TAXONOMY, NOMENCLATURE, AND VARIATION WITHIN THE *PINUS FLEXILIS* COMPLEX

Thesis for the Degree of Ph. D.

MICHIGAN STATE UNIVERSITY

Raphael John Steinhoff

1964

This is to certify that the

thesis entitled

TAXONOMY, NOMENCLATURE, AND VARIATION
WITHIN THE PINUS FLEXILIS COMPLEX

presented by

Raphael John Steinhoff

has been accepted towards fulfillment
of the requirements for

PhD degree in Forestry

John W Andresen
Major professor

Date 19 February 1964

O-169

ABSTRACT

TAXONOMY, NOMENCLATURE, AND VARIATION WITHIN THE *PINUS FLEXILIS* COMPLEX

by Raphael John Steinhoff

The *Pinus flexilis* complex is composed of two populations of 5-leaved pines of the subgenus *Haploxylon* of the genus *Pinus*. The northern population, usually known as *Pinus flexilis* James, has a range from southern Alberta to northern New Mexico. The southern population ranges from southern Colorado into northern Mexico. This population is referred to as *Pinus strobiformis* Engelm., *Pinus flexilis* var. *reflexa* Engelm., *Pinus reflexa* Engelm., or *Pinus ayacahuite* var. *brachyptera* Shaw.

The primary purposes of the study were to evaluate the extent of differences between the taxa and to evaluate the variation within each. The results were to be used to attempt clarification of the nomenclature and classification of the taxa.

Materials for the study were collected in 1959 and 1960 from 61 native stands in the mountains of the western United States and Alberta, Canada. Cones, seed, and a single branch of foliage were collected from each tree. The cones and foliage were measured and scored for several characteristics. The seed were planted in a replicated nursery test in 1961. Observations and measurements were made on the resulting seedlings during their first two years of growth.

Distinct differences between the taxa were exhibited in the seedling test. Cotyledon number, length of secondary leaves, and height growth were the most satisfactory characters for distinguishing between the taxa.

Traits measured on the cone and foliage specimens from the parental trees exhibited less distinctive differences between taxa. Secondary leaf length was the most reliable parental character for separating the taxa. Other traits which served to distinguish the taxa were: (1) seed weight, (2) number of rows of stomata on the dorsal leaf surface, (3) length of cones, and (4) degree of cone scale reflexing.

It was concluded from the results of the study that the taxa deserve separate specific rank. According to the rules of nomenclatural priority the proper name for the northern species is Pinus flexilis James. The proper name for the southern species is Pinus strobiformis Engelm.

The patterns of variation in the regions where the species' ranges are contiguous or sympatric indicate that hybridization has occurred in the past and may still be taking place.

Within the northern species, P. flexilis, the population structure had three principle characteristics. First, there was very little variation in either seedlings or parental specimens from that portion of the range extending from Alberta to central Colorado. Second, seedlings of southern origins grew faster and the cones from the parents were longer than those of northern origin. Third, seedlings from three restricted and isolated areas performed like those of the southernmost origins. These areas were in east-central Idaho, near Pine Bluff, Wyoming, and in Douglas County, Colorado.

Variation within P. strobiformis was more random than in P. flexilis. Seedlings from the northernmost origins grew more slowly than those of more southern sources. The parental specimens from northern Arizona trees had shorter leaves, smaller cones, and less cone scale reflexing than those from central and southern Arizona. Both seedling and parental leaves of New Mexico and Texas sources were shorter and less serrulate than those from central and southern Arizona.

Significant differences between progenies within one or more stands were found for all 13 seedling traits investigated. In some of the northern areas within-stand differences were almost as large as between-stand differences.

TAXONOMY, NOMENCLATURE, AND VARIATION WITHIN THE *PINUS FLEXILIS* COMPLEX

By

Raphael John Steinhoff

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

1964

ACKNOWLEDGMENTS

Financial support for various phases of the study has been provided by the American Museum of Natural History, Michigan State University, and the National Science Foundation.

Special thanks are due to the many co-operators who have collected materials used in the study and to the staff of the Bogue Experimental Nursery for assistance in processing the specimens and conducting the nursery test.

Dr. W. B. Critchfield of the Pacific Southwest Forest and Range Experiment Station has generously supplied supplemental information for the species' range map.

The author wishes to express his appreciation to the members of the guidance committee for their continuing assistance and encouragement throughout the study.

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INTRODUCTION

This paper is concerned with members of the Pinus flexilis complex which occur in western North America. Taxa in the complex belong within the group Flexiles, sensu Shaw (1914:24-28), of subsection Cembra of the Haploxylon or soft pines. Members of this subgenus are characterized by non-decurrent leaf-fascicle bracts and a single fibro-vascular leaf-bundle. The subsection Cembra contains those members of the Haploxylon with terminal cone-scale umbos. Members of the group Flexiles of the subsection Cembra have wingless seeds and dehiscent cones.

The two taxa under consideration will be referred to as species and the specific epithets first published for them will be used. The northern species, Pinus flexilis James, or limber pine, has been described as follows: Leaves in five-leaved clusters, thick, rigid, 35 to 75 millimeters in length with several rows of stomata on the dorsal surface, cones 75 to 250 millimeters long, scales rounded or pointed at the apex; tree 13 to 16 meters in height with a short, massive trunk 0.6 to 1.2 meters or more in diameter (Sargeant 1897, XI:35-37). Some other authors consider the maximum cone length to be considerably less, e.g. Engelmann (1863) 110 millimeters. The species is found from southwestern Alberta, south along the Rocky Mountains and related chains, to northern New Mexico and Arizona. It also occurs from Nevada westward to the Sierra Nevada Range with western outposts in southwestern California and the Wallowa Mountains in Oregon. At the eastern extreme it is found in isolated stands in western North and South Dakota (Figure 1).

The southern species, Pinus strobiformis Engelm., or Mexican border white pine, is found in the mountains of extreme southern Colorado, Arizona, New Mexico, Texas, and northern Mexico (Figure 1). Sargent (1897, XI:33-34) gave the following description for the species: Leaves in clusters of five, slender, from 85 to 100 millimeters in length, usually without stomata on the dorsal leaf surface, leaves sharply serrate or entire; cones 125 to 225 millimeters long, their scales thin and reflexed; tree 26 to 32 meters in height with diameters ranging to 0.6 meters.

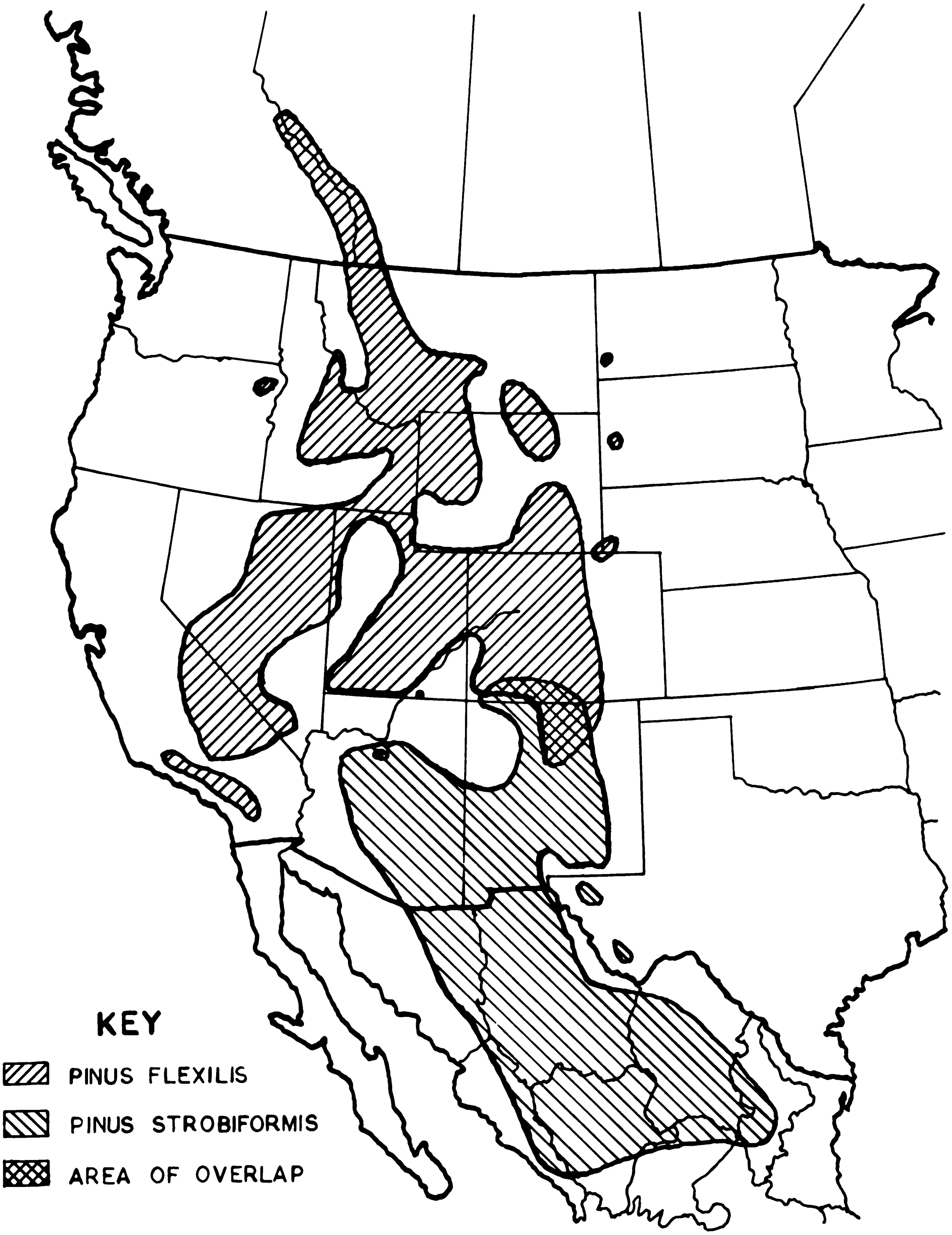


Figure 1. Distribution of members of the *Pinus flexilis* complex.

In the days before railroad transportation, P. flexilis was the primary lumber source for the desert regions of Nevada (Jepson 1910:75). The tree also has value as protection for watershed lands and its windswept forms add beauty to the mountain scene. Its seeds are large and edible. They were gathered by Indians and trappers for food (James 1823;II:34). The nutritious seeds are also an important item in the diet of many rodents (Hatt 1943). Rodents are the prime agents in seed dispersal (Eggler 1941). P. flexilis has been recommended for shelterbelt planting in Wyoming and western Nebraska (U. S. Dept. of Agriculture 1949:848).

Pinus strobiformis, on the other hand, grows on less exposed sites than does P. flexilis and, under mesic conditions, develops to a size and quality that is quite satisfactory for producing lumber. A trial planting of 150,000 seedlings is currently being grown in central Colorado for use in reforestation efforts (Milodragovich, R. R. 1963. Personal communication to Dr. J. W. Andresen, Dept. of Forestry, Michigan State University).

Examples of typical members of the two species and the associations in which they occur are presented in Figure 2.

Pinus flexilis near Nye, Montana.
Elevation: 1509 meters.

Pinus strobiformis near Springerville, Arizona.
Elevation: 2910 meters.

Figure 2. Examples of naturally occurring stands of members of the Pinus flexilis complex.

PURPOSES

Two primary purposes prompted the study: first, a desire to clarify the correct taxonomic rank of the two taxa through an analysis of the differences between the two as well as the variation within each; second, to recommend proper specific epithets which are consistent with good usage and accepted nomenclatural rules.

The study also has long-range objectives. Among them are: (1) The establishment of plantations containing materials of known origin for continuing anatomical, morphological, and physiological studies of the species, (2) Correlation of juvenile with mature performance, (3) Production and evaluation of hybrids between members of the *Pinus flexilis* complex and other 5-leaved soft pines, and (4) Evaluation of the timber potentialities of the species in the Midwest.

LITERATURE REVIEW

Taxonomy and Synonymy.

The discovery and naming of *Pinus flexilis* by James (1823,II:34-35) initiated a series of nomenclatural controversies and confusions which have persisted until the present day. Unfortunately, James did not collect specimens and his later description was based only on his field notes. Engelmann (1863) published a Latin description of *P. flexilis* and attributed the inconsistencies in the account of James to the inclusion of observations on another 5-leaved species of pine, which was later named *Pinus aristata* Engelm.. This assumption might explain James's description of the cones as being erect and smaller than those of *Pinus rigida* Mill. However, the prominent arming of the cones of *P. aristata* and James's note that those of *P. flexilis* are unarmed made such confusion seem unlikely. Nuttall (1853,III:107) attempted to elaborate on the earlier description by James, but his text and poor figure did little to clarify the situation.

A questionable nomenclatural addition placed in the synonymy by some authors (e.g. Sudworth 1897:16) was made by Hooker (1838,II:161) in *Flora Boreali-Americana*. He listed a variety of sugar pine, *Pinus lambertiana* var. *β* Hooker, which may have referred to either *P. flexilis* or *P. albicaulis* Engelm. The collection upon which the varietal description was based was made by Drummond (1830) in Canada while portaging from the Red Deer River to the Columbia River at "Height of Land". Drummond's description of the foliage would fit either *P. flexilis* or *P. albicaulis* but the cones which he observed had been attacked by rodents or birds. Because the cones are necessary for distinguishing between these species no positive conclusions can be drawn from his brief remarks about the species of pine represented. Endlicher (1847:150) questioned Hooker's interpretation and altered the varietal epithet to *P. lambertiana* var. *B. brevifolia* in his synopsis of the conifers.

As late as 1855, Carrière (1855:392), in *Traité général des Coniferes*, attributed authorship of *P. flexilis* to Wislizenus. This designation was based on a note by Engelmann (1848) in his description of the collections of Wislizenus regarding a specimen sent to him by A. Fendler from Sante Fe, New Mexico. Because Fendler was unable to collect at high elevations it is questionable if his specimen was *P. flexilis*, but rather *P. strobiformis*.

Although not pertinent to the question of similarity or difference between *P. flexilis* and *P. strobiformis*, Rydberg (1905) proposed that *P. flexilis* should be called *Apinus flexilis* (James) Rydb. to conform to the nomenclature of the classification system of Necker (1790,III:269).

The initial description of *Pinus strobiformis* was published by Engelmann (1848) when he described material collected by Wislizenus in northern Mexico near Cosihuiriachi, Chihuahua. However, the specific epithet does not appear in Engelmann's later works (1878, 1880, and 1882). Shaw (1909:11) attributes this ommision to the fact that Engelmann did not learn of Ehrenberg's (1838) description of *Pinus ayacahuite* until after 1848 and that Engelmann then considered what he had named and described as *P. strobiformis* as synonymous with *P. ayacahuite*. The range ascribed by Parlatore (1868, XVI,pt.II:406-407) to *P. ayacahuite* Ehrenb. includes some areas where *P. strobiformis* is found. He also considered the two species as synonymous.

After abandoning *P. strobiformis* as the name for the trees found in northern Mexico, Engelmann (1878), in describing specimens collected by Wheeler's Expedition in Arizona, assigned varietal rank under the species *Pinus flexilis* to various forms which display some of the characteristics he attributed to *P. strobiformis*. These characteristics included serrulation of leaves, reduction in number or lack of stomatal rows on the dorsal leaf surface, elongation of cones, and elongation and reflexion of cone scales. The varieties were designated as: var. *α* -*serrulata*- referring specifically to the serrulate leaves, var. *β* -*macrocarpa*- cones enlarged, and var. *γ* -*reflexa*- cone scale apophyses elongated and reflexed. In the "Revision of the Genus *Pinus*" Engelmann (1880) did not mention the varietal forms of *P. flexilis*. However, he soon (Engelmann 1882) proposed raising the variety *reflexa* to specific rank as *Pinus reflexa*.

Based on their analysis of leaf anatomy, Coulter and Rose (1886) considered *P. flexilis* and *P. reflexa* to be distinct at the species level.

After examining specimens collected by Pringle in 1887 in the same area where Wislizenus collected the specimen described by Engelmann as *P. strobiformis*, Sargent (1889) concluded that *P. reflexa* and *P. strobiformis* were identical. He suggested that *P. strobiformis* was probably only a northern form of *P. ayacahuite* with short leaves and small cones. Shortly afterward, Lemmon (1892:3) used the epithet *P. ayacahuite* var. *strobiformis* Sargent, to refer to the "Arizona white pine" even though Sargent had not proposed the varietal designation. Lemmon also specifically mentioned *P. reflexa* as being synonymous with *P. ayacahuite* var. *strobiformis*. As part of the synonymy for *P. flexilis* var. *reflexa*, Shaw (1909:12) listed, in *Pines of Mexico*, *P. ayacahuite* var. *strobiformis* Lemmon and cited the above article as the reference.

The nomenclatural confusion was further increased when Sargent (1897, XI:33-34) in *Silva of North America* assigned specific rank to *Pinus strobiformis* and cited Engelmann as the authority. This was a complete reversal of his 1889 opinion that *P. strobiformis* was only a form of *P. ayacahuite*. Sudworth (1897:17) accepted and concurred with Sargent's 1897 position and, in his *Nomenclature of Arborescent Flora*, listed *P. strobiformis* Engelm., for which he listed as synonyms *P. flexilis* var. *reflexa* Engelm., *P. reflexa* Engelm., and *P. ayacahuite* var. *strobiformis* Lemmon.

Two of Engelmann's varieties of *P. flexilis* were separated by Sudworth (1897:16) from *P. strobiformis*. *Pinus flexilis* var. *serrulata* Engelm. was placed as a synonym under *P. flexilis*; *P. flexilis* var. *macrocarpa* Engelm. was placed by itself as *P. flexilis megalocarpa*.

The synonymy was further expanded when Voss (1907) considered that *P. reflexa* Engelm. should be designated as *P. ayacahuite* var. *reflexa* Voss. In his treatment *P. strobiformis* Engelm. was placed as a synonym of *P. ayacahuite* Ehrenb.

When Shaw (1909) authored *The Pines of Mexico*, he held that *P. strobiformis* Engelm. was synonymous with the northern form of *P. ayacahuite* which he then designated as a new variety, namely *Pinus* *ayacahuite* var. *brachyptera*. *Pinus flexilis* var. *reflexa* was retained as a variety of *P. flexilis* with *P. ayacahuite* var. *strobiformis* Lemmon and *P. strobiformis sensu* Sudworth and Sargent as synonymy. Shaw evidently did not feel that the *P. strobiformis* of Engelmann, Sudworth, and Sargent was the same tree.

By the time *The Genus Pinus* was published (Shaw 1914), the controversy had completed a full circle. In that publication Shaw considered *P. strobiformis* Engelm. as synonymous with *P. ayacahuite* and all other types previously mentioned as being only forms of *P. flexilis*. Only *P. reflexa* Engelm. and *P. strobiformis* Sargent are mentioned in the synonymy of *P. flexilis*.

After the publication of Shaw's *The Genus Pinus* in 1914, Sudworth (1917:12-13) pointed out that *P. strobiformis*, *P. reflexa*, and *P. ayacahuite* var. *brachyptera* all referred to the same tree. He called attention to the fact that the name *strobiformis* was the oldest and thus implied the idea of priority in his preference for the continued use of *P. strobiformis* to refer to the species. However, Sudworth's views seem to have found little favor until very recently, for *P. reflexa* or *P. flexilis* var. *reflexa* are the names most commonly seen in publications from the intervening years.

Sargent (1922), in the second edition of the *Manual of the Trees of North America* dropped *Pinus strobiformis* Engelm. from the place he gave it in the first edition. As a synonym for *P. flexilis* he listed *P. strobiformis* Sarg., not Engelm. This change represents a complete reversal of Sargent's opinion of the status of the trees first described and named *P. strobiformis* by Engelmann.

In the *Trees and Shrubs of Mexico*, Standley (1920:54-55) assigned separate specific rank to *P. flexilis* and *P. reflexa*. He placed *P. strobiformis* Engelm. in the synonymy of *P. ayacahuite* Ehrenb.

The native student of the Mexican pine flora, Martinez (1948:104-105) accepted Shaw's 1909 treatment of *P. ayacahuite* but separated *P. reflexa* Engelm. from *P. flexilis* James at the specific level. *Pinus strobiformis* Sudworth and *P. ayacahuite* var. *strobiformis* Lemmon were placed in the synonymy of *P. reflexa*. After a year of study in Mexico and British Honduras, Loock (1950), produced an English language treatise on the Mexican pines which paralled and concurred with the taxonomic treatment of Martinez.

A study of *P. flexilis* and *P. reflexa* samples led Douglas (1958) to conclude that the criteria used by previous authors for separation were not valid. She felt that a gradient of morphological characters connected *P. flexilis* var. *flexilis*, *P. flexilis* var. *macrocarpa*, and *P. flexilis* var. *reflexa* but that they were sufficiently distinct to warrant subspecific rank.

The French taxonomist Gaussen (1960:202-205), however, listed both *P. strobiformis* Engelm. and *P. reflexa* Engelm. as separate species in addition to *P. flexilis*. Mirov (1961:34-35), after analysis of the gum turpentines of *P. flexilis* and *P. reflexa* concluded that they should be regarded as separate species. A preliminary investigation of *P. flexilis* and *P. reflexa* disclosed that the species were attacked by different forms of dwarf mistletoe (*Arceuthobium campylopodum*). *Pinus flexilis* was attacked by *A. campylopodum* forma *cyanocarpum* and *P. reflexa* by *A. campylopodum* forma *blumeri* (Hawksworth, F. G. 1962. Personal communication to Dr. J. W. Andresen, Dept. of Forestry, Michigan State University).

During the past decade the views of the U. S. Forest Service dendrologist, E. L. Little, Jr., have changed from the position that the complex should be treated as the species *P. flexilis* with varieties *flexilis* and *reflexa* (Little 1950:13-14, 1953:265-266) to the view that the more correct treatment would be to designate the two as separate species, namely *P. flexilis* James and *P. strobiformis* Engelm. (Keng and Little 1961, Little 1962:88).

