN	1.70	.45	9.4	48	24	9	7
6-PENN	1.84	.39	4.9	42	33	4	3
9-PENN	1.90	.44	7.0	47	21	22	3
10-N Y	1.91	.45	6.6	47	36	5	4
12-N Y	1.90	.45	5.9	45	29	15	4
13-MASS	1.90	.47	5.2	50	41	4	3
14-MAIN	1.97	.44	3.4	36	35	10	4
15-IOWA	------	------	------	------	26	9	6
16-OHIO	------	------	------	------	27	12	2
18-WIS	------	------	------	------	27	12	12
19-MINN	1.94	.42	6.2	48	29	14	3
20-N S	1.89	.47	5.9	44	24	7	16
21-N B	1.90	.44	4.9	40	28	9	9
23-QUE	------	------	------	------	26	36	3
24-ONT	1.90	.38	5.6	45	28	4	5
25-ONT	1.92	.46	5.9	49	26	15	3
28-MINN	1.91	.42	5.9	50	31	12	3
29-MICH	1.85	.43	7.6	50	26	19	4
31-WIS	------	------	------	------	35	14	3
32-MICH	------	------	------	------	21	14	6
35-MINN	------	------	------	------	30	12	4

[1] Concentration of the listed elements and monoterpenes was consistent between plantations. (After Hilton 1968).

more than 50 percent of the total variance in alpha-pinene, beta-pinene, camphene, and 3-carene.

Response to daylength and to night temperature.—Mergen (1963b) found differences between provenances in response to daylength. One series of 3-year-old seedlings, potted the previous autumn, was given 8-hour days during the winter. Northern origins flushed earliest, but none of the seedlings grew vigorously. Another series was given 16-hour days. In that series, southern trees grew 3 to 5 inches, significantly more than northern ones.

In another experiment he tested reaction to varying night temperature (day temperature remained at 60° F.). The seedlings grew best when kept at a night temperature of 60° F. At that temperature and at night temperatures of 80° F., southern origins grew fastest. However, southern Appalachian trees grew very little when maintained at 39° F. during the night.

Winter cold damage.—As far north as southern Michigan, all white pines in the Forest Service provenance study survived 10 winters unscathed. Farther north in the Lake States, southern Appalachian origins suffered no visible injury but grew slowly.

Mergen (1963b) conducted a small *in vitro* experiment, using detached needles from dormant and actively growing seedlings. In midwinter he placed the needles at temperatures varying from −10° F. to −75° F., allowed them to thaw, and measured damage. In the series taken from dormant seedlings, southern Appalachian origins subjected to the lowest temperatures suffered some damage, but northern origins did not. In the series taken from actively growing seedlings, two North Carolina origins suffered almost three times as much damage as did the others.

Local Variation Patterns

The Michigan half-sib progeny test includes open-pollinated progeny from 123 parents located in 16 stands in 15 counties of the State. Height was measured at ages 2 and 3 (nursery) and 6 (four plantations in Lower Michigan). The most striking differences were between regions. The 6-year heights (strongly correlated with the nursery data) were as follows:

Region of origin	Range in stand means	Average for region
	Percent of experiment mean	
Upper Peninsula	78–86	82
Northeastern Lower Peninsula	88–95	92
West-central Lower Peninsula	100–111	106

The Upper Peninsula, represented by progenies from five widely separated localities, is separated from the rest of the State by the Straits of Mackinac. The Straits are wide enough to provide an effective barrier to pollen and seed migration. The slow growth rate probably represents an adaptation to the generally cool days and short growing seasons prevailing in northern Michigan.

The rather large differences in climate within the Lower Peninsula do not help explain the differences in growth rate between northeastern and west-central trees. Both areas have a similar range in rainfall, temperature, and length of growing season. Soils in the counties bordering Lake Huron are, however, less well drained than in the west-central part of Lower Michigan. Perhaps the soil differences were responsible for the differentiation into types with medium and with fast growth.

The separation of Upper and Lower Peninsula populations is a natural one. Separation of two Lower Peninsula ecotypes, while justified by the data, is more arbitrary. There is no range gap, and between the two areas there was a large unsampled strip which may contain intermediate trees.

Hilton (1968) sampled monoterpene content in many of the half-sib progenies. The concentration of alpha-pinene was consistently highest in seedlings from Lower Michigan. The concentration of myrcene and limonene also differed appreciably between Upper and Lower Peninsula trees. The percentage content of 3-carene and gamma-terpinene varied significantly from stand to stand within the same region.