For comparative purposes the descriptions assigned to members of the complex by some of the more prominent authors are presented in Table 1.

A summary of the preceding literature review yields the following synonymy:

Pinus flexilis James.

Pinus flexilis James, Account of an expedition from Pittsburg to the Rocky Mountains. II:27 and 34-35 (1823).

Pinus lambertiana var. *β* Hooker, Flora Boreali-Americana. II:161 (1838).

Table 1. Comparison of descriptions assigned to members of the *Pinus flexilis* complex by various authors.

	Leaf characteristics			Cone characteristics		
	Length (mm)	Serration	Dorsal stomata	Length (mm)	Scale reflexing	Apophysis elongation
Northern population						
P. flexilis						
Engelmann (1863)	30-50	slight	present	75-115	--	--
Sargent (1897)	40-75	none or slight	--	75-255	none or slight	--
Shaw (1914)	30-90	none	present	65-255	none or reflexed	often prolonged
Little (1950)	30-65	slight	2 rows	100-200	none	none
Southern population						
P. flexilis v. *reflexa* = *P. reflexa*						
Engelmann (1882)	--	slight	none	100-200	yes	yes
Martínez (1948)	65-115	serrate	none	125-225	yes	yes
Little (1950)	40-75	--	0(1-2) rows	--	much reflexed	yes
P. strobiformis						
Engelmann (1848)	65-75	slight	--	255	--	--
Sargent (1897)	90-100	distinct or none	none	125-225	much reflexed	--
P. ayacahuite v. *brachyptera*						
Shaw (1914)	100-200[a]	serrate	none	200-500	pronounced	pronounced
Martínez (1948)	90-125	serrate	none	150-300	pronounced	pronounced

[a] Shaw's description applies to *P. ayacahuite in toto*.

Pinus lambertiana var. *B. brevifolia* Endl., Synopsis coniferarum. 150 (1847).

Apinus flexilis (James) Rydb., Bull. Torr. Bot. Club. 32:258 (1905).

Pinus strobiformis Engelmann.

Pinus strobiformis Engelm., Sketch of the botany of Dr. A. Wislizenus's expedition. Sen. Misc. Doc. No. 26 (1848).

Pinus flexilis var. *α serrulata* Engelm. Coniferae of Wheeler's expedition. *in* Report upon U.S. geographical surveys west of the one hundreth meridian. VI:258 (1878).

Pinus flexilis var. *β macrocarpa* Engelm. Coniferae of Wheeler's expedition. *in* Report upon U.S. geographical surveys west of the one hundreth meridian. VI:258 (1878).

Pinus flexilis var. *γ reflexa* Engelm. Coniferae of Wheeler's expedition. *in* Report upon U.S. geographical surveys west of the one hundreth meridian. VI:258 (1878).

Pinus flexilis var. *megalocarpa* Sudworth. Nomenclature of the arborescent flora of the United States. USDA, Div. of For. Bull. No. 14:17 (1897).

Pinus reflexa Engelm.. Bot. Gaz. 7:4 (1882).

Pinus ayacahuite Ehrenb.. Linnaea. 12:492 (1838).

Pinus ayacahuite var. *strobiformis* Sargent ex Lemmon. Handbook of west-American cone-bearers. 4 (1892).

Pinus ayacahuite var. *reflexa* Voss. Deut. Dendrol. Gesell. Mitt. 16:92 (1907).

Pinus ayacahuite var. *brachyptera* Shaw. Pines of Mexico. Pubs. Arnold Arb. No. 1:11 (1909).

Experimental Study of Variation and Speciation

The transition from the observational to the experimental approach in taxonomic investigation permitted greater evaluation of variation in morphological characteristics. Experimentation allowed an estimate of the degree to which variation was due to the genetic potential of the organism and the degree to which the final expression was influenced by differences in the environment.

Recent studies which have examined the relative importance of heredity, environment, and their interactions received their prime impetus from the extensive investigations of Turesson (1922a, 1922b, and 1930). This Swedish worker grew specimens of numerous herbaceous species from a variety of habitats together in a common garden and compared the resultant plant forms with those found in native habitats. He recognized the differences between populations from different environments and the part played by the local conditions in altering the genetic composition of the population of a particular area. At the same time, Turesson called special attention to the variability present in all populations. The variability was often masked by the special environmental conditions in effect in the native habitat but was readily seen and compared with that of other populations in the common test site. Turesson (1922a) proposed the term "ecotype" to apply to an ecological unit to cover "the product arising as a result of the genotypical response of an ecospecies to a particular habitat". He inferred discontinuity between ecotypes but did not stress the point very much.

Extensive transplanting studies were conducted in California by Clausen, Keck, and Hiesey (1940). They utilized three transplanting areas at elevations of 30, 1400, and 3050 meters. Clonally propagated material from each collection was transplanted to each area. More than 50 species were studied. Each species was represented by several specimens from a number of locations. Transplants were generally taken from an east-west transect from Montara on the Pacific Coast west of Palo Alto, thence through the Coast Ranges, San Joaquin Valley, and Sierra Nevada to Benton in the Great Basin. For a few species the collection area was extended north to southern Oregon and south to southern California.

Each species maintained its identity when transplanted into the new environments. Although extensive modification of some organs occurred the modified parts did not assume the form characteristic of other species. The results showed that species differences were strongly controlled by hereditary factors rather than being mere adaptations to envirnomental conditions.

Maritime and Coast Range clones were usually reduced in size at the mid-altitude station, Mather. At the Timberline station they were unable to set ripe seed and soon died. The dormant period of mid-altitude plants was considerably shortened at the lowest station, Stanford. Mid-altitude forms generally made greatest growth at the mid-altitude station, with less at the low-altitude station, and a great reduction at Timberline. High-elevation clones generally made greater growth at the mid-elevation station than at Timberline but less at Stanford. Other characteristics which showed extensive modification included; number of stems per propagule, number of flowers per stem, size of leaves, time of flowering, and length of dormant period.

In a review paper on the study of ecotypic variation, Böcher (1963) called attention to the idea that the most important goal of comparative cultivations should be the study of the variation itself and the factors responsible for the variation. He proposed the separation of taxonomical and morphological motivations.

History of Provenance Testing in Forest Trees

Extensive general reviews of the provenance testing literature may be found in the works of Kalela (1937), Schütt (1958), or Wright (1962). The first provenance test to be reported in the literature was initiated by a French nurseryman, Louis de Vilmorin during the years 1820 to 1850. He made several unreplicated plantings of Scotch pine (*Pinus sylvestris* L.) from different origins (cited from Wright 1962:142). Numerous investigations similar to those of de Vilmorin during the remainder of the century led to the establishment of a several-nation co-operative study under the auspices of the International Union of Forest Research Organizations (IUFRO) in 1907. Wiedemann (1930) compiled and compared the results obtained in the various plantations which survived the war years.

An extensive study of the variability of foliar dry matter content and the relation of this measure to frost hardiness of Scotch pine seedlings was undertaken by Langlet (1936) in Sweden in the early 1930's. He collected seed from 582 areas in Sweden and grew the resultant seedlings for 2 years in an unreplicated nursery trial. In 1936 the IUFRO Congress initiated another series of studies on variability in Scotch pine, Norway spruce [*Picea abies* (L) Karst], and European larch (*Larix decidua* Miller).

In 1952 Veen (1952) visited most of the test plantations and recommended measurement procedures. The Czechoslovakian, New Hampshire, and Michigan plantings of Scotch pine have been the subject of published reports covering variation in several growth, wood, and chemical properties.

After 1945 many geographic variation studies were initiated. In the United States two large co-operative tests were organized. The Southwide Pine Seed Source Study was initiated in 1951. Collections were made and plantation established in 16 states (Wakely 1961). These studies have been carried out with the four southern pines: P. echinata Mill., P. elliottii Engelm., P. palustris Mill., and P. taeda L.. Approximately 50 collection areas and slightly over 100 plantations are included in the study. These plantations, in addition to providing a study of variation, can also provide materials for intra- and inter-specific hybridization programs. In the north central states the NC-51 program was initiated in 1960. Co-operating agencies in 10 states are currently conducting geographic variation studies in 9 species. In several of the NC-51 tests, the progeny of individual trees have been kept separate to allow examination of the relative amounts of within-and between-stand variation. Currently, variation studies are being conducted on some three-score species throughout the world.

During the past century many changes have occurred in the design, analysis, and philosophy of studies of geographic variation. For example, in Scotch pine, sampling intensity has varied from 12 widely scattered origins in the 1907 IUFRO test, to 582 origins from Sweden alone, in Langlet's study during the 1930's. At present, most studies attempt to get a broad, even sampling for the initial phase of a test and a more intensive sampling in follow-up studies in areas of special interest.

In early variation studies little consideration was given to the test design. Consequently, the conclusions to be drawn from such tests were very limited. Then experiments began, about 1940, to follow the work in other fields such as agriculture and horticulture. Ideas and practices on replication, plot size and shape, and selection of test areas were adapted to forestry problems. Finally, experiments were conducted to devise experimental designs which were specifically intended to provide the information desired. Prior to 1940 most tests utilized either short-term nursery results or field plantation measurements but not a combination of both. Analyses have progressed from the stage of recognition of differences between areas of origin, to comparison of growth of seedlings to that of the stands where the seeds were collected, to comparison of growth at early and later ages, and finally to the evaluation of differences between and within stands from a particular region.

The philosophy behind variation studies has changed as much as the methods employed. The early tests were set up to examine the existence and extent of possible differences between various origins of a species. Soon afterwards the practical approach of testing to find the most suitable source for making seed collections became prominent.

This practical attitude continues at present but is tempered to allow or encourage the simultaneous investigation of theoretical aspects as well. Included in this latter category are the study of variability of anatomical features and physiological processes, the evaluation of taxonomic affinities through breeding tests, the study of ways to improve experimental design and analysis, and the determination of heritability estimates for use in future selection and breeding programs.

The literature on geographic variation in trees is too voluminous to be reviewed completely here. However, work done with species which grow in areas where *Pinus flexilis* grows and with species related to *P. flexilis* will be reviewed.

Geographic Variation in Rocky Mountain Conifers

Ponderosa pine (*Pinus ponderosa* Laws.).--A 21-origin provenance test of ponderosa pine was started at Priest River, Idaho in 1911. The test contained a single plot of each origin. When examined at age 40 there was a good correlation between height at age 12 and at age 40 (Squillace and Silen 1962). In an earlier report on the same test Weidmann (1939) presented evidence for close correspondence between growth rate of the progeny and growth rate of trees in the

parental locality. Differences in several traits were evident. There was a 5 to 3 growth rate difference between the fastest growing trees from northern Idaho and the slowest growing ones from eastern and southern origins. South Dakota trees had a high proportion of two-leaf fascicles as compared to others which had mostly three. One California seedlot was completely eliminated by sudden freezing weather.

A second provenance test was started in 1926 that included 10 origins and outplantings at six locations in Washington and Oregon. Two-year nursery heights were strongly correlated with 30-year plantation heights (Squillace and Silen 1962). These same authors compared the results of these two studies and a third one conducted in New Zealand and found very close agreement in the relative heights of progenies from similar regions in all three tests.

The effect of altitude of origin on seedling growth has been followed for a 20-year period in California (Mirov et al. 1952, Callaham and Metcalf 1959, and Callaham and Liddicoet 1961). Until age 12, mid-elevation origins outgrew low-and high-elevation ones at all three planting sites (290, 830, and 1700 meters). At 15 years, Callaham and Hazel (1961) found a significant correlation between the second year growth increment and 15-year height. They also found that within elevational zones, 39 percent of the variation in height growth was due to genetic causes. By age 20, differences due to elevation of origin had disappeared at the high-altitude but not at the other test sites. At all ages high-elevation origins performed poorly at low-and mid-elevation planting sites.

In a 2-year nursery test of 60 origins grown in Michigan, Wells (1962) found a sharp break between sources from Arizona and southern New Mexico and those from farther north. Seedlings of these southern interior origins grew taller, had longer leaves, and formed a greater number of secondary leaves in the first year than did others. There was approximately a 2 to 1 difference between the greatest and the least development in these characters. Northern origin progenies of the coastal variety formed more terminal buds in the first year than southern ones and were less subject to winter injury.

Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco].--A test of 120 single tree progenies from 13 coastal sources was started in 1912 in Washington and Oregon (Munger and Morris 1936 and 1942). The first seedlings were outplanted in 1915 to six test areas. The individual progenies were planted in the same sequence in each plantation. A second, smaller replicate was planted at each site a year later. There were no significant relationships between the maternal parent's altitude of origin, age, or soil type and growth of the progeny. Two seed source progenies from Granite Falls and Darrington, Washington exceeded the height-growth average for all stocks on every plantation. Time of bud-bursting was studied on three of the plantations by Morris et al. (1957). The three earliest and latest origins to burst buds did so very consistently in all areas. Relative time of bud-bursting was related to the spring temperature pattern at the place of origin. Sources from areas with warm days and cold nights began growth later than those from areas where warm days and nights were prevalent.

In a 24-year-old German test of Douglas-fir from Colorado, Oregon, Washington, and British Columbia, the Colorado progenies grew very slowly in all test areas (Schober 1954 and Schober and Meyer 1955). They were also very susceptible to needle blight and frost damage. Coastal Washington sources performed best in maritime planting areas and those from the Fraser River Valley of British Columbia performed best at intermediate elevations.

Douglas-fir from a high-elevation New Mexican source showed the best survival and growth after 5 years in the field in a New Hampshire test (Baldwin and Murphy 1956). Among the remaining three origins, those from Idaho were next best and were followed by Montana and California progenies. In a 19-origin Christmas tree test in Pennsylvania, seedlings from the central and southern Rocky Mountains were heavily damaged by late spring frosts but did not suffer from winter cold (Byrnes et al. 1958). Coastal and western interior sources were heavily damaged by cold winters but not by late spring frosts.

In an Oregon test involving only origins of the coastal variety of Douglas-fir, Irgens-Möller (1958) found that higher elevation progenies grew less at Corvallis than lowland origins because they stopped growth earlier in the season. Two-year nursery results from another Oregon test of Oregon, Washington, and British Columbia sources showed that most northern sources were faster growing than southern ones (Ching and Bever 1960). Most northern sources also had longer leaves. Southern sources began growth earlier and continued to grow longer than northern ones.

First-year results from a 135 origin test in Michigan show origins from extreme northern Idaho and adjacent Montana to be the fastest growing ones from the Rocky Mountains (personal communication from Dr. J. W. Wright, Dept. of Forestry, Michigan State University).

Lodgepole pine (*Pinus* *contorta* Dougl.).--Most early studies of the species were concerned primarily with the differences between the coastal and inland forms and not with variation within regions. For an extensive review of these works see Edwards (1954 and 1955). However, Critchfield's (1957) study of *P. contorta* was quite similar to the present investigation. He utilized both seedlings and parental specimens in analysing variation patterns. However, in his study the emphasis was placed on the parental specimens. In contrast, the seedlings were considered of greater importance in the present study. His study also sought to clarify the complex nomenclatural and taxonomic treatment of the species.

Samples of lodgepole pine were collected from 40 native stands throughout the species' range during the 4-year period from 1952 to 1955. Leaves from adult trees growing in the Sierra Nevada were wider, on the average, than those from other geographic regions. An increase in leaf width with an increase in altitude was also observed. Mendocino Coastal and White Plains populations were distinct from all others in their lack of leaf resin canals. Leaves from interior stand collections were slightly longer than those from coastal collections. However, for seedling materials, leaves from interior sources were shorter than those from coastal sources.

The angle between the cones and the branch on which they were borne was much more uniform for coastal *P. contorta* sources than for those from the interior. In particular, cones from the northern Rocky Mountain collections had grown at a wide variety of angles.

Frequently the cone position overlapped the angular range characteristic of Pinus banksiana Lamb.. These results supported the earlier observations of Moss (1949) of hybridization and introgression between P. contorta and P. banksiana in Alberta.

With regard to the specific gravity of cones, those from the Rocky Mountains had the highest values and those from the Sierra Nevada the lowest. Cones from the coastal regions and the Cascade and Blue Mountains had intermediate values. The light cones from the Sierra Nevada usually shed their seed soon after maturity and did not persist for long on the tree. The denser cones from other regions were often indefinitely indehiscent and persistent.

On the basis of his findings, Critchfield assigned subspecific rank to the four most distinct elements of the species.

White fir [Abies concolor (Gord. and Glend.) Hoopes].-- The first preliminary results of a geographic origin study being conducted jointly by Michigan State University and the University of California indicated that among southern Rocky Mountain origins those seedlings from Arizona and southern New Mexico grew fastest, had long and straight leaves, and were light in color (personal communication from Dr. J. W. Wright, Dept. of Forestry, Michigan State University). Seedlings from Utah were shortest, had shorter and curved leaves, and were darder colored. Northern New Mexico and Colorado origins were intermediate.

Geographic Variation in the White Pines

Eastern white pine (Pinus strobus L.).--In a test of 67 origins from the vicinity of Petersham, Massachusetts, Pauley et al. (1955) found only random variation in growth rate. For another portion of the test involving sources from scattered locations throughout the species range, seedlings of Massachusetts origins grew fastest during the first two years while those from more distant sources grew progressively slower. After 14 and 15 years growth in field tests, the local origins were superior with regard to diameter growth.

Results of a rangewide test of P. strobus initiated by the Northeastern Forest Experiment Station in 1957 have been reported from three areas: (1) New Jersey (Santamour 1960), (2) Southern Appalachians (Sluder 1963), and (3) southern Michigan (Wright et al.

1963). In all areas seedlings from the more southern origins have made the fastest growth. Contrary to the expected reaction, seedlings of northern origins had the most lammas shoot growth in Michigan.

Western white pine (*Pinus monticola* Dougl.).--Differences in growth rate were found among progenies originating as little as one-half mile apart in Idaho by Squillace and Bingham (1958). Seedlings produced by moist site and low elevation sources grew faster on the lower and better planting sites than did those from dry or high sources. At high elevation planting sites seedlings from high sources did best after recovering from nursery and transplanting effects.

At Placerville, California, 15-year height of *P. monticola* seedlings from Idaho is greater than that of California Sierra Nevada sources.

Limber pine (*Pinus flexilis* James).--Although the botanical descriptions of members of the *Pinus flexilis* complex indicate considerable variation in morphological traits there has been very little systematic investigation of the variation. A study of the variability present in native *P. flexilis* stands in Colorado was begun by Douglas and Douglas (1955), but illness forced discontinuation of the work.

MATERIALS AND METHODS

Materials

Acquisition.--The study was initiated in June of 1959 by Dr. J. W. Andresen of Michigan State University. Requests for seed from several widely scattered areas throughout the range of the complex were sent to selected co-operators. A portion of the seed received was planted in 1960 to determine the best methods of handling the larger scale test which was to follow.

The majority of the collections for the study were made in 1960. To provide the widest possible sample of naturally occuring populations of the complex, U.S. Forest Service personnel, state foresters, and botanists were asked to co-operate in making the collections. The co-operators were asked to gather cones and a foliage specimen from up to 10 trees per stand and to keep the materials from each tree separate. Edaphic, ecologic, and geographic data pertinent to the collection sites was also requested. All collections were forwarded to East Lansing, Michigan for further processing. In addition, Dr. Andresen has spent the summers of 1960 to 1962 supplementing the collections and notes of the co-operators. The distribution of collections is presented in Figure 3.

Handling.--When the collections arrived in East Lansing they were assigned accession numbers in accordance with the Michigan State Forest Genetics (MSFG) system of identifying new acquisitions. The cones were dried to facilitate seed extraction and the foliage specimens were dried and pressed in preparation for mounting on herbarium sheets. After the seeds had been removed, the cones and foliage specimens were stored for later measurements and observations. The seeds were cleaned after extraction to eliminate foreign materials and then placed in 95% ethyl alcohol to float off any that were not completely filled. The alcohol flotation technique does not distinguish between seed which are filled and have a sound, living embryo and those which are filled but not sound. It also may eliminate some seeds which have germinative potential even though not completely filled.

The filled seed were placed in cold storage at 45° F. until sowing time some 180 days later. The seed were not stratified because of a

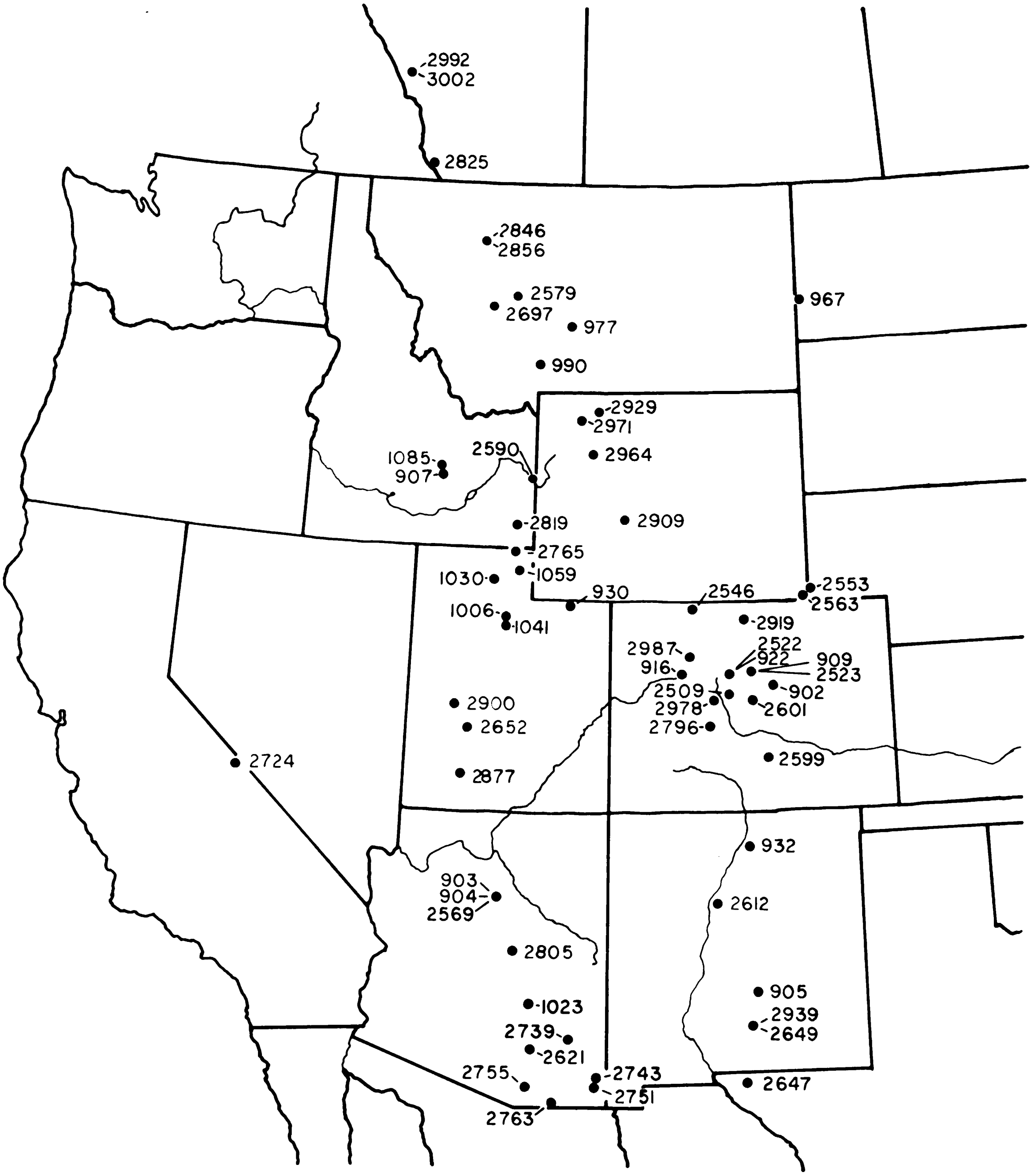


Figure 3. Location of stands sampled for this study.

desire to test the effect of place of origin on time of germination. In all, seed from 325 collections representing 61 stands, have produced seedlings for this study.

Methods

Design and installation of the nursery test.--A randomized complete block design with four replications was used in planning and establishing the experiment. Plots within replicates consisted of a single row which contained seed from a single tree with the exception of seven of the collections made in 1959. In each of these seven collections seed from several trees had been mixed together.

Planting was done at the Bogue Experimental Nursery on the Michigan State University campus on May 20, 1961. The nursery soil was a sandy clay loam. It had been maintained at a high fertility level prior to the test. No fertilizers were applied during the course of the experiment. The nursery beds had been treated with "MILON", a combination fungicide and herbicide, in the autumn of 1960. The seed were planted at 4 centimeter intervals in rows 100 centimeters long. The rows were perpendicular to the length of the bed and were 15 centimeters apart. Seeding was started at the north end of each row to provide a common reference point for those cases where sufficient seed was not available to fill the row. Accurate spacing was accomplished by using a steel tape measure and a wooden template which made a slight depression in the soil at each seed-spot. After sowing, a thin layer of fine sand was spread over the seed. The nursery beds were lined with 4-inch boards which served to prevent disturbance of the edges. The boards were also used to support wire screen and lath to provide shade and protect against bird damage.

Adequate soil moisture was maintained by sprinkler irrigation. Weeding was done by hand in conjunction with regular measurement activities. A one-half-inch sawdust mulch was applied in November of 1961 to reduce seedling damage by frost heaving.

Measurement of seedling traits.--Traits chosen for analysis in this study are listed in Tables 2 and 3. The criteria for selecting a trait was either: (1) That it exhibited such pronounced row-to-row differences as to make the presence of between-progeny differences

Table 2. Two-year growth data for Pinus flexilis progenies, summarized by stand-progeny.

MSFG Number	State or Province	Number of Progenies in Stand	North Latitude	East Longitude	Elevation	Date of Mean Germination (1)	Date of Bud Set (2)	Length of Growing Season (3)	Cotyledon Number (4)	Cotyledon Length (5)	Diameter of Hypocotyl (6)	Trees Forming Secondary Leaves in First Year (7)	1-year Foliage Color (8)	2-year Foliage Color (9)	Length of Secondary Leaves (10)	Degree of Leaf Serrulation (11)	Number of Dorsal Stomatal Rows (12)	1-year Height (13)	2-year Height (14)	Amount of Second Growth Increment (15)
		no.	° '	° '	feet	day of year		days	no.	mm.	mm.	%	--grade---		mm.	grade	no.	------mm.------		
2992	Alta.	7	51 00	115 10	4700	200	250	50	8.4	26	1.0	10	2.4	3.6	30	0.0	1.8	25	43	5
3002	Alta.	7	51 00	115 10	4200	166	229	63	8.0	25	1.1	10	1.7	3.1	25	0.0	1.6	25	43	3
2825	Alta.	9	49 20	114 20	5100	172	236	64	8.8	25	1.0	15	2.1	3.6	25	0.2	1.5	28	43	2
2846	Mont.	10	47 50	112 40	5800	212	243	31	8.6	25	1.0	5	1.9	3.3	23	0.1	1.6	25	43	3
2856	Mont.	8	47 50	112 40	5000	216	250	34	8.8	26	1.0	10	1.8	3.0	25	0.1	1.5	23	41	3
2579	Mont.	1	46 50	111 43	7800	181	229	48	8.4	20	1.0	45	3.0	3.2	30	0.0	1.5	28	48	8
2697	Mont.	4	46 36	112 20	7200	214	257	43	9.0	23	1.0	5	1.9	3.2	23	0.2	1.4	20	41	3
977	Mont.	8	46 15	110 15	6500	205	236	31	9.0	26	1.1	10	1.6	3.2	25	0.5	1.5	25	43	2
990	Mont.	2	45 28	111 02	7200	217	250	33	9.0	23	1.0	15	1.5	3.1	25	0.0	1.5	25	48	5
967	N. Dak.	5	45 45	104 00	2500	211	264	53	9.0	27	1.2	10	2.0	3.3	28	0.1	1.6	30	48	5
2929	Wyo.	10	44 45	109 20	6300	188	243	55	9.2	28	1.3	20	1.8	3.4	30	0.3	1.4	30	53	8
2971	Wyo.	3	44 29	109 49	----	175	250	75	9.8	24	1.0	30	2.0	3.0	30	1.0	2.0	30	56	10
2964	Wyo.	3	43 48	109 35	6500	180	229	49	8.4	26	1.0	25	1.4	3.2	28	0.7	1.8	30	51	8
1085	Idaho	4	43 27	113 35	5800	209	250	41	9.2	28	1.2	10	1.6	3.2	30	1.0	2.0	30	53	8
907	Idaho	-[a]	43 20	113 30	5000	198	257	59	9.8	32	1.5	10	2.5	3.2	36	0.0	2.5	30	53	8
2590	Idaho	2	43 18	111 05	6000	217	250	33	8.8	33	1.8	15	1.5	3.8	33	0.5	2.0	36	66	13
2819	Idaho	1	42 25	111 31	8900	212	250	38	8.8	26	1.0	15	2.0	3.8	30	1.0	1.5	30	58	13
2909	Wyo.	10	42 33	108 45	8300	189	236	47	8.0	24	1.0	15	1.6	3.2	25	0.1	1.7	28	46	5
2765	Utah	3	42 10	111 30	7200	193	243	50	9.0	26	1.1	15	2.1	3.3	30	0.0	1.6	25	53	10
1059	Utah	1	41 35	111 20	8500	200	250	50	8.4	27	1.0	55	1.2	4.0	30	0.0	2.0	25	51	5
1030	Utah	7	41 22	112 02	9300	200	236	36	9.2	28	1.2	15	1.7	3.1	28	0.0	1.6	30	48	5
930	Utah	-[a]	40 55	110 08	7800	190	243	53	7.8	27	1.0	20	1.0	2.2	30	0.0	1.5	36	56	13
1006	Utah	3	40 40	111 40	9700	202	250	48	9.8	30	1.4	10	1.8	3.2	36	1.0	1.0	38	58	10
1041	Utah	2	40 31	111 41	9600	194	229	39	8.6	28	1.0	25	1.8	3.1	28	0.5	2.2	25	46	8
2553	Nebr.	10	41 40	104 02	5200	188	271	83	10.0	27	1.7	5	2.3	4.2	38	0.2	2.1	38	61	10
2563	Wyo.	5	41 00	104 04	5300	179	264	85	9.6	32	1.8	0	2.8	4.2	43	0.4	2.0	41	58	5
2724	Calif.	10	37 30	118 10	10000	187	236	49	7.2	24	1.0	25	1.9	3.4	25	0.2	1.6	23	43	5
2546	Colo.	4	40 50	106 58	8800	213	264	51	8.2	29	1.1	20	1.7	3.2	33	0.2	2.0	28	48	8
2919	Colo.	2	40 38	105 41	10200	171	250	79	9.2	24	1.0	15	1.6	3.8	28	0.0	2.0	20	41	5
2522	Colo.	1	39 40	106 08	9900	198	250	52	8.2	24	1.0	15	1.8	3.0	20	0.0	2.0	25	41	0
922	Colo.	7	39 32	106 08	9900	171	236	65	8.0	26	1.1	25	1.6	3.4	28	0.1	1.6	28	46	5
909	Colo.	7	39 40	105 36	10600	166	236	70	7.8	27	1.2	20	1.6	3.3	28	0.0	1.7	28	48	8
2523	Colo.	6	39 36	105 36	10500	190	243	53	8.2	25	1.0	10	1.7	3.6	25	0.1	1.8	25	46	5
2509	Colo.	10	39 13	106 05	10900	173	236	63	8.2	25	1.1	30	1.5	3.6	30	0.3	2.0	28	46	5
2601	Colo.	10	39 05	105 33	10600	187	250	63	8.6	27	1.2	10	1.9	3.6	28	0.1	1.8	28	48	8
2987	Colo.	2	39 55	107 05	8300	175	236	61	8.6	27	1.4	10	1.6	3.2	28	0.2	1.7	30	64	13
916	Colo.	5	39 36	107 14	9300	209	257	48	8.4	29	1.2	15	1.8	3.4	33	1.0	2.0	30	56	10
2978	Colo.	6	39 05	106 28	11000	163	236	73	8.6	28	1.5	15	2.0	3.5	33	0.2	1.9	33	56	10
902	Colo.	-[a]	39 20	105 00	8500	166	243	77	9.6	28	2.0	10	2.2	4.0	36	0.0	2.0	38	64	15
2900	Utah	9	39 00	112 50	9500	210	250	40	9.4	30	1.6	10	2.4	3.5	33	0.4	1.7	33	61	13
2652	Utah	10	38 31	112 31	8500	200	250	50	9.8	29	1.6	15	2.3	3.4	36	0.3	1.8	41	69	13
2877	Utah	3	37 40	112 40	8600	167	236	69	9.4	30	1.8	10	2.0	3.5	33	0.0	2.0	41	66	13
2796	Colo.	5	38 36	106 38	9800	169	250	81	9.4	32	1.8	10	3.2	4.0	36	0.0	1.7	43	74	18
2599	Colo.	2	38 00	105 10	9000	167	250	83	9.2	31	2.0	0	2.6	4.1	30	0.0	2.0	41	66	10
2612	N. Mex.	3	35 12	106 27	10500	167	264	97	10.4	28	1.9	0	3.2	4.6	33	0.8	1.9	43	74	13
Standard deviation of a progeny mean						4.8	10.5	7.1	0.5	1 0	0.2	5.0	0.3	0.2	3.5	0.1	0.4	3.3	5.8	4.1
$LSD_{.05}$ between progeny means						16.8	37.1	24.8	1.6	3.5	0.6	17.5	0.9	0.8	10.7	0.4	1.3	11.7	20.6	14.2
$LSD_{.01}$ between progeny means						21.1	46.2	31.2	2.0	4.4	0.7	22.0	1.1	1.0	15.4	0.5	1.7	14.5	25.7	17.9

[a] Collected for the pilot study -- progenies within the stand grouped at time of collection.

KEY TO GRADES

Character	(8) 1-year Foliage Color	(9) 2-year Foliage Color	(11) Degree of Leaf Serrulation
Grade 0			Serrulations absent or extremely minute and very scarce
Grade 1	Yellow-green	Yellow-green	Serrulations few in number and minute but readily discernable
Grade 2	Light green	Light green	Serrulations prominent and numerous
Grade 3	Green	Green	
Grade 4	Dark green	Dark green	
Grade 5	Blue-green	Blue-green	

Table 3. Two-year growth data for Pinus strobiformis progenies, summarized by stand-progeny.

MSFG Number	State or Province	Number of Progenies in Stand	North Latitude	East Longitude	Elevation	Date of Mean Germination (1)	Date of Bud Set (2)	Length of Growing Season (3)	Cotyledon Number (4)	Cotyledon Length (5)	Diameter of Hypocotyl (6)	Trees Forming Secondary Leaves in First Year (7)	1-year Foliage Color (8)	2-year Foliage Color (9)	Length of Secondary Leaves (10)	Degree of Leaf Serrulation (11)	Number of Dorsal Stomatal Rows (12)	1-year Height (13)	2-year Height (14)	Amount of Second Growth Increment (15)
		no.	° '	° '	feet	day of year		days	no.	mm.	mm.	%	--grade---		mm.	grade	no.	------mm.-----		
903	Ariz.	-[a]	35 20	111 40	9600	171	264	93	11.2	31	2.2	0	3.2	4.5	56	0.0	2.0	64	117	37
904	Ariz.	-[a]	35 20	111 40	9100	170	271	101	11.0	29	2.2	5	3.8	4.8	51	1.0	1.5	69	99	25
2569	Ariz.	5	35 20	111 42	8800	165	264	99	11.4	36	2.8	0	3.6	4.4	53	0.8	1.4	76	142	36
2805	Ariz.	7	34 26	111 11	7400	166	271	105	10.8	35	2.4	0	4.2	5.0	69	1.6	0.6	69	127	33
1023	Ariz.	5	33 18	110 50	7700	175	278	103	11.2	37	2.9	0	4.7	5.0	76	1.3	1.0	76	130	31
2739	Ariz.	2	32 40	109 55	8400	163	271	108	13.2	37	3.0	0	4.9	5.0	69	1.0	1.8	94	150	28
2621	Ariz.	7	32 26	110 46	8000	185	285	100	11.4	38	2.8	0	4.6	5.0	71	1.4	0.3	71	135	43
2743	Ariz.	5	31 55	109 15	7600	178	285	107	12.0	37	2.7	0	4.1	4.7	66	1.4	1.0	71	109	15
2755	Ariz.	3	31 41	110 51	6500	170	278	108	12.4	34	2.0	0	4.0	5.0	58	1.0	1.5	76	94	18
2751	Ariz.	3	31 46	109 15	8000	167	285	118	14.0	40	2.6	0	3.4	4.4	74	1.1	1.0	66	117	20
2763	Ariz.	1	31 24	110 18	7200	163	292	129	12.0	36	2.8	0	5.0	5.0	86	2.0	0.2	91	135	18
932	N. Mex.	-[a]	36 20	105 40	7000	171	264	93	11.6	30	2.2	0	4.2	4.8	61	1.0	2.5	76	124	28
905	N. Mex.	-[a]	33 33	105 34	8000	176	285	109	11.8	37	2.8	0	4.5	4.8	61	2.0	1.5	74	127	28
2649	N. Mex.	2	32 57	105 44	8700	163	264	101	12.4	37	3.0	0	4.9	5.0	53	1.0	2.0	84	150	33
2939	N. Mex.	2	32 57	105 44	8700	159	278	119	12.0	38	3.0	0	4.0	5.0	69	0.5	1.5	64	140	56
2647	Texas	2	31 51	105 50	7700	170	285	115	12.6	39	3.0	0	4.5	5.0	69	1.5	1.8	89	119	23
Standard deviation of a progeny mean						4.8	10.5	7.1	0.5	1.0	0.2	5.0	0.3	0.2	3.5	0.1	0.4	3.3	5.8	4.1
$LSD_{.05}$ between progeny means						16.8	37.1	24.8	1.6	3.5	0.6	17.5	0.9	0.8	10.7	0.4	1.3	11.7	20.6	14.2
$LSD_{.01}$ between progeny means						21.1	46.2	31.2	2.0	4.4	0.7	22.0	1.1	1.0	15.4	0.5	1.7	14.5	25.7	17.9

[a] Collected for the pilot study -- progenies within the stand grouped at time of collection.

KEY TO GRADES

Character	(8)	(9)	(11)
	1-year Foliage Color	2-year Foliage Color	Degree of Leaf Serrulation
Grade 0			Serrulations absent or extremely minute and very scarce
Grade 1	Yellow-green	Yellow-green	Serrulations few in number and minute but readily discernable
Grade 2	Light green	Light green	Serrulations prominent and numerous
Grade 3	Green	Green	
Grade 4	Dark green	Dark green	
Grade 5	Blue-green	Blue-green	

likely, or (2) That considerable variation in the trait had been reported in the species' descriptions. The validity of the assumption of differences was tested by analysing data from the pilot study. Measurements were always begun at the start of replicate one and continued in sequence to the end of replicate four. To reduce bias, the measurement for each plot was obtained before the identity of the row was checked. The plot mean is the measure used in all computations.

1. Germination date was recorded for all seed in each plot. Seedlings were recorded when the hypocotyl became visible. Germination counts were made twice a week for 5 weeks after the first seedlings appeared. Further observations were recorded at weekly intervals for 4 weeks and then at 3-week intervals until the ground froze in November. Mean germination date was calculated as follows:

$$\bar{x} = \frac{f_a x_a + f_b x_b + f_c x_c \; . \; . \; . \; . \; . \; . \; . + f_n x_n}{f_a + f_b + f_c \; . \; . \; . \; . \; . \; . \; . + f_n}$$

where $\bar{x}$ = day of the year mean germination was reached.

x_a, x_b, x_c, etc. = day of the year for the mid-point of each observation period.

f_a, f_b, f_c, etc. = number of seeds germinated since the previous examination.

2. Date of bud set, or terminal bud formation was recorded at weekly intervals. Bud set was reported to have occurred when one-fifth (1/5) of the seedlings in a plot had visible terminal buds.

3. Length of growing season was obtained by subtracting date of germination from date of bud set.

4. Cotyledon number was obtained by counts of five seedlings per plot.

5. Cotyledon length was measured on the longest cotyledon on each of the same five seedlings used to determine number.

6. Diameter of hypocotyl was estimated to the nearest 1 millimeter for the plot as a whole.

7. The percentage of seedlings forming secondary leaves in the first year was determined by counting.

8,9. First- and second-year foliage color were recorded according to a series of color grades which were established at the time of observation in November 1961 and September 1962. The seedlings with leaves exhibiting the most yellow coloring were always scored as Grade 1. Seedlings with blue-green foliage were at the other extreme and were scored as Grade 5.

10. Length of secondary leaves was measured to the nearest millimeter on leaves collected at the end of the second growing season. For each plot the sample consisted of one fascicle of leaves from each of five seedlings.

11. Degree of leaf serrulation was scored under a dissecting microscope on leaves from one replicate that had been used for length measurements. The grades used were 0 (no serrulation), 1, and 2 (serrulations prominent and numerous).

12. The number of dorsal leaf surface stomatal rows were counted with the aid of the microscope at the time that the leaf serrulation estimates were made. Incomplete rows were counted as half-rows.

13. First-year height was determined by measuring the tallest and shortest seedlings on each plot. Only epicotyl growth was measured, i.e. the distance from the upper surface of the cotyledons at the point of insertion into the stem to the tip of the terminal bud. The validity of means based on the tallest and shortest seedlings had previously been established by O. O. Wells on ponderosa pine, by J. B. Genys on Japanese larch [Lariz leptolepis (Sieb. and Zucc.) Gord.], and by J. W. Wright on Scotch pine in the same nursery (personal communications).

14. Second-year height was determined by measuring five seedlings on each plot to an accuracy of 1 millimeter.

15. The amount of the second growth increment in the second year was measured from a point 5 millimeters above the last-formed secondary leaves to the tip of the new shoot. The measurements were made on the same seedlings used for second-year height measurements.

Measurement of mature traits on herbarium specimens.--Traits chosen for measurement are listed in Tables 4 and 5. Leaf length,

Table 4. Data for adult characteristics of *Pinus flexilis* trees, summarized by stands.