Genys' (1968) Maryland study sampled New England and New York intensively. Each of four origins from relatively mild Connecticut was fast-growing, averaging 18 centimeters tall at age 2. In the remainder of the region, however, there was no evident relation between elevation or winter temperatures at place of origin and growth. Western Maryland and adjacent West Virginia were also sampled intensively. One group of seedlings, representing elevations above 2,300 feet, grew 14 to 16 centimeters tall. Another group of seedlots, representing elevations of 800 to 2,200 feet in nearby counties, grew significantly more—17 to 19 centimeters.

Inheritance of Growth Rate

Kriebel started a half-sib progeny test at the Ohio Research and Development Center in 1962, using open-pollinated seed collected from native trees in a northeastern Ohio stand. The test was well replicated. The seedlings were grown for 3 years in individual pots, each pot constituting a plot. Height differences among the 75 progenies were significant and accounted for 19 percent of the total variance.

In 1963 and 1964 he conducted full-sib progeny tests of many of the same parents, using the same experimental techniques. He measured height at ages 2 (1963 test) or 3 (1964 test). The data were analyzed on the basis of three different assumptions. When so analyzed the theoretical heritabilities were as follows:

Assumption	Theoretical heritability	
	1963 test	1964 test
Parents were unrelated	0. 21	0. 24
Parents were half-sib to each other	. 31	. 22
Parents were full-sib to each other	. 22	. 15

In the Michigan half-sib progeny test, started in outdoor nursery beds with multiple-tree plots, there were no significant differences in height at age 2 among families from the same stand. In one of the four test plantations measured at age 6, the differences among families from the same stand were significant at the 1-percent level; they were not significant in the other tree plantations. Nor were single progenies consistently superior from plantation to plantation.

Pellati (1967) reported on a 7-year-old half-sib progeny test in Italy, using open-pollinated seed from 19 trees growing in an Italian plantation. One family was thought to contain some natural hybrids with *Pinus griffithii.* The between-family differences were large and accounted for 34 percent of the total variance of plot means. The family means ranged from 87 to 128 centimeters.

Dwarf White Pines

Rehder (1940) listed three dwarf cultivars of eastern white pine. They are propagated by grafting and are usually found only in rare-plant gardens. The ones the author has seen, even though a half century old, have not flowered.

Chisman and Lylo (1958) reported 47 dwarf eastern white pines growing naturally in the woodlands of Pennsylvania State University. They were globe-shaped and grew 1 to 3 inches per year. One was 18 inches tall at age 16. In the vicinity were 375 normal seedlings and 3 normal old white pines, one of which was thought to have produced all the dwarfs. If so, the dwarf habit was controlled by a recessive mutation or by gross chromosomal change acting as a recessive, and the old parent produced a high percentage of selfs. Alternatively, the dwarf habit was controlled by a dominant mutation or chromosome change acting as a dominant, but in that case the seed was produced by a dwarf no longer alive at the time of Chisman and Lylo's examination.

Breeding for Blister Rust and Weevil Resistance

A breeding program to develop blister-rust resistance in eastern white pine was started in 1937 in Wisconsin by A. J. Riker and continued by J. E. Thomas and R. F. Patton. The original work consisted of selection of rust-free trees in heavily cankered areas, a clonal test of grafted trees, and an open-pollinated progeny test. In the clonal test one-fourth of the 160 selections remained uninfected. The average level of resistance was the same in progenies of selected and unselected trees, but it was higher (significance unstated) in a few progenies (Patton and Riker 1966).

Additional selections have been made and grafted. Also, experiments were performed in the last 15 years to test a suspected relation between age and susceptibility. The experiment shows increased resistance with age of tree and that this increased resistance is transmitted by grafting. This provoked a reevaluation of the original clonal experiment, with the conclusion that some clonal differences in susceptibility might be nongenetic.

The age effect was noticeable in seedling progeny tests. Of 700 control-pollinated seedlings inoculated at age 1, only two seedlings survived 3 years later. The same two crosses were retested and inoculated at age 4. Two years later, 25 percent of the trees were disease free, in contrast to 1 percent in progenies of average trees. Later inoculation is now recommended as most useful.

One full-sib progeny test included 153 crosses among 37 old trees selected for freedom from blister rust infection. Progeny of the canker-free parents did not, on the average, possess a higher degree of resistance than did average seedlings. Six of the 37 parents proved able to transmit enough resistance to warrant inclusion in a long-term breeding program. In essence, family selection was effective whereas mass selection was not.