													Degree of Cone Scale Reflexing		
MSFG Number	State or Province	North Latitude	East Longitude	Elevation	Number of Seed per Gram	Length of Secondary Leaves	Number of Dorsal Stomatal Rows	Degree of Leaf Serrulation	Length of Peduncle	Cone Length	Cone Width	Length of Apophysis	Terminal 1/3 of Cone	Central 1/3 of Cone	Basal 1/3 of Cone
					(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	(25)	(26)
		° '	° '	feet	no.	mm.	no.	grade	mm.	mm.	mm.	mm.	°	°	°
2992	Alta.	51 00	115 10	4700	11	53	2.3	0.1	0	84	51	5	0	30	40
3002	Alta.	51 00	115 10	4200	13	58	2.4	0.0	0	84	46	3	0	30	50
2825	Alta.	49 20	114 20	5100	11	53	2.6	0.1	0	81	53	4	0	10	30
2846	Mont.	47 50	112 40	5800	11	46	2.4	0.0	0	76	48	4	0	20	40
2856	Mont.	47 50	112 40	5000	10	53	2.6	0.3	1	81	51	4	10	50	60
2579	Mont.	46 50	111 43	7800	12	51	2.3	0.0	2	81	51	4	0	0	10
2697	Mont.	46 36	112 20	7200	12	46	2.5	0.3	0	71	53	4	0	10	10
977	Mont.	46 15	110 15	6500	11	43	2.6	0.1	3	86	53	5	0	10	40
990	Mont.	45 28	111 02	7200	12	51	2.7	0.0	3	81	48	4	0	0	20
967	N. Dak.	45 45	104 00	2500	9	53	2.4	0.0	4	84	48	4	0	10	30
2929	Wyo.	44 45	109 20	6300	11	51	2.4	0.1	1	79	48	5	0	30	50
2971	Wyo.	44 29	109 49	----	10	53	2.4	0.5	1	81	51	6	10	30	50
2964	Wyo.	43 48	109 35	6500	11	51	2.4	0.6	1	89	53	6	0	30	50
1085	Idaho	43 27	113 35	5800	9	51	2.2	0.0	2	89	53	7	0	20	50
907	Idaho	43 20	113 30	5000	6	--[a]	---	---	-	---	--	-	--	--	--
2590	Idaho	43 18	111 05	6000	7	46	2.2	1.0	0	86	51	6	0	50	90
2819	Idaho	42 25	111 31	8900	12	51	2.5	0.4	2	86	53	5	0	20	40
2909	Wyo.	42 33	108 45	8300	15	46	2.3	0.1	1	69	43	6	0	20	50
2765	Utah	42 10	111 30	7200	13	46	2.0	0.2	5	76	48	6	0	10	50
1059	Utah	41 35	111 20	8500	10	48	2.5	0.1	5	89	53	5	0	0	10
1030	Utah	41 22	112 02	9300	9	56	2.6	0.2	2	89	56	6	0	0	40
930	Utah	50 55	110 08	7800	10	--[a]	---	---	-	---	--	-	--	--	--
1006	Utah	40 40	111 40	9700	9	56	2.6	0.1	5	91	58	7	10	40	50
1041	Utah	40 31	111 41	9600	10	56	2.5	0.0	5	91	56	6	10	20	50
2553	Nebr.	41 10	104 02	5200	9	58	2.2	0.7	4	91	53	6	0	20	40
2563	Wyo.	41 00	104 05	5300	8	64	2.7	0.8	5	102	56	8	20	50	80
2724	Calif.	37 30	118 10	10000	14	56	2.9	0.1	0	74	51	5	0	0	30
2546	Colo.	40 50	106 58	8800	10	43	2.4	0.0	2	91	56	8	0	50	60
2919	Colo.	40 38	105 41	10200	11	53	2.9	0.0	0	71	53	5	0	0	30
2522	Colo.	39 40	106 08	9900	15	46	2.5	0.0	3	76	51	3	0	0	0
922	Colo.	39 32	106 08	9900	12	--[a]	---	---	-	---	--	-	--	--	--
909	Colo.	39 40	105 36	10600	11	--[a]	---	---	-	---	--	-	--	--	--
2523	Colo.	39 36	105 36	10500	11	46	2.8	0.0	1	74	51	5	0	10	20
2509	Colo.	39 13	106 05	10900	12	53	3.2	0.0	1	81	53	4	0	0	10
2601	Colo.	39 05	105 33	10600	9	53	2.3	0.2	1	89	53	5	0	0	40
2987	Colo.	39 55	107 05	8300	12	53	2.6	0.2	3	71	48	6	0	10	40
916	Colo.	39 36	107 14	9300	10	--[a]	---	---	-	---	--	-	--	--	--
2978	Colo.	39 05	106 28	11000	9	53	2.5	0.3	0	79	53	4	0	20	40
902	Colo.	39 20	105 00	8500	7	--[a]	---	---	-	---	--	-	--	--	--
2900	Utah	39 00	112 50	9500	8	58	2.8	0.5	1	96	58	8	10	40	50
2652	Utah	38 31	112 31	8500	8	--	---	---	2	91	56	5	0	30	50
2877	Utah	37 40	112 40	8600	9	56	2.2	0.1	4	89	56	6	0	10	20
2796	Colo.	38 36	106 38	9800	8	58	2.2	0.1	2	102	61	7	0	30	40
2599	Colo.	38 00	105 10	9000	7	53	2.6	0.1	0	96	56	6	0	10	40
2612	N. Mex.	35 12	106 27	10500	7	48	1.8	0.5	6	96	51	6	0	20	50
Standard deviation of a progeny mean					0.73	2.94	0.16	0.22	1.08	3.78	1.27	0.79	5.01	9.52	7.49
$LSD_{.05}$ between progeny means					2.55	10.3	0.56	0.77	3.78	13.6	4.45	2.64	17.5	33.3	26.2
$LSD_{.01}$ between progeny means					3.21	12.9	0.70	0.97	4.74	16.7	5.59	3.46	22.1	41.8	32.9

[a] Collected for the pilot study -- no parental materials collected.

KEY TO DEGREE OF LEAF SERRULATION GRADES

Grade 0 - Serrulations absent or extremely minute and very scarce
Grade 1 - Serrulations few in number and minute but readily discernable
Grade 2 - Serrulations prominent and numerous

Table 5. Data for adult characteristics of Pinus strobiformis trees, summarized by stands.

													Degree of Cone Scale Reflexing		
MSFG Number	State or Province	North Latitude	East Longitude	Elevation	Number of Seed per Gram	Length of Secondary Leaves	Number of Dorsal Stomatal Rows	Degree of Leaf Serrulation	Length of Peduncle	Cone Length	Cone Width	Length of Apophysis	Terminal 1/3 of Cone	Central 1/3 of Cone	Basal 1/3 of Cone
					(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)	(24)	(25)	(26)
		° '	° '	feet	no.	mm.	no.	grade	mm.	mm.	mm.	mm.	°	°	°
903	Ariz.	35 20	111 40	9600	5	--[a]	---	---	--	---	--	--	--	---	---
904	Ariz.	35 20	111 40	9100	6	--[a]	---	---	--	---	--	--	--	---	---
2569	Ariz.	35 20	111 42	8800	5	69	1.8	0.9	7	99	58	5	0	0	20
2805	Ariz.	34 26	111 11	7400	7	71	1.1	1.3	5	137	64	8	30	50	80
1023	Ariz.	33 18	110 50	7700	6	71	0.5	1.6	11	117	61	9	20	70	90
2739	Ariz.	32 40	109 55	8400	4	76	1.5	1.5	9	132	61	8	30	60	90
2621	Ariz.	32 26	110 46	8000	4	79	0.3	0.9	7	125	61	9	30	80	90
2743	Ariz.	31 55	109 15	7600	5	81	0.7	1.4	12	130	58	12	50	100	130
2755	Ariz.	31 41	110 51	6500	5	84	0.7	1.0	7	120	58	12	70	120	130
2751	Ariz.	31 46	109 15	8000	5	96	0.8	1.2	6	112	56	10	50	90	110
2763	Ariz.	31 24	110 18	7200	4	86	0.0	1.0	12	122	56	13	50	100	100
932	N. Mex.	36 20	105 40	7000	7	--[a]	---	---	--	---	--	--	--	---	---
905	N. Mex.	33 33	105 34	8000	4	--[a]	---	---	--	---	--	--	--	---	---
2649	N. Mex.	32 57	105 44	8700	5	69	1.8	0.7	3	107	53	6	0	70	70
2939	N. Mex.	32 57	105 44	8700	5	81	1.0	1.0	3	112	56	8	50	50	90
2647	Texas	31 51	105 50	7700	7	79	1.0	0.8	6	114	53	8	60	80	100
Standard deviation of a progeny mean					0.73	2.94	0.16	0.22	1.08	3.78	1.27	0.79	5.01	9.52	7.49
LSD$_{.05}$ between progeny means					2.55	10.3	0.56	0.77	3.78	13.6	4.45	2.64	17.5	33.3	26.2
LSD$_{.01}$ between progeny means					3.21	12.9	0.70	0.97	4.74	16.7	5.59	3.46	22.1	41.8	32.9

[a] Collected for the pilot study -- no parental materials collected.

KEY TO DEGREE OF LEAF SERRULATION GRADES

Grade 0 - Serrulations absent or extremely minute and very scarce
Grade 1 - Serrulations few in number and minute but readily discernable
Grade 2 - Serrulations prominent and numerous

serrulation, and stomatal patterning were chosen to correspond to similar measurements made on the seedlings. Cone characteristics were chosen to investigate points of controversy among the early descriptions. A single branch about 18 inches long had been collected from each tree. Leaves to be measured were removed from the main stem of the branch. They were taken from the central portion of the growth produced in the year prior to collection of the specimen. An average of 10 to 15 cones had been collected from each tree.

16. The number of sound seed per gram was calculated at the time the seed lots were weighed in preparation for sowing.

17. Leaf length was measured to the nearest millimeter. Five fascicles of leaves were measured for each specimen.

18,19. Number of dorsal surface stomatal rows and degree of leaf serrulation were observed under the dissecting microscope using the same procedures employed for the seedling leaves. The leaves used for length measurements were used for these observations.

20. Length of peduncle was measured to the nearest 5 millimeters on five cones taken at random from the collection. More accurate measurement was not warranted because of the difficulty of determining the point of attachment without destroying the cone base.

21,22. Cone length and cone width were measured to the nearest millimeter on each of five cones. Cone width was measured at the widest point on each cone.

23. Length of cone scale apophyses was measured on five scales from the central portion of each of five cones to an accuracy of 1 millimeter.

24, 25, and 26. Cone scale reflexing was estimated as the angle between a line extending parallel to the adaxial surface of the cone scale and the adaxial surface of the apophysis. The estimates were based on scales in the center of the terminal, central, and basal one-third of each of five cones.

Statistical analysis.--Two basic types of statistical analyses were applied to the data: viz. analysis of variance and correlation. Most of the computations were performed by an electronic computer (MISTIC). In addition, the results of the analysis of variance tests for several characters were combined by using the "Summation of Differences" approach of Wright and Bull (1962). The combined analyses were used to evaluate the patterns of variation for any evidence of discontinuity.

Analyses of variance were performed on the data for each nursery character. Plot means of the 278 progenies represented in all four replicates were used as items. The form of the analyses was as follows:

Source of variation	Degrees of Freedom	Parameters estimated
Stands	60	$\sigma^2 + r\sigma_T^2 + rt\sigma_S^2$
Trees within stands	217	$\sigma^2 + r\sigma_T^2$
Replication (error)	834	σ^2
Total	1111	

Where: r = the number of replicates = 4

and t = the harmonic mean of the number of trees per stand = 4.16

The appropriate value for testing the differences between individual trees, the standard error of a progeny mean ($s_{\bar{x}_t}$) is equal to the square root of the error mean square divided by the number of replications (r), viz. $s_{\bar{x}_t} = \sqrt{\frac{\text{Error mean square}}{(r)}}$. An approximate value for testing the differences between stands, the standard error of a stand-progeny mean ($s_{\bar{x}_s}$), is equal to the square root of the mean square for trees within stands divided by the harmonic mean (t) of the number of trees per stand multiplied by the number of replicates (r), viz. $s_{\bar{x}_s} = \sqrt{\frac{\text{Mean square for trees within stands}}{(t) \times (r)}}$

A standard error of a stand-progeny mean is strictly valid only if there were no significant differences between trees within stands.

Such differences were present in some stands but the amount of within-stand variation was generally small enough for the above formulas to be valid.

Data from measurement of herbarium specimens collected from 51 stands in 1960 were also subjected to analyses of variance. There was no replication of single trees so only between stand comparisons are possible. To maximize sample size, observations from all trees sampled in a stand were included in the analyses even though some did not produce seedlings. The form of the analyses was as follows:

Source of variation	Degrees of freedom	Parameters estimated
Stands	50	$\sigma^2 + t\sigma_s^2$
Trees within stands	342	σ^2
Total	392	

The appropriate value for testing the differences among stands ($s\bar{x}_s$) is equal to the square root of the mean square for trees divided by the harmonic mean of the number of trees per stand (t), viz.

$$s\bar{x}_s = \sqrt{\frac{\text{Mean square for trees}}{(t)}} .$$

Differences among stands were tested by the methods of Duncan (1955). The appropriate standard error of the mean was multiplied by a factor from Duncan's tables to obtain a "Least Significant Difference" (L.S.D.). A single multiplying factor was chosen to represent a rank difference of 20 for the complete experiment. This value was chosen to facilitate separation of stands which occur in or near the area where the ranges of the two taxa overlap for placement with the correct taxon. At the same time the value is not so large as to obscure differentiation within each taxon. Choosing a single multiplier tends to underestimate the significance of differences between similar means. In actual practice, however, there were very few instances in which the use of the single multiplier caused any loss of precision.

In order to combine data from several characters the "Summation of differences" technique of Wright and Bull (1962) was employed.

These summations made it possible to compare the progenies as entities rather than trait by trait. Differences for the analyses were calculated by subtracting the least significant difference (L.S.D.$_{.05}$) from the actual difference between two stand means for each character. This process eliminated non-significant differences from further consideration. The remainder was multiplied by four and divided by the L.S.D.$_{.05}$. The factor "4" was an arbitrary one to eliminate the need for decimals. The process was repeated for each character. Finally, the resulting values were summed to give a single value applicable to a stand-pair. The procedure described is represented by the following formula taken from Wright and Bull (1962:36):

$$\Sigma \frac{4\ (\text{Difference} - \text{L.S.D.}_{.05})}{\text{L.S.D.}_{.05}} \quad .$$

Two hypothetical examples may serve to illustrate the use and interpretation of the analyses. Consider a series of stands sampled along a given transect, e.g. latitudinal or altitudinal. In Example A, Table 6, each stands differs only slightly from the adjacent one but by continuously greater amounts from more distant ones. In Example B, some widely separated stands, a and f were similar whereas the neighboring stands f and g were different. The pattern presented in Example B would usually be interpreted as discontinuous variation.

Stand means were used as items for computing all possible simple correlations among seedling traits, parental traits, and geographic origin data. Only the 50 stands which were represented by both seedling and parental materials were included in the analyses.

Table 6. Examples of hypothetical, idealized, summation of differences tables.

Example A. Continuous variation pattern.

	Differences between stands listed below and on the left.							
Stands								
a	a							
b	1	b						
c	2	1	c					
d	3	2	1	d				
e	4	3	2	1	e			
f	5	4	3	2	1	f		
g	6	5	4	3	2	1	g	
h	7	6	5	4	3	2	1	h

Example B. Discontinuous variation pattern.

	Differences between stands listed below and on the left.								
Stands									
a	a								
b	1	b							
c	2	1	c						
d	3	2	1	d					
e	1	0	1	2	e				
f	3	2	1	0	2	f			
g	12	11	10	9	11	8		g	
h	14	13	12	11	12	10		2	h

GENERAL NURSERY OBSERVATIONS

Germination began on June 6, 1961 and continued during the summer and fall until the ground froze in November. Some germination also occurred during May 1962, especially among seed lots which had late germination during the first season. Second year germination was concentrated during a 10 day period.

Several seedlots contained less than the desired 100 seed. A small percentage of the seed failed to germinate. Rodents consumed many seed and emerging seedlings even though poisoning and trapping were employed to reduce such losses. The combination of these factors reduced the stocking of nursery beds well below the planned maximum. Approximately one-fifth of the rows had fewer than 6 seedlings, one-fifth had 6 to 10, one-fifth had 11 to 15, one-fifth had 16 to 20, and one-fifth had 21 to 25 seedlings.

Fumigation of the nursery beds in the fall preceding planting with "MILON", a combination fungicide and herbicide reduced fungus and weed problems to a minimum. Application of "CAPTAN" as germination progressed further reduced damping-off losses. Minor weeding was done by hand in conjunction with regular observations and measurements. Because a test on some extra seedlings indicated that the "Stoddard solvent" normally used to control weeds in the nursery had a detrimental effect on the seedlings, at least during the first year of growth, it was not applied to the experimental materials.

A sawdust mulch was applied to control frost heaving during the 1961-62 winter. The treatment was successful except in low spots where water was occasionally trapped on the surface.

The spacing employed in planting appeared adequate during the two year period. There was no competition between rows for light or space. There was competition between seedlings within rows of the fastest growing progenies. The roots of most seedlings were long enough to interlace with those from seedlings in other rows. However, the resultant competition did not noticeably restrict or favor seedling growth.

Seedling color and growth rate served to indicate that soil nutrients and moisture were maintained at adequate levels.

DIFFERENCES BETWEEN THE TAXA

In discussing the differences between the taxa the author prefers to use the specific names originally proposed, *Pinus flexilis* for the northern taxon and *P. strobiformis* for the southern. It was felt that the use of specific names would help clarify the discussion by reducing the terminology.

Seedling Differences

Form and size differences among seedlings in the nursery that indicated the presence of different taxa were apparent within two months after germination began. A portion of a seedbed showing differences at the end of the second growing season is illustrated in Figure 4.

Individual characters.--Data resulting from the measurement of seedling characters are presented as stand averages in Tables 2 and 3 for *P. flexilis* and *P. strobiformis*, respectively. Figure 5 summarizes the data of Tables 2 and 3 by areas of origin.

In Figure 5, the two taxa appear to be distinct with regard to most characteristics. Stand-progeny means were used as items in analyses of variance to test the difference between the species' means for each character. All differences between the species' means were significant at the 0.1 percent level. F values ranged from a low of 14 for the number of dorsal surface stomatal rows, to a high of 370 for 1-year height. The analyses are available on request.

A more critical series of analyses was performed to further test the differences between the species. In these analyses seedling progenies from the southern extreme of the range of *P. flexilis* were compared with those from the northern extreme of the range of *P. strobiformis*. Six stand-progenies were chosen to represent *P. flexilis*; the three most southern ones from Utah, the two most southern ones from Colorado, and the one from northern New Mexico. Four stand-progenies were chosen to represent *P. strobiformis*; the one from northern New Mexico and the three most northern ones from Arizona. The results of these analyses are presented in Table 7.

There was very little overlap between species in the characters of cotyledon number, length of secondary leaves, and height growth.

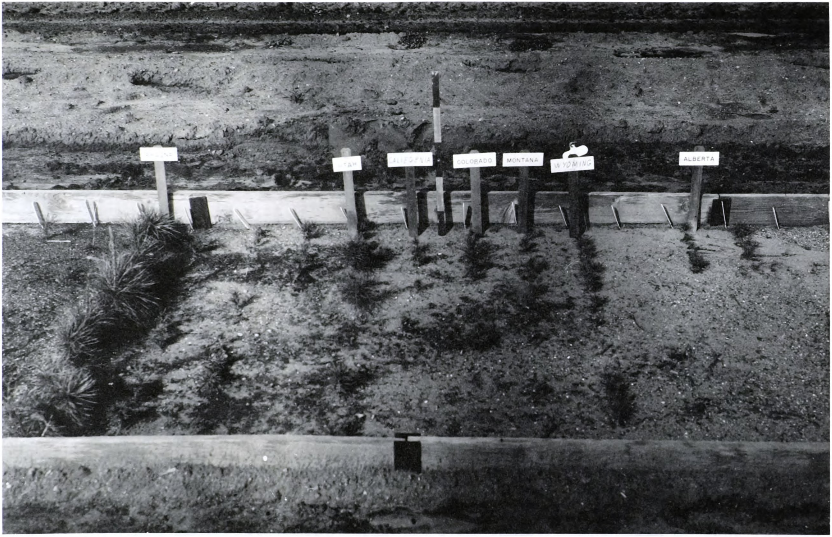


Figure 4. Portion of a nursery bed illustrating differences among seedling progenies.

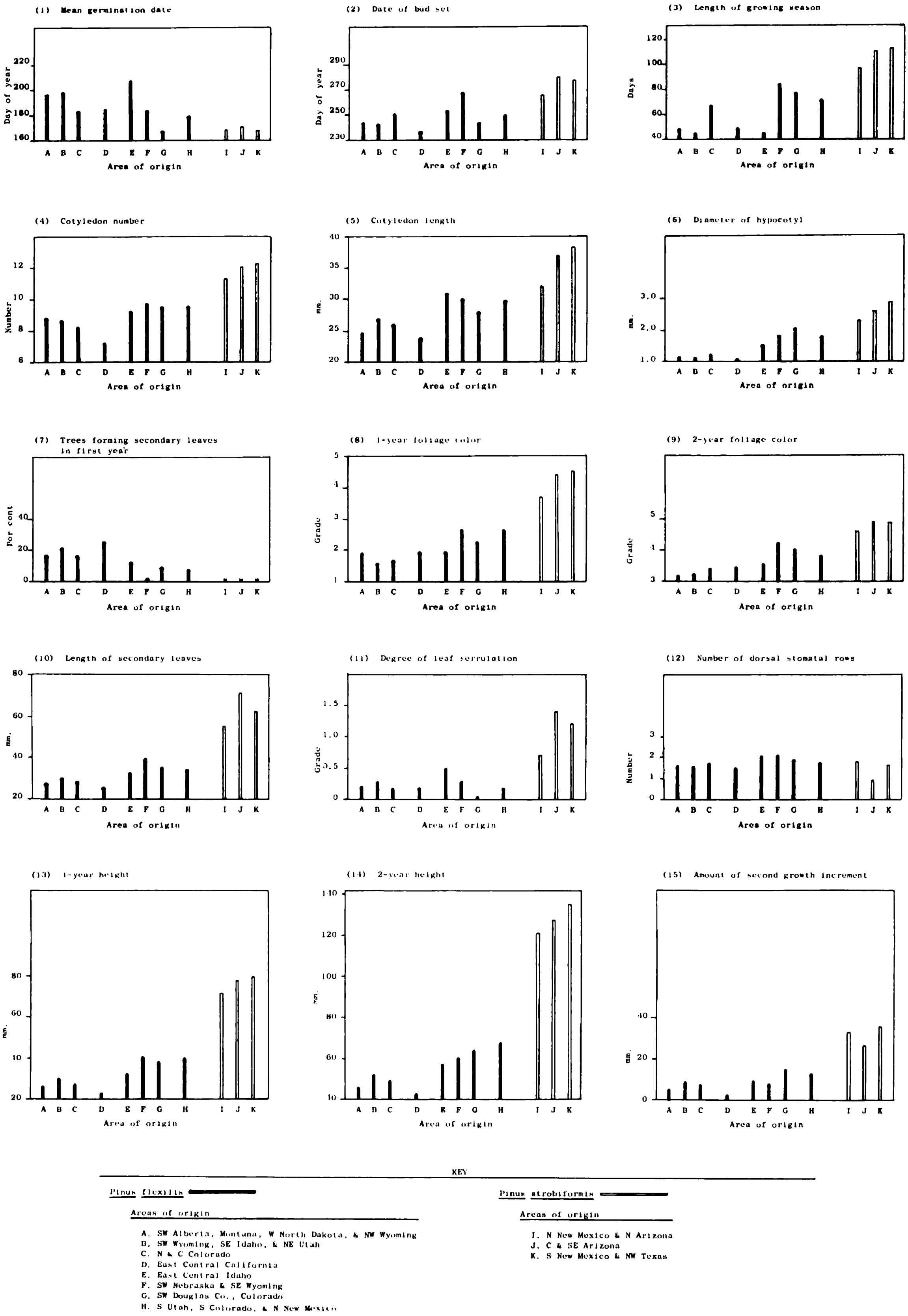


Figure 5. Mean values for seedling characteristics of Pinus flexilis and Pinus strobiformis stands grouped by area of origin.

Table 7. Results of analysis of variance tests of differences between the southernmost Pinus flexilis and northernmost Pinus strobiformis seedlings.

Character	Value of F resulting from the test of differences between species[(a)]	Percent of total variance attributable to differences between species
	Number	$\frac{\sigma_B^2}{\sigma_B^2 + \sigma_W^2} \times 100$
1. Mean germination date	6.7*	54
2. Date of bud set	11.1*	68
3. Length of growing season	5.7*	49
4. Cotyledon number	47.9***	91
5. Cotyledon length	1.1	2
6. Diameter of hypocotyl	15.4**	75
7. Seedlings forming secondary leaves in the first year	3.6	35
8. 1-year foliage color	13.1**	72
9. 2-year foliage color	9.4*	64
10. Length of secondary leaves	110.8***	96
11. Degree of leaf serrulation	9.4*	64
12. Number of dorsal stomatal rows	0.0	0
13. 1-year height	104.3***	96
14. 2-year height	48.4***	91
15. Amount of second growth increment	37.0***	88

(a) For each analysis degrees of freedom were 1 and 8 for between- and within-species variation respectively.

* Greater than 5.32 needed for significance at the 5 percent level.
** Greater than 11.26 needed for significance at the 1 percent level.
*** Greater than 25.4 needed for significance at the 0.1 percent level.

With respect to these traits both stand-and single-tree-progenies could usually be assigned definitely to one species or the other.

Date of mean germination, date of bud set, length of growing season, diameter of hypocotyl, first and second year foliage color, and degree of leaf serrulation were less satisfactory as diagnostic characters. There was little overlap between species if the means applicable to regions of origin were considered. However, there was considerable overlap if stand-progeny and single-tree-progeny means were considered.

Cotyledon length, number of dorsal stomatal rows, and secondary leaf formation during the first year were of little value in differentiating the species. Variation was almost as great within as between species.

Simultaneous consideration of several characters.--The summation-of-differences technique was used to combine the data from eleven characters:

(2) Date of bud set
(3) Length of growing season
(4) Cotyledon number
(5) Cotyledon length
(6) Diameter of hypocotyl
(8) 1-year foliage color
(10) Length of secondary leaves
(11) Degree of leaf serrulation
(13) 1-year height
(14) 2-year height
(15) Amount of second growth increment

The summations for *P. flexilis* are presented in Table 8. The bottom line of that table contains the summations for progeny 903, the most *flexilis*-like of the *P. strobiformis* seedlings. Study of the summations in that line shows that, all traits considered, progeny 903 is more different from all *P. flexilis* than is almost any *P. flexilis* progeny from any other in the same species. In other words, there is almost no overlap between the species.

Species distinctness is also indicated in Table 9, which includes the summations for *P. strobiformis* and the two southernmost *P. flexilis* progenies (Nos. 2599 and 2612). Considering all traits, almost all

Table 8. Summation of differences for seedling characteristics of Pinus flexilis and one Pinus strobiformis stand-progenies.

Progeny, state, or province		Total difference (in summation-units)[a] between progeny listed below and progeny on left.																																													
2992	Alta.	2992																																												
3002	Alta.	0	3002																																											
2825	Alta.	0	0	2825																																										
2846	Mont.	0	0	0	2846																																									
2856	Mont.	0	1	0	0	2856																																								
2579	Mont.	2	3	1	2	3	2579																																							
2697	Mont.	0	0	0	0	0	1	2697																																						
977	Mont.	0	0	0	0	0	2	0	977																																					
990	Mont.	0	0	0	0	0	2	0	0	990																																				
967	N. Dak.	0	2	0	0	0	4	2	0	2	967																																			
2929	Wyo.	0	0	0	0	0	5	1	0	1	0	2929																																		
2971	Wyo.	0	2	0	0	0	2	0	0	0	0	0	2971																																	
2964	Wyo.	0	0	0	0	0	5	0	0	0	0	0	0	2964																																
1085	Idaho	0	2	0	0	0	7	2	0	2	0	0	1	0	1085																															
907	Idaho	6	9	7	7	5	11	9	6	9	3	4	6	2	2	907																														
2590	Idaho	9	11	9	9	8	15	13	8	11	4	5	8	8	4	0	2590																													
2819	Idaho	0	0	0	0	0	2	0	0	0	1	0	0	0	1	7	9	2819																												
2909	Wyo.	2	0	2	2	3	4	1	2	1	4	2	4	2	4	12	13	1	2909																											
2765	Utah	0	0	0	0	1	3	0	0	0	2	0	1	0	2	7	10	0	0	2765																										
1059	Utah	1	1	0	0	0	5	1	0	1	0	0	0	0	2	5	5	2	3	1	1059																									
1030	Utah	0	3	1	1	0	6	3	0	3	0	0	1	0	0	2	3	1	5	2	0	1030																								
930	Utah	2	1	1	1	0	6	1	0	1	0	0	1	0	0	7	6	0	3	2	0	0	930																							
1006	Utah	1	5	2	2	2	7	5	0	5	2	2	2	1	0	1	1	2	7	4	1	0	1	1006																						
1041	Utah	0	1	0	0	0	2	0	0	0	0	0	1	0	0	7	9	0	3	1	0	1	0	3	1041																					
2553	Nebr.	3	5	2	3	3	8	6	1	4	0	0	2	2	0	3	3	3	7	3	5	0	5	0	3	2553																				
2563	Wyo.	6	12	8	9	8	11	14	8	12	4	2	6	7	3	0	1	6	14	8	6	3	7	0	8	1	2563																			
2724	Calif.	1	0	2	1	3	2	1	1.	1	4	2	4	1	4	12	14	1	0	1	2	5	6	8	4	9	15	2724																		
2546	Colo.	0	2	1	1	1	6	2	1	2	0	0	3	0	0	3	5	0	4	1	0	0	0	1	1	2	3	5	2546																	
2919	Colo.	0	0	0	0	0	3	0	0	0	0	1	0	0	1	7	12	0	2	0	0	1	0	3	0	4	13	2	2	2919																
2522	Colo.	2	0	2	2	3	3	1	2	1	4	3	4	2	5	13	14	1	0	0	4	5	3	8	3	9	13	0	5	2	2522															
922	Colo.	0	0	0	0	0	4	0	0	0	1	0	1	0	1	8	9	0	1	0	0	1	0	3	0	3	9	0	0	0	1	922														
909	Colo.	0	0	0	0	0	5	1	0	0	0	0	1	0	0	3	3	0	2	0	0	0	0	1	0	2	7	1	0	0	2	0	909													
2523	Colo.	0	0	0	0	0	3	0	0	0	0	0	1	0	0	7	8	0	2	0	0	1	0	3	0	3	9	0	1	0	2	0	0	2523												
2509	Colo.	0	0	0	0	0	4	0	0	0	1	0	1	0	1	8	9	0	1	0	0	2	0	4	0	3	8	0	1	0	1	0	0	0	2509											
2601	Colo.	0	2	0	0	0	4	2	0	2	0	0	0	0	0	3	4	1	4	2	0	0	0	0	0	0	3	3	0	0	5	1	0	0	1	2601										
2987	Colo.	0	0	0	0	0	5	1	0	1	1	0	0	0	1	6	6	0	1	0	0	1	0	1	0	1	5	0	0	1	2	0	0	0	0	1	2987-									
916	Colo.	0	2	4	1	0	7	2	0	2	0	1	4	2	0	3	4	0	4	1	0	0	0	0	1	1	3	3	0	4	7	3	0	2	4	0	0	916								
2978	Colo.	0	2	0	0	0	5	3	0	2	0	2	1	0	5	5	2	1	5	2	0	0	0	0	0	0	1	5	0	1	5	1	0	0	1	0	1	0	2978							
902	Colo.	5	8	6	7	5	10	9	4	8	2	4	2	3	2	1	2	3	11	6	5	2	6	1	5	0	0	11	3	7	12	5	5	6	5	3	4	3	0	902						
2900	Utah	3	5	4	4	2	9	6	2	6	1	1	4	3	0	0	1	4	8	4	2	0	5	0	3	1	0	9	0	5	9	7	3	4	4	0	2	0	0	0	2900					
2652	Utah	2	6	4	5	3	7	8	2	6	0	1	2	2	0	1	2	3	8	4	3	0	3	0	2	0	0	9	1	6	12	5	2	4	4	0	2	0	0	0	0	2652				
2877	Utah	5	7	4	5	6	8	9	4	7	1	0	4	2	1	1	1	4	8	6	3	1	3	0	6	3	0	12	2	8	9	4	2	5	4	2	1	1	0	0	0	0	2877			
2796	Colo.	8	13	10	11	11	13	14	10	12	5	4	7	8	4	2	2	7	14	10	8	4	9	2	11	1	0	16	6	10	18	10	9	10	11	6	5	3	2	0	0	0	1	2796		
2509	Colo.	10	10	9	10	10	13	14	8	12	3	5	7	8	3	0	1	8	13	9	8	2	7	1	10	1	0	16	4	12	15	8	7	10	10	4	5	3	1	0	0	0	0	0	2509	
2612	N.Mex.	8	13	10	10	10	13	12	10	12	5	6	6	9	5	2	5	8	16	10	10	6	11	2	11	0	1	16	10	12	16	12	11	11	12	7	6	7	3	0	0	0	1	1	0	2612
903[b]	Ariz	31	37	34	35	34	36	37	35	36	26	24	26	34	23	16	15	28	39	32	31	27	31	19	35	16	12	39	29	34	42	35	33	34	34	28	27	25	21	12	15	13	14	10	13	15	903

[a] Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 11 different characters.

[b] Pinus strobiformis stand included for comparative purposes.

Table 9. Summation of differences for seedling characteristics of *Pinus strobiformis* and two *Pinus flexilis* stand-progenies.

Progeny, state or province		Total difference (in summation-units)[a] between progeny listed below and progeny on the left.																	
		Pinus flexilis																	
2599	Colo.	2599																	
2612	N. Mex.	0	2612																
				Pinus strobiformis															
903	Ariz.	13	15	903															
904	Ariz.	15	13	0	904														
2569	Ariz.	23	22	1	2	2569													
2805	Ariz.	21	17	0	0	0	2805												
1023	Ariz.	28	28	4	5	0	0	1023											
2739	Ariz.	45	38	10	15	0	3	0	2739										
2621	Ariz.	30	28	0	5	0	0	0	1	2621									
2743	Ariz.	24	20	0	0	0	0	0	0	0	2743								
2755	Ariz.	16	12	0	0	1	0	0	2	2	2	2755							
2751	Ariz.	26	26	6	6	0	0	0	1	0	0	0	2751						
2763	Ariz.	39	35	12	11	1	1	0	0	3	0	1	1	2763					
932	N. Mex.	21	15	0	0	0	0	0	4	0	0	0	0	3	932				
2649	N. Mex.	33	30	7	7	0	0	0	0	0	0	3	1	0	0	2649			
905	N. Mex.	26	23	4	1	0	0	0	0	0	0	0	0	0	0	0	905		
2939	N. Mex.	29	24	0	5	0	0	0	7	0	0	4	0	8	3	2	0	2939	
2647	Texas	33	30	6	7	0	0	0	0	0	0	0	0	0	0	0	0	0	2647

[a] Summation-unit = $\Sigma\ 4(\text{actual difference} - \text{LSD}_{.05}) / \text{LSD}_{.05}$ for 11 different characters.

the *P. strobiformis* progenies are more similar to each other than to *P. flexilis*.

Parental Differences

Individual characters.--Data on parental characters are presented by stands in Tables 4 and 5 and by broad areas of origin in Figure 6. The sampling was less complete than in the case of the progeny characters. This was especially true of the northern *P. strobiformis* area (Area "I") which was represented by parental material from only a single stand (No. 2569).

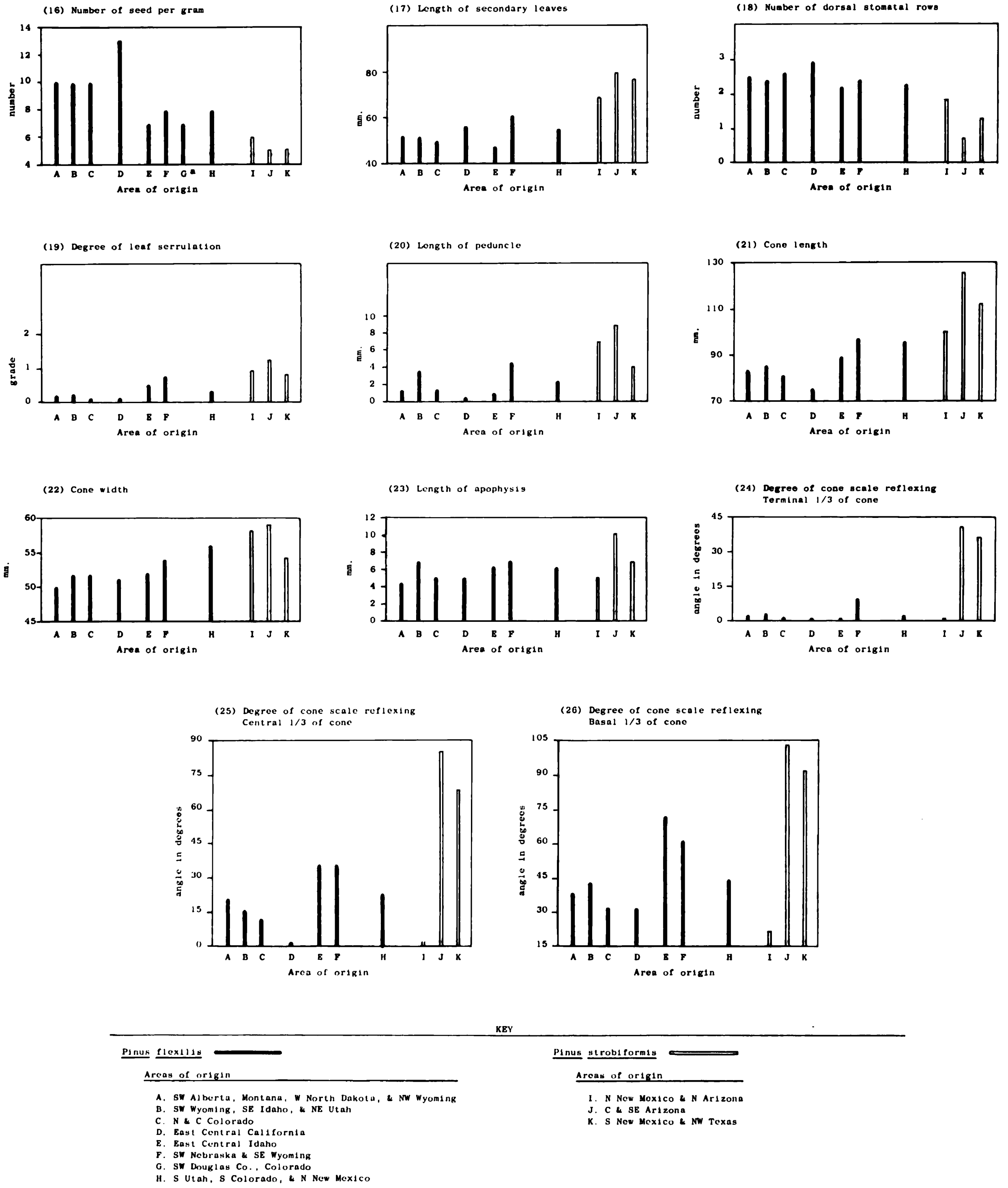
The length of secondary leaves is the best diagnostic character for separating the species. Stand means range from 43 to 64 millimeters for *P. flexilis* and from 69 to 96 millimeters for *P. strobiformis*.

Other characters for separating the species were: (1) The number of sound seed per gram, (2) The number of dorsal surface stomatal rows, and (3) The length of cones. The degree to which cone scales were reflexed provided distinct separation between species for all materials except those from stand 2569.

There was considerable overlap between stand means of both species for four characters: (1) Leaf serrulation, (2) Length of peduncle, (3) Cone width, and (4) Length of apophysis.

Simultaneous consideration of several characters.--Values for all parental characters were included in the summation-of-differences analyses which yielded the results presented in Tables 10 and 11. The arrangement of these tables is similar to that of Tables 8 and 9 with one or two stand values for the opposite species included for comparison.

When all parental characters were considered the distinction between species was smaller than for seedling characters. Materials from two *P. strobiformis* stands, No. 2569 from north-central Arizona and No. 2649 from central New Mexico were unusual. They were more different from those of most other *P. strobiformis* stands than from materials of some *P. flexilis* stands. These stands were *flexilis*-like in their parental traits and *strobiformis*-like in their progeny traits. That might be explained in either of two ways. First, the sites on which the stands were growing were so atypical as to result in abnormal



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[a] Single stand collection, MSFC # 902, collected for the pilot study; no parental materials other than seed available.

Figure 6. Mean values for adult characteristics of Pinus flexilis and Pinus strobiformis stands grouped by area of origin.

Table 10. Summation of differences for adult characteristics of *Pinus flexilis* and one *Pinus strobiformis* stand-progenies.

Progeny, state, or province		Total difference (in summation-units)[a] between progeny listed below and progeny on left.																																						
2992	Alta.	2992																																						
3002	Alta.	0	3002																																					
2825	Alta.	0	0	2825																																				
2846	Mont.	0	0	0	2846																																			
2856	Mont.	1	2	3	1	2856																																		
2579	Mont.	2	2	0	1	7	2579																																	
2697	Mont.	2	2	0	1	7	0	2697																																
977	Mont.	0	1	0	0	2	1	2	977																															
990	Mont.	1	0	0	0	5	0	0	0	990																														
967	N. Dak.	1	3	1	1	4	1	2	0	1	967																													
2929	Wyo.	0	0	0	0	1	2	2	0	1	0	2929																												
2971	Wyo.	0	1	0	0	0	3	3	0	3	0	0	2971																											
2964	Wyo.	0	0	0	0	0	2	4	0	0	0	0	0	2964																										
1085	Idaho	0	3	1	0	1	3	6	0	1	0	0	0	0	1085																									
2590	Idaho	7	6	8	7	4	13	13	8	12	8	3	3	2	1	2590																								
2819	Idaho	0	0	0	0	1	2	3	0	0	1	0	0	0	1	7	2819																							
2909	Wyo.	3	1	2	2	4	3	3	4	2	5	2	3	4	6	11	3	2909																						
2765	Utah	2	2	3	2	7	2	4	1	2	2	2	2	1	2	8	4	2	2765																					
1059	Utah	5	5	2	3	9	0	4	1	0	0	5	5	3	2	12	3	9	3	1059																				
1030	Utah	0	3	0	0	3	3	5	0	1	0	0	0	0	0	7	1	6	3	2	1030																			
1006	Utah	3	6	4	4	3	6	9	0	5	1	2	2	2	0	5	1	8	4	4	1	1006																		
1041	Utah	2	4	2	3	2	3	7	0	2	0	2	1	1	0	6	0	7	2	3	0	0	1041																	
2553	Nebr.	1	3	1	2	0	3	6	1	1	0	0	0	0	0	5	1	6	3	2	0	0	0	2553																
2563	Wyo.	11	13	15	16	6	18	21	12	16	13	7	4	3	4	6	10	17	13	13	7	2	3	5	2563															
2724	Calif.	3	0	1	1	7	1	0	1	0	4	3	5	2	5	14	0	1	4	5	4	10	7	8	22	2724														
2546	Colo.	1	4	6	4	1	6	10	3	7	6	0	0	0	0	3	1	5	4	7	2	0	0	2	4	11	2546													
2919	Colo.	1	0	0	0	5	1	0	1	0	1	1	2	2	3	12	1	3	4	4	1	5	5	5	18	1	8	2919												
2522	Colo.	5	3	4	4	10	1	1	4	1	6	6	9	6	9	18	3	4	3	3	7	13	9	7	26	1	14	3	2522											
2523	Colo.	0	0	0	0	3	0	0	0	0	0	0	2	1	1	11	0	3	4	3	1	5	6	3	18	1	6	0	2	2523										
2509	Colo.	5	4	1	3	6	2	2	2	0	3	5	6	4	6	16	4	5	7	3	4	9	6	6	20	0	10	1	3	0	2509									
2601	Colo.	0	2	0	0	3	2	4	0	1	0	0	0	0	0	7	1	6	4	3	0	3	2	0	11	5	4	2	6	1	4	2601								
2987	Colo.	0	0	0	0	3	1	1	1	0	1	0	0	1	2	11	1	1	1	2	2	3	2	3	13	0	5	0	4	0	2	2	2987							
2978	Colo.	0	2	0	0	1	3	3	0	1	1	0	0	0	0	4	1	4	4	4	0	3	2	1	12	3	2	0	6	0	5	0	1	2978						
2900	Utah	3	5	4	4	2	8	11	2	9	3	3	1	1	1	3	2	10	9	6	2	2	1	1	2	10	1	8	15	6	9	4	6	3	2900					
2877	Utah	2	4	2	2	6	1	5	0	3	0	1	2	0	0	11	1	8	2	1	0	1	2	0	9	9	4	6	6	3	5	1	3	2	4	2877				
2796	Colo.	4	5	3	4	4	7	8	3	5	2	3	2	1	0	6	3	9	6	3	0	1	0	0	4	12	1	7	13	5	11	0	6	3	0	0	2796			
2599	Colo.	2	5	2	4	9	5	7	2	4	1	4	2	2	0	7	3	10	9	4	0	2	3	1	9	7	4	5	11	4	6	0	6	2	1	2	0	2599		
2612	N.Mex.	5	9	8	8	8	7	12	5	8	0	7	4	5	1	5	5	13	6	3	1	0	1	1	7	7	3	8	14	8	8	3	7	5	2	1	2	5	2612	
2569[b]	Ariz.	10	12	13	13	15	10	16	11	13	6	12	11	10	6	14	10	19	10	6	6	6	6	3	13	17	12	16	15	15	16	7	14	10	11	1	3	8	3	2569

a. Summation-unit = $\sum 4(\text{Actual difference} - LSD_{.05}) / LSD_{.05}$ for 11 different characters.

b. *Pinus strobiformis* stand included for comparative purposes.