Selection of parent trees has continued, and the Forest Service has recently taken over the breeding program. In the past 3 years many more controlled pollinations have been made.

For the past 15 years, there has been interest in the development of a strain of eastern white pine resistant to the white-pine weevil (*Pissodes strobi*), with the work now centered in Pennsylvania and New York. The work has emphasized correlations between attack and phenotypic characters such as position in crown canopy, bark thickness, and foliar chemistry. Some progeny and provenance tests are being exposed to weevil attack, but there are no definitive data on genetic differences in susceptibility.

Interspecific Hybridization

White pine hybridization started in the 1930's at the Institute of Forest Genetics, [at] Placerville, Calif. A few natural hybrids of *Pinus strobus* X *P. griffithii* had been reported prior to that time. In the 1940's, hybridization experiments were pursued by the Northeastern Forest Experiment Station, the Cabot Foundation of Harvard University, and by Canada's Southern Forest Experiment Station at Maple, Ontario. More recently, work has been done by the University of Wisconsin, the Forest Service Forestry Sciences Laboratory at Moscow, Idaho, the Ohio Agricultural Research and Developmental Center, the Quetico-Superior Wilderness Research Center, Pennsylvania State University, Michigan State University, and German workers.

In the decade just after World War II, the Bureau of Plant Industry of the U.S. Department of Agriculture issued an annual newsletter which was circulated among all white pine workers. It promoted exchange of pollen, seed, scions, and information. As a result, crosses which were successful at one place were soon attempted elsewhere. This review is based upon the newsletter, on personal correspondence with H. B. Kriebel and R. F. Patton, and on published papers by Duffield (1952), Duffield and Righter (1953), Wright (1959), Heimburger (1962), and Patton (1966).

Status of hybridization work.—At Placerville, different racial combinations of the cross *Pinus strobus* X *P. monticola* were made. Seed sets were similar, but the hybrids differed markedly in growth characters, depending on whether California or Idaho *P. monticola* was used as a parent. Elsewhere the hybridizations involved a single race of each species, or parents for which there were no origin data. Many clones have been used in *P. strobus* and *P. monticola;* about 20 clones in *P. griffithii;* a few clones each in *P. peuce*, *P. cembra*, *P. parviflora*, and *P. koraiensis;* and a single clone of dubious status in *P. ayacahuite*. Thus much work remains to be done in the use of selected parents to make interspecific hybrids.

In Philadelphia the average date of pollen shedding varied by 9 days, from May 22 (*Pinus cembra*) to May 31 (*P. monticola*). The short period facilitated reciprocal crossing, and many species combinations have been made in both directions, although never in enough quantity to test reciprocal differences. The most commonly used female parents have been *P. strobus* in the east and *P. monticola* in the west.

Crossability patterns reported by different workers and from different places have generally been similar. There are, however, considerable year-to-year and tree-to-tree fluctuations. Near Philadelphia, these were most noticeable in crosses between *Pinus griffithii* female and *P. strobus* male. Yields of sound seed per cone were 15 or more on two young and three old female trees; 0 to 5 on seven other trees. The yields changed from year to year on the same tree.

Several F_1 hybrid combinations have been made in small quantities. Their testing has been limited to a few localities and to observations on growth characters. There has been some testing for resistance to blister rust in the case of *Pinus strobus* X *P. griffithii* and *P. strobus* X *P. monticola*, but even that has been incomplete.

Crossability patterns and growth of hybrids.—The soft pine or *Haploxylon* subgenus includes two series of species with less than five needles and three series with five needles. Most hybridization has been done within series *Strobi* (five needles) which includes the following species:

- *P. strobus* L. from Eastern United States and Canada.
- *P. monticola* Dougl. ex D. Don from Western U.S. and Canada.
- *P. lambertiana* Dougl. from California and Oregon.
- *P. ayacahuite* Ehrenb. from Mexico and Guatemala.
- *P. chiapensis* (Martinez) Andresen from Central America.
- *P. parviflora* Sieb. and Zucc. from Japan.
- *P. formosana* Hayata from Taiwan.
- *P. griffithii* McClel. from the Himalayas.
- *P. peuce* Griseb. from Southeastern Europe.

All except *Pinus chiapensis* and *P. formosana* have been used in crossing work.