Table 11. Summation of differences for adult characteristics of *Pinus strobiformis* and two *Pinus flexilis* stand-progenies.

Progeny, state or province		Total difference (in summation-units)[a] between progeny listed below and progeny on the left.													
		Pinus flexilis													
2599	Colo.	2599													
2612	N. Mex.	5	2612												
				Pinus strobiformis											
2569	Ariz.	8	3	2569											
2805	Ariz.	24	16	10	2805										
1023	Ariz.	29	17	13	2	1023									
2739	Ariz.	27	14	9	0	0	2739								
2621	Ariz.	32	23	18	0	0	0	2621							
2743	Ariz.	47	33	29	7	2	3	0	2743						
2755	Ariz.	44	34	29	8	9	7	1	0	2755					
2751	Ariz.	34	26	18	4	1	1	0	0	0	2751				
2763	Ariz.	45	33	29	9	0	4	0	0	2	0	2763			
2649	N. Mex.	7	4	3	3	6	3	9	24	20	11	24	2649		
2939	N. Mex.	20	12	9	0	0	0	0	9	6	0	9	0	2939	
2647	Texas	27	18	13	0	0	0	0	2	0	0	3	3	0	2647

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[a] Summation-unit = $\Sigma\ 4(\text{actual difference} - LSD_{.05}) / LSD_{.05}$ for 11 different characters.

development of the parental trees. If so, their phenotypic appearance might not be a reliable indicator of their genetic potentialities. Second, the parents might be members of a hybrid swarm which was surrounded by *P. strobiformis* pollinators. If so, the offspring would be expected to be much more *strobiformis*-like than the parents. However, they would not be expected to be indistinguishable from pure *P. strobiformis* as was actually the case.

The primary question which the study sought to answer was: "Are there two distinguishable taxa within the *Pinus flexilis* complex?" When based on seedlings grown together in a nursery the answer is an unqualified "Yes". On the basis of parental performance under field conditions the answer is "Yes" but with reservations about materials from stands 2569 and 2649.

The second question to be answered was: "If the taxa are distinct, what taxonomic rank does each merit?" The author feels that the differences are of sufficient magnitude that the taxa merit equal rank as species. This ranking is in accord with the general level of species distinctiveness recognized within the genus *Pinus*.

According to the rules of nomenclatural priority in the *International Code of Botanical Nomenclature*, Article 11, (1961) the proper name to be applied to the northern species is *Pinus flexilis* James. The proper name for the southern species is *Pinus strobiformis* Engelm..

DIFFERENCES BETWEEN STANDS WITHIN SPECIES

The analysis of the materials for evidence of distinctness of species also revealed the presence of variation within each. The next logical step was to analyze the differences between the stand-collections for each species.

Pinus flexilis

Seedling characters.--The outstanding feature of the geographic variation pattern is the performance of progenies 2553 and 2563 from a small area near Pine Bluff, in southeastern Wyoming and the adjacent part of southwestern Nebraska. These seedlings had the most cotyledons and the longest secondary leaves of any of the limber pine. They also set first-year buds latest, formed the fewest secondary leaves during the first growing season, and had the greenest leaves. They were among the fastest growing origins (see Table 2 and Figure 5).

Progenies 907, 1085, and 2590 from east-central Idaho had the longest cotyledons. They were nearly equal to seedlings from the Pine Bluff with regard to cotyledon number, length of secondary leaves, and lateness of bud set. Also outstanding was progeny 902 from Douglas County, Colorado, It was from the easternmost collecting area in the state. Although not extreme in any character, it had considerably more and longer cotyledons, greater height, longer leaves, and darker foliage than other seedlings from the same latitude.

There was only one collection from the western part of the species' range. Stand-progeny 2724 from the Sierra Nevada of east-central California had the fewest cotyledons recorded. It also had short cotyledons, short leaves, and a slow growth rate.

The main body of the species occupies high elevations in the Rocky Mountains from southern Alberta to northern New Mexico. Within this broad area, there were no trends evident in that portion of the range extending from southern Alberta to central Colorado. Progenies from this area had the shortest cotyledons and secondary leaves, were the yellowest, and grew the slowest.

Southern Colorado, southern Utah, and northern New Mexico progenies were the tallest within the species. They also had long

cotyledons and secondary leaves.

When several traits are considered simultaneously by the "Summation-of-Differences" method (Table 8), stand progenies from three areas show differentiation from those of the main portion of the range of the taxon. These areas are in:(1) east-central Idaho, (2) the Pine Bluff region of Nebraska and Wyoming, and (3) Douglas County, Colorado. Seedlings from the more highly differentiated stands in these areas very closely resemble seedlings from the southern portion of the species range.

Progeny of the single California collection are very similar to those from the main body of the species. Within the main range from Alberta to central Colorado, the differences between stands are small and mostly of random nature.

Southern Utah and especially southern Colorado and New Mexico progenies show considerable differentiation from the more northern ones.

Parental characters.--The collections from the Pine Bluff area were again outstanding (see Table 4 and Figure 6). These specimens had the longest leaves, the most extensive leaf serrulation, the longest cones, and the longest peduncles. The cone scales were among the most reflexed.

Cones from east-central Idaho had the heaviest seeds, as reflected in the low number per gram sample, and the most reflexed cone scales. However, the leaves from adult trees were among the shortest for the species in contrast to the long leaves of the progenies.

The Douglas County, Colorado collection was represented only by seed. These were among the heaviest obtained for the species.

Materials from the California collection were distinctive in several ways. The seeds were the lightest, the cones and their peduncles the shortest, and the cone scales the least reflexed. The leaves had the most rows of stomata on the dorsal surface and the least serrulation.

Within the main portion of the species' range the specimens were remarkably uniform. Cones from this area were narrowest and their cone scales had the shortest apophyses. In general, materials from northeastern Utah and adjacent areas showed slightly greater

development than those from Alberta, Montana, and northern Wyoming or northern and central Colorado.

When all characters are considered together the entire species shows little consistent differentiation (Table 10). However, the results indicate that the samples from within any given area were more variable than were their progeny. One collection from the Pine Bluff area and one from east-central Idaho are seen to be quite different from all others. In general, it was not as easy to differentiate between the southernmost stands and those from the northern and central areas on the basis of parental specimens as it was by observing their progeny.

Pinus strobiformis

Seedling characters.--Within the portion of the range of the taxon represented in this study, variation was not extensive (see Table 3 and Figure 5). Seedlings from northern Arizona and New Mexico had fewer and shorter cotyledons, thinner hypocotyls, shorter leaves, and more rows of stomata on the dorsal leaf surface than more southern origins. They also had the shortest growing season and the least serrulate leaves, grew the slowest, and were the lightest colored.

Central and southern Arizona progenies had the longest secondary leaves. The leaves from these progenies also had the most pronounced serrulations and fewest dorsal surface stomata.

Progenies of southern New Mexico and northern Texas stands had the longest cotyledons, the thickest hypocotyls, and the fastest growth rates. They were about equal to Arizona progenies in length of growing season, number of cotyledons, and foliage color.

The "Summation-of-Differences" analysis indicates that the northern stand-progenies have differentiated slightly from the southern ones (Table 9). Within all three areas the variability is nearly random.

Parental characters.--The single northern Arizona stand from which parental materials were available was very different from more southern stands in Arizona, New Mexico, and Texas (Table 5 and Figure 6). The specimens from this stand had the shortest leaves of any. The leaves also had the most rows of dorsal surface stomata. This collection had

the shortest cones, the shortest apophyses, and the least cone scale reflexing.

Among other Arizona collections there were slight north to south trends. Seed weight, leaf length, length of apophysis, and cone scale reflexion increased from north to south but cone length and width decreased. Central and southern Arizona trees had the longest leaves with the fewest dorsal stomatal rows and the most pronounced serrulation. Their cones were longest and widest, had the longest apophyses, and showed the greatest amount of scale reflexing. Cone scales with apophyses 25 millimeters long and reflexed into a full curl were observed.

Specimens from New Mexico and Texas stands showed slightly less development than those from central and southern Arizona in almost all characters.

When all characters were considered together the northern Arizona stand appeared to be very different from other *P. strobiformis* stands and almost intermediate between *P. strobiformis* and *P. flexilis* (Table 11). However, when judged by seedling characters it was definitely associated with *P. strobiformis*. A slight amount of differentiation between the Arizona and New Mexico - Texas populations appears to have taken place.

Area-of-origin groupings used in preparing Figures 5 and 6 were rather arbitrarily made by utilizing a combination of geographic features and the results of the "Summation-of-Differences" analyses (Tables 8, 9, 10, and 11). The outlines of these areas are illustrated in Figure 7 superimposed on the map of the collection locations.

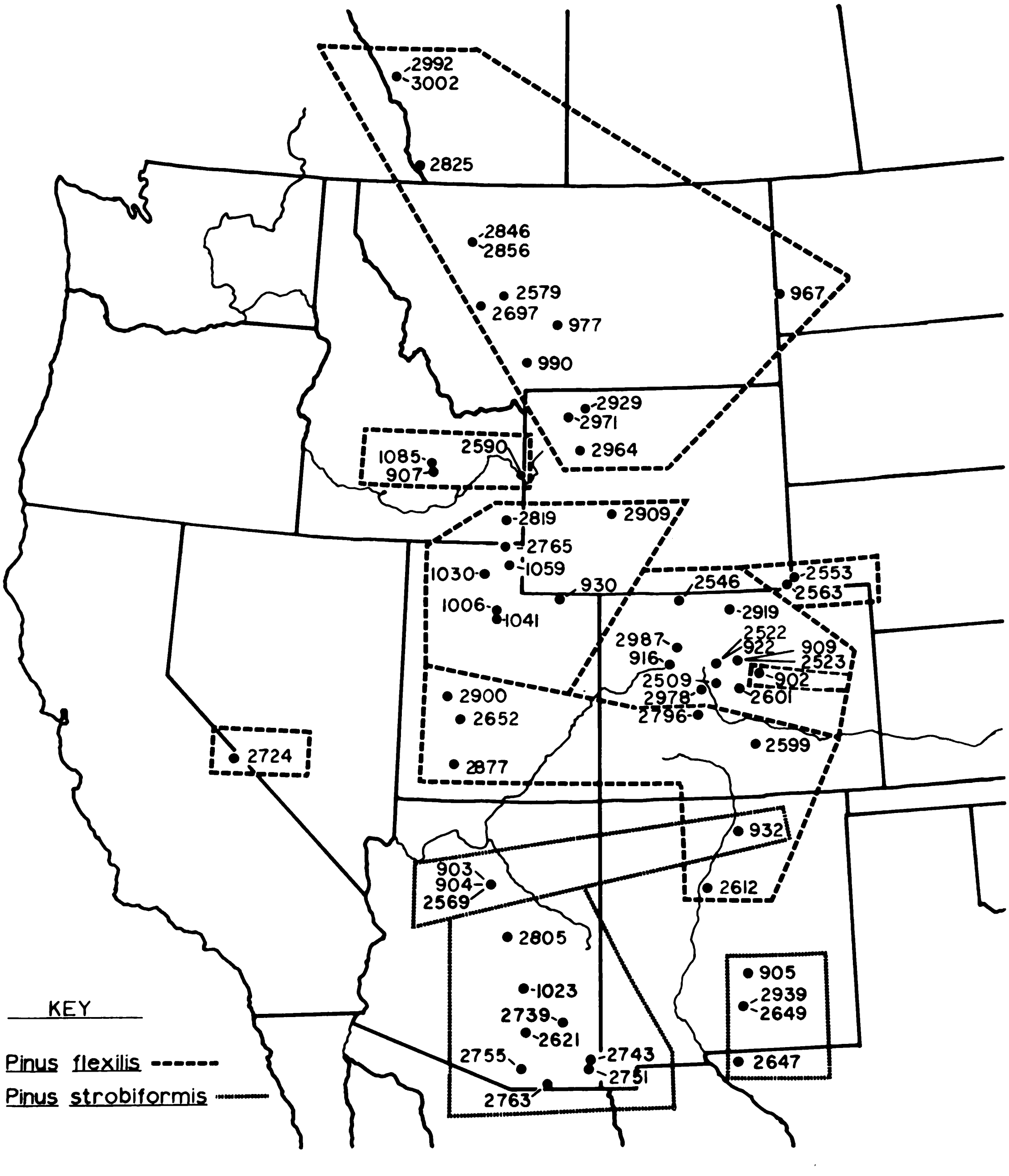

Figure 7. Boundaries of area of origin groupings of stand collections.

DIFFERENCES BETWEEN PROGENIES WITHIN STANDS

Preceding evidence has shown that the taxa and stands within taxa differed. The next step is the examination of the stands for differences among the individual trees. Sampling of parental materials involved the collection of only one herbarium specimen from each tree. With one specimen per tree it is possible to derive a figure showing the amount of variation within a stand but it is not possible to state whether the variation is due to genetic or environmental factors. That can be done only with a replicated test, as when the progenies from each parent are represented several times in the nursery. For that reason all conclusions as to within-stand variability are based on progeny performance. Only stands represented by four or more individual tree progenies were considered in the analyses.

Significant differences between progenies within stands were found for all 13 traits analyzed. Eight of the traits were selected for presentation and further discussion in this report (see Table 2). The characters selected to illustrate the variability are: (1) Length of growing season, (2) Cotyledon number, (3) Cotyledon length, (4) Trees forming secondary leaves in the first year, (5) 1-year color, (6) Secondary leaf length, (7) 1-year height, and (8) 2-year height. Dates of germination and bud set were not presented because they are functions of length of growing season. Height was considered to be a better measure of 1-year growth than stem diameter. The patterns of within-stand variation in first- and second-year color were similar. No test of within-stand differences was possible for leaf serrulation and number of dorsal stomatal rows because observations were made on only one replicate. Two-year total height includes the amount of growth during the second increment so the latter measure was not presented.

Differences between progenies within stands are numerous in comparison with the small number of differences between stands from most regions.

Significant within-stand differences in length of growing season were found in approximately half of the stands. The stands with differences were uniformly distributed throughout both species.

In slightly over half of the <u>P. flexilis</u> stands there were

Table 12. Differences between progenies within stands for eight selected characters.

MSFG number	Length of growing season	Cotyledon number	Cotyledon length	1-year secondary leaves	1-year color	Secondary leaf length	1-year height	2-year height
Pinus flexilis								
2992	+[a]	+	+	+	-	-	+	-
3002	-	-	+	+	-	-	+	-
2825	+	+	+	+	-	-	+	-
2846	+	-	+	-	-	-	+	-
2856	-	-	+	+	-	-	+	-
2697	+	-	+	+	-	-	-	-
977	+	+	+	-	+	-	+	-
967	-	-	+	+	-	-	+	-
2929	+	+	+	+	-	+	+	+
1085	-	-	+	-	-	-	+	+
2909	+	+	-	+	+	-	+	-
1030	+	+	+	+	-	-	+	-
2553	+	+	+	-	+	+	+	+
2563	-	-	+	-	+	-	+	-
2724	-	-	+	-	-	-	-	-
922	-	-	-	+	-	-	+	-
909	-	+	+	+	-	-	+	-
2523	-	+	+	-	-	-	+	-
2509	+	+	+	+	+	-	+	-
2601	+	+	+	+	-	-	+	-
916	-	-	+	+	+	-	+	+
2978	-	+	+	-	+	+	+	+
2900	+	+	+	+	+	-	+	+
2652	+	-	+	+	+	-	+	+
2796	+	+	+	-	-	-	+	-
Pinus strobiformis								
2569	+	-	+	-	-	+	+	+
2805	-	-	-	-	-	-	+	+
1023	-	-	+	-	-	-	+	+
2621	+	+	+	-	+	+	+	+
2743	-	-	+	-	+	+	+	+

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[a] + indicates a significant difference between progenies within the stand.
- indicates no significant difference between progenies within the stand.

significant differences in the number of cotyledons per seedling. However, only within one of five P. strobiformis stands were differences evident. Within-stand differences in cotyledon length were present in almost all stands of both taxa. One might expect the number of cotyledons per seedling to be genetically controlled. However, cotyledon length is probably strongly related to seed size or weight because cotyledon growth is nearly complete by the time the reserve food supply of the seed is expended. Correlation coefficients presented in the following chapter indicate that seed weight is related to both measures. However, the use of plot means in the analyses may have masked the extent of the relationships.

Pinus flexilis progenies within half of the stands differed in the production of secondary leaves in the first year. Pinus strobiformis seedlings uniformly lacked first-year secondary leaves.

Approximately 40 percent of the stands had first year color differences among the individual tree progenies. The within-stand variation was more prominent in stands from the more southern collection areas for both species.

Significant differences in the length of secondary leaves were found in 3 of 5 stands of P. strobiformis but in only 3 of 26 stands of P. flexilis. The greater range of variation in leaves of P. strobiformis (60 millimeters) as compared to that of P. flexilis (40 millimeters) may account for the higher proportion of within-stand differences.

First-year height differences were present within all but 3 of 26 stands of P. flexilis but only 7 of 26 had significant differences at the end of the second year. In contrast, significant within-stand differences were present in all P. strobiformis stands in both years. The first-year height was probably confounded by seed-size differences.

In every case where significant within-stand differences in secondary leaf length were present there were also differences in second-year height. However, the reverse condition did not hold.

Single-tree progenies within stand 2724 from California differed in only one of eight traits. There were two stands with differences between progenies for only two characters (stands 922 and 2805). At the opposite extreme, there were four stands with differences between

progenies for seven of the eight traits and three with differences in six of the eight traits.

At the end of the second year there were few noticeable within-stand differences for *P. flexilis*.

ANALYSES OF CORRELATIONS BETWEEN CHARACTERS

Simple correlations were calculated for all possible combinations of seedling and parental characters measured and between these characters and geographic origin data. Stand means were used as items in the analyses. The 38 P. flexilis and 12 P. strobiformis stands for which both seedling and parental data were available were included in the overall species analyses. In addition, individual analyses were performed for those areas of origin represented by collections from five or more stands.

Five traits were eliminated from the discussion and tables for the sake of brevity. The measure of length of growing season was retained in preference to the dates of germination and bud set because it incorporates both. First- rather than second-year color data was included because it reflected greater differentiation between stands. The color measures were correlated at the 1 per cent level or greater. In like manner, the measure of cone scale reflexing based on the central portion of the cone was given preference over data from the tip and basal portions. Again, all measures of reflexing were correlated at the 1 per cent level or greater.

Correlations which were significant at the 5 per cent level or greater for either species or any area are presented. For comparative purposes the corresponding values for the other areas are presented whether significant or not. When used in the text the words "significant" and "highly significant" refer to significance at the 5 and 1 per cent levels respectively.

Correlations Between Seedling Characters

With the exception of some correlations involving length of growing season there is no apparent causal relationship implied in the correlation coefficients presented in Table 13. When the entire range of P. flexilis was considered almost all the correlations were significant. However, for smaller areas only about 18 per cent were. This type of situation is not unusual when a species with a wide range is considered. A hypothetical example illustrating this type of pattern is presented in Figure 8. A strong correlation between the two characters is apparent over the range of the species but within less extensive areas, only population A shows significant correlation.

Table 13. Correlations between seedling characters of Pinus flexilis and Pinus strobiformis.