Trees in the limber-border pine complex (series *Flexiles*) have been used as parents by several hybridizers. Crosses between trees identified at the time as *Pinus flexilis* James (probably *P. strobiformis* Engelm.) and *P. griffithii* have given high seed sets and have exhibited hybrid vigor. With one exception, crosses between *P. flexilis* or *P. strobiformis* have been unsuccessful. The exception occurred in Philadelphia where one tree X tree combination produced seven seeds of which four germinated. The *P. flexilis* male parent grew slowly as did the hybrids.

Crosses have also been attempted between *Pinus strobus* and series *Cembrae* (*P. cembra* L., P. *koraiensis* Sieb. and Zucc.) and series *Flexiles* (*P. armandi* Franchet). The pollinations usually resulted in full-size cones and many empty seeds but no authentic hybrids.

In earlier years, before pine crossability patterns were known, a few crosses were attempted between *Pinus strobus* and totally dissimilar hard pines or two-needled soft pines. Such crosses did not induce cone set.

Pinus lambertiana of California has not been crossed with *P. strobus*. The range of *P. lambertiana* overlaps that of *P. monticola*, and this seems to have resulted in the formation of genetic barriers to hybridization. All other attempted hybridizations in series *Strobi* have been successful, and those F_1's which have grown sufficiently large have been fertile. This indicates that the species have been prevented from crossing only by geographic barriers, genetic barriers being almost nonexistent.

The species which cross readily are similar morphologically. Most are distinguished by quantitative traits. Hybrids usually need to be grown for 3 or 4 years before they can be authenticated. First-year identification is reliable only if the hybrids are grown under extremely precise conditions in a well-replicated experiment, with nonhybrid seedlings from the same female parent trees to serve as controls. However, hybrids involving *Pinus flexilis* or *P. strobiformis* as male parents are exceptions. The nonserrate needles characteristic of both species are also characteristic of F_1 hybrids.

Some hybrid combinations possess hybrid vigor and other useful traits, and can be produced easily. Mass production should be considered as a practical tree improvement measure in the near future although no hybrids are planted commercially now. Because *Pinus strobus* produces cones long before it produces pollen, seedlings could be planted and economically hand pollinated. The same is true of *P. peuce*, and most open-pollinated seed now produced by American trees is hybrid. A pollenless, isolated 34-year-old tree of *P. ayacahuite* in Philadelphia was a miniature seed orchard capable of producing more than 10,000 hybrid (*P. ayachuite* X *P. strobus*) seed per year, with no care.

Pinus strobus X *P. monticola* hybrids have grown well at a number of eastern and western localities. They are often heterotic and fertile. Development of a fast-growing, blister-rust-resistant strain by crossing selected parents of both species holds promise and is being pursued in Idaho and Wisconsin. Also, the hybrids may be valuable in eastern areas with heavy weevil populations because of resistance inherited from *P. monticola.*

Embryogeny in species crosses.—Kriebel (1968) studied embryo development in *Pinus strobus*, and after pollinating *P. strobus* with *P. cembra*, *P. koraiensis* and *P. flexilis.* Those crosses rarely if ever have given germinable seed. The pollen tubes grew normally and effected fertilization in all species combinations. Both nonhybrid and hybrid embryos started to develop within 2 or 3 days of fertilization, and grew rapidly. They developed a suspensor system with several embryonal segments extending into a well-developed corrosion cavity. But then hybrid embryos degenerated rapidly.

Wright (1959) found evidence that the development of *Pinus strobus* and *P. strobus* X *griffithii* embryos reacts differently to different external conditions. Intra- and inter-specific pollinations were made in several different years on many different planted trees near Philadelphia. Seed yields were similar, averaging 2.3 sound seeds per cone. Then the hybridization work was transferred to native trees in the Pocono Mountains. There was a slight decrease in yield of hybrid seed but a large increase (up to 40 sound seeds per cone) in yield of nonhybrid seed.

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1970. Genetics of Eastern White Pine (*Pinus strobus* L.) USDA Forest Serv. Res. Pap. WO-9, 16 p.

Eastern white pine (*Pinus strobus* L.) is one of the most widely ranging conifers of Eastern United States and Eastern Canada. Characteristics of eastern white pine including reproductive development, pollination techniques, propagation, geographic variation, and progeny and provenance tests are reviewed as they apply to the genetic improvement of the species. Status of interspecific hybridization work is discussed and suggestions regarding further work are offered.

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