Characters to which correlation applies		Pinus flexilis					Pinus strobiformis	
		Entire species	Alta. Mont. N Wyo.	SW Idaho SE Wyo. N Utah	N Colo. C Colo.	S Colo. S Utah N. Mex.	Entire species	Ariz.
(3) Length of growing season	(4) Cotyledon number	+.533**	+.377	+.261	+.231	+.606	+.507	+.472
	(5) Cotyledon length	+.353*	+.110	+.416	-.302	-.251	+.263	+.114
	(6) Diameter of hypocotyl	+.612**	+.123	+.267	-.112	+.796	-.009	-.166
	(7) 1-year secondary leaves	+.330*	-.206	-.364	+.219	+.712	+.307	+.240
	(8) 1-year foliage color	+.560**	+.251	-.348	+.546	+.740	+.311	+.115
	(10) Length of secondary leaves	+.548**	+.560*	+.651	-.541	.000	+.787**	+.662
	(11) Degree of leaf serrulation	+.116	+.302	+.230	-.702	+.294	+.743**	+.577
	(12) Number of stomatal rows	+.449**	+.560*	-.413	+.366	+.318	-.380	-.390
	(13) 1-year height	+.670**	+.636*	+.326	-.211	+.826	+.432	+.129
	(14) 2-year height	+.549**	+.661*	+.573	-.418	+.870	-.131	-.365
	(15) Second growth increment	+.330*	+.587*	+.166	-.536	+.080	-.724**	-.738*
(4) Cotyledon number	(5) Cotyledon length	+.415*	+.102	+.879**	-.115	-.860	+.496	+.440
	(6) Diameter of hypocotyl	+.560**	+.190	+.906**	+.173	+.155	+.147	-.011
	(7) 1-year secondary leaves	+.449**	-.128	+.484	+.276	+.453	+.115	+.209
	(8) 1-year foliage color	+.440**	-.150	+.370	+.012	+.538	+.077	-.250
	(10) Length of secondary leaves	+.555**	+.164	+.794*	+.120	+.148	+.220	+.094
	(11) Degree of leaf serrulation	+.367*	+.580*	+.306	-.380	+.890*	+.040	-.332
	(13) 1-year height	+.680**	+.310	+.749	-.336	+.248	+.393	+.174
	(14) 2-year height	+.606**	+.496	+.704	+.043	+.570	+.060	-.153
	(15) Second growth increment	+.443**	+.367	+.444	+.275	+.019	+.521	-.518
(5) Cotyledon length	(6) Diameter of hypocotyl	+.809**	+.574*	+.850*	+.660	+.026	+.581*	+.523
	(7) 1-year secondary leaves	+.401*	+.424	+.119	+.103	-.340	-.066	-.070
	(10) Length of secondary leaves	+.663**	+.083	+.742	+.722*	+.048	+.270	+.266
	(13) 1-year height	+.730**	+.203	+.647	+.680	+.026	+.041	-.296
	(14) 2-year height	+.732**	+.092	+.534	+.668	-.176	+.186	+.182
	(15) Second growth increment	+.613**	-.065	+.070	+.754*	+.255	+.029	+.127
(6) Diameter of hypocotyl	(7) 1-year secondary leaves	+.522**	+.150	+.480	+.065	+.834	-.300	-.286
	(8) 1-year foliage color	+.542**	-.160	+.186	+.434	+.207	+.534	+.448
	(10) Length of secondary leaves	+.691**	+.284	+.696	+.516	-.477	+.246	+.378
	(13) 1-year height	+.904**	+.485	+.819*	+.872**	+.732	+.524	+.409
	(14) 2-year height	+.860**	+.331	+.450	+.860**	+.482	+.747**	+.818**
	(15) Second growth increment	+.670**	+.128	+.180	+.833*	-.338	+.253	+.334
(7) 1-year secondary leaves	(8) 1-year foliage color	+.333*	-.417	+.767*	+.447	+.262	-.404	-.281
	(13) 1-year height	+.414*	-.570*	+.617	-.014	+.366	-.180	-.011
(8) 1-year foliage color	(10) Length of secondary leaves	+.474**	+.457	+.175	+.039	+.407	+.576*	+.506
	(11) Degree of leaf serrulation	-.029	-.316	+.402	-.222	+.407	+.617*	+.551
	(13) 1-year height	+.578**	+.089	+.363	+.408	+.496	+.807**	+.683*
	(14) 2-year height	+.493**	-.020	+.402	+.134	+.814	+.636*	+.440
	(15) Second growth increment	+.393*	+.219	+.774*	+.100	+.490	+.003	+.112
(10) Length of secondary leaves	(11) Degree of leaf serrulation	+.280	+.271	+.565	+.707*	.000	+.882**	+.785*
	(12) Number of stomatal rows	+.242	+.428	-.020	+.071	-.609	-.630*	-.623
	(13) 1-year height	+.737**	+.782**	+.646	+.383	+.236	+.482	+.282
	(14) 2-year height	+.694**	+.702**	+.844*	+.425	+.480	+.244	+.205
	(15) Second growth increment	+.630**	+.832**	+.578	+.087	+.968**	-.326	-.184
(13) 1-year height	(14) 2-year height	+.900**	+.889**	+.683	+.844**	+.862	+.600*	+.521
	(15) Second growth increment	+.719**	+.760**	+.420	+.661	+.336	-.210	-.112
(14) 2-year height	(15) Second growth increment	+.903**	+.929**	+.816*	+.915**	+.547	-.012	+.509
Number of progenies in analysis		38	13	7	8	5	12	9
Value of r significant at 5 percent level (= *)		.325	.553	.754	.707	.878	.576	.666
Value of r significant at 1 percent level (= **)		.418	.684	.875	.834	.959	.708	.798

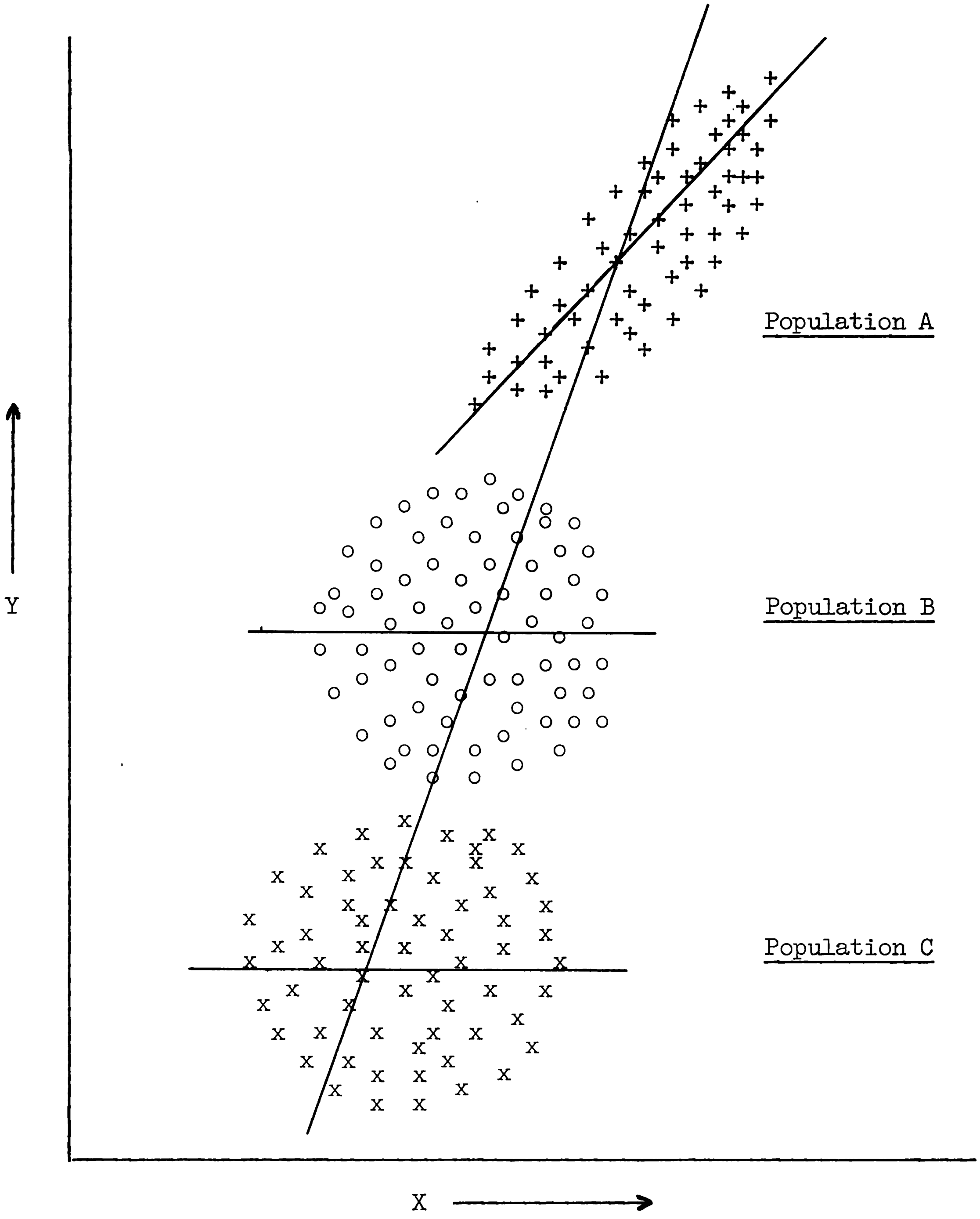

Figure 8. Hypothetical scatter diagram illustrating correlation patterns.

Most of the P. strobiformis collections available for correlation analysis were from Arizona. Most correlations which were significant for the species were also significant for the Arizona population.

The most consistent correlations among P. flexilis characteristics involved hypocotyl diameter, secondary leaf length, 1- and 2-year heights, and amount of growth during the second increment of the second year. Seedlings that were tallest at the end of the first year were also tallest at the end of the second year. The seedlings that were tallest at the end of the second year were the ones which made the most growth during the second growth increment. The relationships between secondary leaf length and degree of serrulation and number of dorsal stomatal rows were inconsistent.

In P. strobiformis seedlings, long secondary leaves were strongly correlated with more pronounced serrulation and fewer stomatal rows. There was a highly significant correlation between hypocotyl diameter and 2-year height but 1- and 2-year heights were only weakly related.

Correlations Between Parental Characters

In four of the eight groupings among the correlation coefficients applicable to P. flexilis (Table 14), the signs of the coefficients were consistently reversed within some populations as compared to the entire species. For example, correlations involving the length of secondary leaves were positive for the species as a whole and the southern Idaho-northern Utah and southern Colorado-southern Utah-northern New Mexico populations. For the Alberta-Montana-northern Wyoming and northern and central Colorado populations the correlations were negative.

Several interesting comparisons between P. flexilis and P. strobiformis may be seen in the correlation coefficients presented in Table 14. Longer leaves of P. flexilis had more dorsal stomata than short ones but the opposite condition prevailed for P. strobiformis. Collections of P. strobiformis with long leaves and few dorsal stomata also had cones with long and reflexed apophyses. These characters were not consistently related for P. flexilis. For both species longer cones were also wider and those cones with longer apophyses exhibited more reflexing of the scales. In P. flexilis the wider cones had longer cone scale apophyses. For P. strobiformis there was almost no relationship for the species as a whole and,

Table 14. Correlations between parental characters of <u>Pinus</u> <u>flexilis</u> and <u>Pinus</u> <u>strobiformis</u>.

Characters to which correlation applies		Pinus flexilis					Pinus strobiformis	
		Entire species	Alta. Mont. N Wyo.	SW Idaho SE Wyo. N Utah	N Colo. C Colo.	S Colo. S Utah N. Mex.	Entire species	Ariz.
(16) Number of seed per gram	(17) Length of secondary leaves	-.346*	-.116	-.828*	-.225	-.625	-.322	-.485
	(19) Degree of leaf serrulation	-.470**	-.296	+.110	-.400	-.416	+.040	+.349
	(21) Cone length	-.786**	-.345	-.941**	-.524	-.380	-.023	+.001
	(23) Length of apophysis	-.631**	-.419	-.524	-.514	-.035	-.203	-.305
	(25) Degree of cone scale reflexing	-.413*	-.238	+.019	-.482	+.084	-.150	-.321
(17) Length of secondary leaves	(18) Number of stomatal rows	+.238	-.126	+.765*	+.349	+.591	-.576*	-.491
	(21) Cone length	+.452**	+.323	+.822*	-.261	+.134	+.076	-.052
	(22) Cone width	+.412*	-.421	+.874*	-.273	+.896*	-.270	-.699*
	(23) Length of apophysis	+.263	-.148	+.727	-.308	+.594	+.693*	+.690*
	(25) Degree of cone scale reflexing	+.184	+.344	+.338	-.534	+.556	+.630*	+.716*
(18) Number of stomatal rows	(23) Length of apophysis	-.183	-.403	+.332	-.265	+.521	-.789**	-.754*
	(25) Degree of cone scale reflexing	-.185	-.210	+.135	-.481	+.413	-.666*	-.755*
(19) Degree of leaf serrulation	(21) Cone length	+.340*	+.150	-.081	+.042	+.102	+.577*	+.439
	(22) Cone width	+.099	+.666*	-.066	-.208	-.338	+.654*	+.393
	(23) Length of apophysis	+.405*	+.693**	-.394	-.052	+.338	+.242	-.019
	(25) Degree of cone scale reflexing	+.484**	+.445	-.204	-.012	+.498	+.093	+.031
(20) Length of peduncle	(21) Cone length	+.428**	+.416	+.596	+.039	-.367	+.346	+.064
	(23) Length of apophysis	+.393*	+.164	+.384	+.190	-.476	+.584*	+.440
(21) Cone length	(22) Cone width	+.713**	+.150	+.950**	+.798*	+.518	+.646*	+.560
	(23) Length of apophysis	+.658**	+.345	+.420	+.407	+.726	+.472	+.338
	(25) Degree of cone scale reflexing	+.426**	+.153	+.032	+.562	+.574	+.409	+.380
(22) Cone width	(23) Length of apophysis	+.599**	+.500	+.600	+.370	+.750	+.008	-.429
(23) Length of apophysis	(25) Degree of cone scale reflexing	+.583**	+.370	+.732	+.828*	+.958*	+.907**	+.965**
Number of progenies in analysis		38	13	7	8	5	12	9
Value of r significant at 5 percent level (= *)		.325	.553	.754	.707	.878	.576	.666
Value of r significant at 1 percent level (= **)		.418	.684	.875	.834	.959	.708	.798

within the Arizona population, the wider cones had shorter apophyses. The longer apophyses of *P. strobiformis* were reflexed to the extent that they did not proportionately increase cone width.

Comparison of correlations between length of leaves and number of dorsal stomatal rows for seedlings (characters 10-12 in Table 13) and parental specimens (characters 17-18 in Table 14) reveals some striking reversals. Seedlings from southern Idaho-southern Wyoming-northern Utah and southern Colorado-southern Utah-northern New Mexico with longer leaves had fewer dorsal stomata. For parental materials the longer leaves had more stomata.

Correlations Between Seedling and Parental Characters

Seed weight, as measured by the number of seed per gram, was strongly correlated with almost all seedling characters of *P. flexilis* if the entire species range was considered (Table 15). Within smaller areas, however, seed weight was significantly correlated only with cotyledon length and secondary leaf length. There were no significant correlations involving seed weight for *P. strobiformis*. No significant effect of seed weight was found on either first- or second-year height of seedlings from within subdivisions of the ranges of either *P. flexilis* or *P. strobiformis*. A seed weight-height correlation has commonly been found in early growth results for other species. The use of average seed weights and plot means for heights might have obscured such a relationship if it existed.

Length of leaves of parents was not consistently related to any seedling characters of *P. flexilis* for limited areas. There was a surprising absence of correlation between parental and seedling leaf length for *P. strobiformis*.

The number of rows of stomata on the dorsal surface of parental leaves was significantly correlated with the same measure on seedling leaves only for *P. strobiformis*. A correlation between the degree of serrulation of parental and seedling leaves was found for the species as a whole and for the most northern and southern populations of *P. flexilis*.

Length of peduncle, cone length, and cone width were significantly correlated with seedling characters only when the entire ranges of the species were considered.

Table 15. Correlations between parental and seedling characters of <u>Pinus flexilis</u> and <u>Pinus strobiformis</u>.

Characters to which correlation applies		Pinus flexilis					Pinus strobiformis	
Parental characters	Seedling characters	Entire species	Alta. Mont. N Wyo.	SW Idaho SE Wyo. N Utah	N Colo. C Colo.	S Colo. S Utah N. Mex.	Entire species	Ariz.
(16) Number of seed per gram	(3) Length of growing season	-.414*	-.352	-.036	+.400	-.452	+.142	-.344
	(4) Cotyledon number	-.645**	-.474	-.613	-.237	-.336	-.217	-.567
	(5) Cotyledon length	-.764**	-.466	-.762*	-.655	+.120	+.040	-.334
	(6) Diameter of hypocotyl	-.738**	-.174	-.577	-.349	-.478	+.033	-.279
	(7) 1-year secondary leaves	-.336*	+.071	+.091	-.069	-.791	-.196	-.550
	(8) 1-year foliage color	-.378*	+.071	+.154	-.309	-.439	+.043	-.222
	(10) Length of secondary leaves	-.674**	-.280	-.573	-.806*	+.596	+.112	-.120
	(13) 1-year height	-.682**	-.369	-.372	-.179	+.062	+.065	-.472
	(14) 2-year height	-.665**	-.319	-.278	-.234	-.062	-.121	-.183
	(15) Second growth increment	-.548**	-.271	-.028	-.550	+.529	-.033	+.171
(17) Length of secondary leaves	(3) Length of growing season	+.354*	+.587*	-.328	+.027	-.760	+.632*	+.838**
	(4) Cotyledon number	+.260	-.251	+.461	+.634	-.776	+.576*	+.766*
	(6) Diameter of hypocotyl	+.381*	+.078	+.527	+.519	-.665	-.340	-.251
	(8) 1-year foliage color	+.358*	+.134	+.078	-.024	-.355	-.325	-.232
	(10) Length of secondary leaves	+.503**	+.388	+.306	+.261	+.423	+.327	+.382
	(13) 1-year height	+.397*	+.299	+.489	+.179	-.391	-.198	-.114
	(15) Second growth increment	+.266	+.204	+.063	+.446	+.464	-.604*	-.626
(18) Number of stomatal rows	(3) Length of growing season	-.301	-.506	-.049	-.331	-.744	-.600*	-.683*
	(4) Cotyledon number	-.353*	+.113	+.172	+.086	-.708	+.096	+.058
	(10) Length of secondary leaves	-.222	-.701**	+.155	+.002	-.358	-.658*	-.732*
	(11) Degree of leaf serrulation	-.122	-.216	+.404	+.255	-.312	-.601*	-.722*
	(12) Number of stomatal rows	-.078	-.417	-.090	+.177	-.288	+.747**	+.702*
	(13) 1-year height	-.381*	-.551	+.389	-.314	-.781	+.110	+.061
	(14) 2-year height	-.423**	-.450	+.040	-.218	-.839	+.395	+.335
	(15) Second growth increment	-.393*	-.610*	-.179	-.195	-.306	+.325	+.269
(19) Degree of leaf serrulation	(4) Cotyledon number	+.423**	+.308	+.275	+.284	+.650	-.001	+.092
	(5) Cotyledon length	+.473**	+.161	+.078	+.568	-.660	-.072	+.084
	(6) Diameter of hypocotyl	+.482**	-.311	-.086	+.932**	-.431	-.022	+.311
	(10) Length of secondary leaves	+.517**	+.150	+.119	+.358	.000	+.384	+.236
	(11) Degree of leaf serrulation	+.394*	+.789**	+.286	+.257	+.918*	+.109	.000
	(13) 1-year height	+.424**	+.138	+.165	+.757*	-.554	-.061	+.077
	(14) 2-year height	+.501**	+.325	+.604	+.758*	-.126	-.032	+.070
	(15) Second growth increment	+.424**	+.422	+.585	+.732*	-.167	-.212	-.188
(20) Length of peduncle	(4) Cotyledon number	+.427**	+.303	+.408	-.486	+.840	+.030	-.057
	(10) Length of secondary leaves	+.410*	+.158	+.709	-.338	+.263	+.675*	+.443
	(13) 1-year height	+.338*	+.217	+.060	+.222	+.340	+.376	+.451
	(14) 2-year height	+.357*	+.323	+.338	+.216	+.497	+.077	+.059
(21) Cone length	(3) Length of growing season	+.412*	+.019	.000	-.102	+.319	+.251	+.098
	(4) Cotyledon number	+.493**	-.272	+.421	-.382	+.047	-.091	-.116
	(5) Cotyledon length	+.665**	+.341	+.547	+.612	+.435	-.248	-.260
	(6) Diameter of hypocotyl	+.626**	+.072	+.348	+.009	+.019	-.175	-.070
	(8) 1-year foliage color	+.479**	-.187	-.129	+.302	+.825	+.358	+.533
	(10) Length of secondary leaves	+.684**	+.398	+.523	+.454	+.395	+.456	+.309
	(13) 1-year height	+.680**	+.434	+.270	+.155	+.152	+.070	+.073
	(14) 2-year height	+.590**	+.242	+.281	-.079	+.438	-.054	-.038
	(15) Second growth increment	+.450**	+.232	+.148	+.043	+.536	-.163	-.080
(22) Cone width	(4) Cotyledon number	+.334*	+.199	+.634	-.131	-.748	-.429	-.509
	(5) Cotyledon length	+.502**	-.189	+.748	+.366	+.867	-.365	-.306
	(6) Diameter of hypocotyl	+.404*	-.509	+.608	-.213	-.443	-.302	-.036
	(10) Length of secondary leaves	+.504**	+.062	+.623	+.573	+.381	+.113	-.292
	(13) 1-year height	+.445**	-.034	+.507	-.195	-.253	-.223	-.152
	(14) 2-year height	+.359*	+.024	+.364	-.390	-.249	-.004	+.160
	(15) Second growth increment	+.355*	-.141	+.138	-.136	+.508	+.316	+.571
(23) Length of apophysis	(3) Length of growing season	+.297	+.321	.000	-.701	-.384	+.734**	+.828**
	(4) Cotyledon number	+.469**	+.530	+.618	-.044	-.198	+.246	+.291
	(5) Cotyledon length	+.706**	+.265	+.520	+.703	+.407	-.087	-.007
	(6) Diameter of hypocotyl	+.562**	+.077	+.826*	+.098	-.648	-.604*	-.373
	(10) Length of secondary leaves	+.732**	+.585*	+.506	+.588	+.477	+.542	+.446
	(11) Degree of leaf serrulation	+.442**	+.870**	+.491	+.363	+.075	+.531	+.517
	(13) 1-year height	+.629**	+.629*	+.747	+.100	-.479	+.045	+.027
	(14) 2-year height	+.652**	+.733**	+.190	+.353	-.140	-.504	-.648
	(15) Second growth increment	+.638**	+.762**	+.168	+.541	+.508	-.752**	-.768*
(25) Degree of cone scale reflexing	(3) Length of growing season	+.100	+.206	+.148	-.378	-.451	+.701*	+.572*
	(5) Cotyledon length	+.502**	+.536	+.042	+.754*	+.173	+.058	+.004
	(10) Length of secondary leaves	+.493**	+.220	+.344	+.609	+.568	+.487	+.423
	(11) Degree of leaf serrulation	+.368*	+.273	+.743	+.302	+.233	+.484	+.406
	(13) 1-year height	+.337*	+.124	+.723	+.217	-.554	+.163	-.018
	(14) 2-year height	+.267	+.035	+.278	+.212	-.156	-.412	-.669*
	(15) Second growth increment	+.259	+.097	+.419	+.337	+.528	+.682*	-.672*
Number of progenies in analysis		38	13	7	8	5	12	9
Value of r significant at 5 percent level (= *)		.325	.553	.754	.707	.878	.576	.666
Value of r significant at 1 percent level (= **)		.418	.684	.875	.834	.959	.708	.798

A surprising result of the analysis was the finding of significant positive correlations between apophysis length and several seedling characters for the northern portion of the range of *P. flexilis*.

Correlations Between Seedling Characters and Geographic Origin Data

Latitude of origin was significantly related to most seedling characters of *Pinus flexilis* when the entire range was considered but only occasionally for smaller areas (Table 16). Although not significantly correlated over the whole range, there was a significant negative correlation between latitude and cotyledon number for two segments of the range of *P. flexilis*, the northernmost and southermost. For *P. strobiformis*, latitude was negatively correlated with length of growing season and cotyledon number and positively correlated with the amount of growth during the second increment.

Negative correlations between longitude and seedling characters of *P. flexilis* when the overall range is considered, reflect a strong correlation between latitude and longitude. The latitudinal effect is probably the most important component of the correlation coefficient.

Fewer dorsal stomata on leaves of seedlings of Arizona - as compared to New Mexico and Texas - origins gave rise to the correlation with longitude.

A decrease in latitude appears to compensate for increasing altitude of origin for more southern *P. flexilis* collections so that no significant correlations between elevation and seedling characters were detected. Elevational effects appear more consistent among *P. strobiformis* progenies.

The relative lack of origin-progeny correlations within areas means that it did not pay to get detailed origin data within regions. Except for 2-year height (inversely correlated with latitude of origin for the Alberta-Montana-northern Wyoming area of *P. flexilis*).it was impossible to forecast progeny performance from origin data.

Correlations Between Parental Characters and Geographic Origin Data

Correlations between both latitude, elevation, and parental characters of *P. flexilis* are very erratic (Table 17). However, for *P. strobiformis* there were several consistent and highly significant

Table 16. Correlations between seedling characters and geographic origin data for *Pinus flexilis* and *Pinus strobiformis*.

Characters to which correlation applies		*Pinus flexilis*					*Pinus strobiformis*	
Geographic data	Seedling characters	Entire species	Alta. Mont. N Wyo.	SW Idaho SE Wyo. N Utah	N Colo. C Colo.	S Colo. S Utah N. Mex.	Entire species	Ariz.
Latitude	(3) Length of growing season	-.424**	-.062	+.053	-.161	-.754	-.646*	-.593
	(4) Cotyledon number	-.174	-.606*	-.314	+.298	-.893*	-.578*	-.593
	(5) Cotyledon length	-.423**	-.058	-.429	+.076	+.814	-.291	-.224
	(6) Diameter of hypocotyl	-.508**	-.217	-.492	-.387	-.504	+.069	+.170
	(10) Length of secondary leaves	-.356*	-.207	-.400	+.169	+.085	-.344	-.472
	(12) Number of stomatal rows	-.402*	-.051	-.043	+.356	-.461	+.030	+.136
	(13) 1-year height	-.459**	-.382	-.297	-.528	-.505	-.175	-.135
	(14) 2-year height	-.530**	-.688**	+.065	-.239	-.608	+.398	+.481
	(15) Second growth increment	-.506**	-.597*	+.110	-.043	+.175	+.658*	+.670*
Longitude	(3) Length of growing season	-.585**	-.229	-.146	-.279	-.854	+.183	-.541
	(6) Diameter of hypocotyl	-.373*	-.514	+.362	+.555	-.796	-.290	-.187
	(12) Number of stomatal rows	-.382*	-.091	-.080	-.202	-.146	-.596*	-.126
	(13) 1-year height	-.366*	-.455	+.106	+.653	-.671	+.066	-.028
Elevation	(3) Length of growing season	+.004	+.083	-.163	+.287	+.556	-.663*	-.528
	(11) Degree of leaf serrulation	-.037	-.014	+.568	-.038	+.786	-.590*	-.443
	(15) Second growth increment	+.319	-.234	-.029	-.349	+.349	+.592*	+.539
Number of progenies in analysis		38	13	7	8	5	12	9
Value of r significant at 5 percent level (= *)		.325	.553	.754	.707	.878	.576	.666
Value of r significant at 1 percent level (= **)		.418	.684	.875	.834	.959	.708	.798

Table 17. Correlations between parental characters and geographic origin data for *Pinus flexilis* and *Pinus strobiformis*.

Characters to which correlation applies		*Pinus flexilis*					*Pinus strobiformis*	
Geographic data	Parental characters	Entire species	Alta. Mont. N Wyo.	SW Idaho SE Wyo. N Utah	N Colo. C Colo.	S Colo. S Utah N. Mex.	Entire species	Ariz.
Latitude	(17) Length of secondary leaves	-.128	+.377	-.821*	-.390	+.917*	-.741**	-.827**
	(20) Length of peduncle	-.356*	-.519	-.648	+.172	-.856	-.238	-.382
	(23) Length of apophysis	-.476**	-.654*	-.751	+.622	+.600	-.759**	-.899**
	(25) Degree of cone scale reflexing	+.181	+.160	-.339	+.571	+.483	-.880**	-.939**
Elevation	(18) Number of stomatal rows	+.147	+.312	+.903**	+.295	-.425	+.651*	+.605
	(23) Length of apophysis	-.156	-.212	+.646	-.629	+.361	-.804**	-.778*
	(25) Degree of cone scale reflexing	-.161	-.191	+.466	-.453	+.414	-.751**	-.767*
Number of progenies in analysis		38	13	7	8	5	12	9
Value of r significant at 5 percent level (= *)		.325	.553	.754	.707	.878	.576	.666
Value of r significant at 1 percent level (= **)		.418	.684	.875	.834	.959	.708	.798

relationships. Length of secondary leaves, apophysis length, and degree of cone scale reflexing all decreased with increased latitude of origin. Higher elevation of origin was related to more dorsal stomata and shorter and less reflexed cone scale apophyses. These parental characters are the ones usually employed to separate P. flexilis and P. strobiformis, yet, all show gradation from the typical P. strobiformis condition toward that of P. flexilis as the boundary between their ranges is approached.

One would logically have expected more origin-parent than origin-progeny relationships. Their relative absence indicates that either the right origin data were not measured, or the origin data chosen had little selective value.

DISCUSSION

The Question of Distinct Species

The taxonomy and nomenclature of the Pinus flexilis complex have been an almost constant source of controversy since the discovery and naming of P. flexilis by James (1823). Most of the disagreement is centered about the status of that portion of the complex which occurs from extreme southern Colorado into northern Mexico. The main question asked is whether there is a continuous gradation between this southern portion of the complex and that from more northern areas. If the gradation is continuous, or nearly so, does it result from hybridization between two separate taxa or is it merely the transition between the extremes of variation in only one?

Seedling materials from a major portion of the range of the complex when grown together in a common nursery indicate that two distinct entities are involved. Although the number of collections from areas where intermediacy might be expected is small, the seedlings are sharply aligned with one group or the other rather than being intermediate. This distinction is maintained also for seedlings from New Mexico sources where the ranges clearly overlap. Although retaining their distinctness, progenies of the two taxa from the zone where the ranges meet and overlap exhibit some variational trends which indicate that hybridization has occurred or is presently occurring.

Parental materials, in contrast, exhibit almost a continuous gradation of variation in several characters. How can the two views be reconciled? The seedling materials represent the expression of heritable differences under a very limited range of environmental conditions. The parental materials reflect the interaction of heredity and environment under widely differing conditions. Most of the intergradation in parental materials was found in traits of the cone. The seedlings do not yet have cones to allow a comparison of the magnitude of genetic and environmental effects on these traits.

Variation Within Pinus flexilis

Within the range of P. flexilis, the northern member of the complex, three main expressions of variation were observed. The first was

the unexpected uniformity of both seedlings and parental materials from collections made in the area from Alberta to central Colorado. The common finding in other studies has been that over a comparable latitudinal range there was significant variation in several traits. The low density and scattered distribution of trees would be expected to restrict gene flow. With restricted gene flow the action of natural selection to effect adaptation to the environment would be very localized. As a result, considerable variation would be expected from place to place throughout the range. The absence of differences between stands might be attributed to several factors. Two of the more apparent possibilities are: (1) lack of genetic diversity upon which selection could act, and (2) uniformity of selective forces throughout the area. The first proposal, however, is opposed by the finding of significant within-stand differences for several traits. The second seems hardly plausible because of the broad elevational and latitudinal ranges involved. These two variables tend to be somewhat compensating, for at higher latitudes the trees grow at lower elevations. Numerous other environmental factors such as exposure, annual precipitation, and soil type vary throughout the area. All of these contribute to the selective pressure exerted in each part of the area. With so many factors involved it seems unlikely that their composite effects could be equal throughout the area.

The second feature of the observed variation concerned the extent of development of seedling and parental materials from isolated areas. The northernmost area was located in southwestern North Dakota. The stand is separated from other areas of P. flexilis by a distance of approximately 200 miles. This collection was made at a lower elevation than any other. Materials from this collection were very similar to those from Montana sources.

The collections from the Pine Bluff region of Wyoming and Nebraska were considerably different from others made at nearly the same latitude. The area is separated from the nearest stands of P. flexilis in the Rocky Mountains by a treeless plain nearly 60 miles wide (Goodding 1923). In most traits, the materials from this area were most like those from the southernmost portion of the species' range. Leaves of both parental and seedling materials were longer than others from similar or more northern sources. Seedlings from the Pine Bluff area also grew faster than all but the most southern progenies.

The areas where collections were made in east-central Idaho are separated from other collection areas to the east and south by the broad Snake River valley. Seedlings from these areas were fast growing. They were similar to seedlings of southern origin in most ways. Both the Idaho and Pine Bluff stands occur at lower elevations than other stands of similar latitude. Also, in both areas materials from one stand showed less extensive development of traits than those from the others.

Progeny of the easternmost stand collection (902) in central Colorado were taller than those from areas slightly farther west. They also had longer leaves and cotyledons. This collection was obtained from the eastern slope of the Front Range whereas the other Colorado collections were from the western slope or farther west. In his study of variation in lodgepole pine, Critchfield (1957:64) also found that materials collected on the eastern and western slopes of the Front Range differed in several characteristics.

The western portion of the species' range was represented by a single collection from the Sierra Nevada in eastern California. Both seedling and parental materials from this collection were very similar to those from high elevations in central Colorado.

The third feature of the variation found in *P. flexilis* was that progenies of southern Colorado, southern Utah, and northern New Mexico trees grew considerably faster than those from northern Utah and Colorado. In Colorado, the Arkansas River appeared to be the dividing line between slower growing progenies to the north and east and faster growing ones to the south and west. The cones from the southern trees were longer and wider than those from northern ones. They also had increased cone-scale reflexing, a trait usually associated with *P. strobiformis*.

Variation Within Pinus strobiformis

Variation between the northern and southern, and eastern and western populations was found in *P. strobiformis*.

Progenies of northern Arizona and New Mexico sources grew slightly slower than more southern ones. They also had shorter

cotyledons and secondary leaves. Parental materials were available for only one northern stand in Arizona. Leaves from this collection were shorter and less serrulate than those from more southern sources. The cones were shorter, and their apophyses shorter and much less reflexed than more southern ones.

Seedlings from New Mexico and Texas sources were slightly faster growing than those from Arizona. However, Arizona progenies had longer and more serrate leaves. When the adult materials are compared, the Arizona collections exhibit greater development of both leaf and cone traits than do those from New Mexico and Texas. It appears that the New Mexico materials show evidence of a slight amount of past or present hybridization with P. flexilis. This is reflected in their shorter leaves and cones, less serrulate leaves with more dorsal stomata, and less reflexed cone scales. In Arizona, the valleys of the Colorado and Little Colorado Rivers separate areas where P. strobiformis occurs from areas to the north and east where P. flexilis or suspected hybrids between P. flexilis and P. strobiformis occur. A possible exception to the general separation may occur in the San Francisco Mountains near Flagstaff, Arizona.

A specimen (Rusby no. 831) seen at the University of Michigan Herbarium, collected in 1883, appears to bear typical P. flexilis foliage. There were no cones present with the collection. Three collections from the San Francisco Mountains were included in the present study. Seedlings from all three collections were distinctly of the P. strobiformis type. Parental materials were available for only one of these three collections. Foliage from trees in this collection was somewhat intermediate between P. flexilis and P. strobiformis. The cones resembled those of P. flexilis in many features. Thus it appears likely that P. flexilis has occurred in that area in the past if it is not presently growing there. Several recent attempts to find P. flexilis in the area have not yielded any likely specimens (personal communication, Dr. J. W. Andresen, Michigan State University).

Differences between progenies within stands were more apparent for P. strobiformis than P. flexilis. Height differences at the end

of the second year were especially noticeable among P. strobiformis progenies.

Correlations Among Characters

Most correlations between characters for P. flexilis were significant when the entire species range was considered. However, within smaller portions of the range only a few correlations were significant and their occurence was erratic. Thus it appears that few, if any, of the traits measured are causally related. For P. strobiformis, the correlations were much more consistent.

Seed size has commonly been found to influence the amount of growth of seedlings during the first few years. No significant effect was found on either first or second year height within subdivisions of the ranges of either P. flexilis or P. strobiformis. The use of average seed weights and plot means for heights might have obscured such a relationship if it existed. However, observations on albino seedlings indicated that the seed provided nutrition to the seedling for only the first 10 to 15 days following germination. Most growth occurs after this time.

Longer leaves had fewer dorsal stomata and more pronounced serrations in P. strobiformis collections but there were no consistent relationships for similar P. flexilis materials.

Parental collections of P. strobiformis that had long leaves with few dorsal stomata also had cones with long and reflexed apophyses.

There was a surprising lack of correlation between parental and seedling leaf length. The number of dorsal stomata on seedling and parental leaves was correlated only for P. strobiformis.

A portion of the confusion encountered regarding the separation of the two taxa may be related to the effects that elevational differences have upon the cones and leaves of P. strobiformis. The leaves of higher elevation sources had more dorsal stomata and the cones had shorter apophyses. The cone scales were also less reflexed. Elevational effects in P. flexilis were significant in only one area and for one character.

SUMMARY AND CONCLUSIONS

The Pinus flexilis complex is composed of two populations of 5-leaved pines of the subgenus Haploxylon. Both members have cones that open at maturity and the seeds of both lack effective wings. The northern population has a range from southern Alberta and British Columbia south to north-central New Mexico. This population is almost universally known as Pinus flexilis James. Members of the southern population occur in northern Mexico, Texas, Arizona, New Mexico, and southern Colorado. The most frequently used names associated with the southern taxon are: Pinus strobiformis Engelm., P. flexilis var. reflexa Engelm., P. reflexa Engelm., and P. ayacahuite var. brachyptera Shaw.

The primary purposes of the study were to evaluate the extent of differences between and within the two taxa of the complex. The results were to be used to attempt clarification of the names and ranks of the taxa.

A review of the literature showed that most authors recognized differences between the two taxa, but disagreed about classification and nomenclature. The suggestion gathered from the literature on experimental studies of variation and speciation in plants and trees was that samples of natural populations from various origins should be grown together in a common test area. This procedure would eliminate most of the differences due to environmental effects and expose the heritable differences.

Collection of materials for the study began in 1959 and continued through 1960. The study utilized two sources of information. The first was drawn from observation of morphological traits of cone and foliage specimens. These specimens were collected from several trees in each of 61 native stands. The second source was obtained from seedlings grown for two years in a nursery at Michigan State University. Seed for this phase of the study was gathered from the same trees sampled for cones and foliage. The nursery test was established in 1961. A randomized block design with four replications was used in the test. Each plot contained seed from a single tree.

Distinct differences between the two taxa were exhibited in the seedling test. Cotyledon number, length of secondary leaves, and

height growth were the most satisfactory characters for distinguishing between the taxa. Both stand- and single-tree progenies could usually be assigned definitely to one taxon or the other on the basis of these traits. Diagnostic characters of less value were germination date, date of bud set, length of growing season, diameter of hypocotyl, first and second year foliage color, and degree of leaf serrulation. Characters of little or no value in differentiating the taxa were: cotyledon length, number of dorsal stomatal rows, and amount of secondary leaf formation during the first year.

Traits measured on the cone and foliage specimens from the parental trees exhibited less distinctive differences between the taxa. Secondary leaf length was the most reliable parental character for separating the taxa. Other traits which served to separate the taxa were: seed weight, number of rows of dorsal stomata, length of cones, and degree of cone scale reflexing. There was considerable overlap with regard to: leaf serrulation, length of cone peduncle, cone width, and length of cone-scale apophyses.

It was concluded from the preceding results that the two taxa under consideration deserve separate specific rank. According to the rules of nomenclatural priority in the International Code of Botanical Nomenclature, Article 11, (1961) the proper name to be applied to the northern species is _Pinus flexilis_ James. The proper name for the southern species is _Pinus strobiformis_ Engelm.

The patterns of variation in the regions where the species' ranges are contiguous or sympatric indicate that hybridization has occurred in the past and may still be taking place. Both seedling and parental materials of _Pinus flexilis_ from southern Utah, southern Colorado, and northern New Mexico indicate the presence of some genes from _P. strobiformis_. There is also an indication that _P. flexilis_ genes are present in the northern _P. strobiformis_ populations. The cones from the parental collections exhibited the most evidence of hybridity. Controlled hybridization studies to test these conclusions will be possible when the outplanted seedlings reach breeding age. Special field studies might detect the presence of hybrid swarms if hybridization is occurring naturally at present.

Within the northern species, _Pinus flexilis_, the population

structure had three principle characteristics. First, there was very little variation in either seedlings or herbarium specimens from their parents in that portion of the range extending from southern Alberta to central Colorado. This uniformity was unexpected because of the common finding of considerable variation in other plants and trees from a similar latitudinal range. A portion of the uniformity may be attributed to the fact that the trees grow at increasing altitudes in more southern areas.

The second characteristic was an increased growth of seedlings from southern origins. Cones from the parent trees were also longer than those of northern origins. These materials appeared to show evidence of immigration of genes from *Pinus strobiformis*.

The third characteristic was the extreme performance of seedlings from three areas: (1) East-central Idaho, (2) The Pine Bluff area of Nebraska and Wyoming, and (3) Douglas County, Colorado. Seedlings from these areas equalled or exceeded those from the southernmost portion of the species range in height growth and foliar development. The parental specimens also resembled those from the southern collections. The stands in these areas were isolated from the main body of the species and were restricted in size. Selective forces acting within these sub-populations might more easily change the genetic composition than in extensive areas where gene migration was less limited.

Variation between stands within *Pinus strobiformis* was much more random than in *P. flexilis*. This randomness can probably be attributed to the fact that *P. strobiformis* occurs only on small, widely separated mountain ranges, or individual peaks. Seedlings from the northernmost origins grew more slowly than those of more southern sources. They also had shorter leaves, fewer cotyledons, and more rows of stomata on the dorsal leaf surface than southern ones. These traits suggest the influence of *P. flexilis* genes. The parental specimens from northern Arizona differed from those of central and southern Arizona in several ways. They had shorter leaves, smaller cones, and less cone scale reflexing.

Central and southern Arizona progenies had the longest leaves. The leaves from these progenies also had the most pronounced

serrulations and the fewest dorsal surface stomata. Cones from parental trees in that area were the largest of any. They also had the most reflexed scales.

Seedlings from eastern New Mexico and northwestern Texas grew the fastest. Both seedling and parental leaves of these sources were shorter and less serrate than those from central Arizona sources.

Variation between trees within stands of either species could be satisfactorily investigated only from the seedlings. Significant differences between progenies within one or more stands were found for all 13 seedling traits studied. Within some portions of the range of either species, differences between progenies within stands were almost as large as differences between stands. The wide spacing found in many stands would be expected to lead to considerable self-pollination or close inbreeding. If that has in fact happened a large amount of random within-stand variation could be expected.

Most correlations between seedling and parental characters were significant when the entire species' range was considered as a unit. However, within smaller portions of the range, the corresponding values often were not significant. The number of observations in any particular area was too small for a completely satisfactory test. More correlations between seedling traits and geographic origin data were significant than those between parental traits and origin data. This finding suggests that either (1) the parental traits studied were not adaptive, or (2) the origin data chosen had little selective value.

The study revealed the need for continuing research on several aspects of the problem. First is the need for more detailed study of samples from the area where the species are contiguous or sympatric. Second, materials from areas which were not sampled should be examined. Among those areas are: (1) Northern Mexico, (2) Southwestern California, (3) Nevada, (4) The Wallowa Mountains of Oregon, and (5) The Black Hills of South Dakota. Third, several areas, e.g., the Pine Bluffs, should be reexamined to determine the extent of ecotypic differentiation.

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