JOHN and MARTIN, 1965). No gross divergence seems to have taken place, as is the case with most species having trans-Bass Strait distributions (PRYOR, 1959), typical *E. globulus* being found both in South Gippsland and Tasmania (*Figure 1*). In fact, intermediates similar to those found in the Otways have been seen by the author in South Gippsland and on Flinders Island (*Figure 1*), suggesting that the rise of sea level since the Last Glacial has swamped a pre-existent pattern of distribution of both putative parent taxa and their mutual intermediates.

The pattern of variation between *E. globulus* and *E. bicostata* is probably the result of the sequence of isolation, divergence and recontact that PRYOR (1959) has postulated for other *Eucalyptus* species, rather than divergence due to selection within a continuous population. The high variability of the Otway stands supports this view.

Most work on intraspecific and interspecific variation in *Eucalyptus* concerns clines that appear to display, compared to this study, a high degree of within site uniformity in the character or complex of characters being studied (e.g. GREEN, 1969; BARBER, 1965).

Although much disturbance has taken place in the Otways, the trees in samples 10 and 16 were individuals who obviously predated European settlement in country untouched by logging to the date of sampling. These are among the more variable and intermediate stands. Thus it seems that the considerable areal extent of the intermediate stands does not fit easily into the hybridization of the habitat hypothesis of ANDERSON (1948) which has been supported for *Eucalyptus* in many cases by PRYOR (1953).


### Acknowledgement

I would like to thank Dr. R. F. PARSONS for his invaluable guidance and criticism.


### Summary


A disjunct occurrence of intermediates between *Eucalyptus globulus* and *E. bicostata* was sampled. With the partial exception of a very narrow coastal strip the populations were found to be highly variable, displaying a complete range of intermediates in two key characters, fruit size and flower number per inflorescence. This probable hybrid swarm cannot wholly be attributed to disturbance.


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# Geographic Variation in Pinus flexilis and Pinus strobiformis and its Bearing on their Taxonomic Status[1])


By R. J. STEINHOFF and J. W. ANDRESEN[2])


In the mountainous areas of western North America and extending into Central America there exists a series of three, apparently closely related, taxa of soft pines. These are: (1) *Pinus flexilis* JAMES, which grows from southern British Columbia and Alberta in Canada south to northern New Mexico and Arizona in the U.S.A. (*Figure 1*); (2) *P. strobiformis* ENGELMANN, which ranges from southern Colorado to San Luis Potosi in Mexico; (3) *P. ayacahuite* EHRENBERG, which extends from Jalisco and Hidalgo in Central Mexico southeastward to El Salvador and Honduras (CRITCHFIELD and LITTLE, 1966; Map 9).

Although these taxa are now accepted as separate species (MIROV, 1967; CRITCHFIELD and LITTLE, 1966), the autonomy and taxonomic position of the central population has long been a source of confusion and controversy. It all began when ENGELMANN (1848) named and described *P. strobiformis* from specimens collected in northern Mexico. Thirty years later he (ENGELMANN, 1878) also proposed that specimens collected in Arizona represented several varieties of P. *flexilis* even though they collectively approximated his earlier description of *P. strobiformis* in leaf serration, cone size, and cone scale reflexing. He soon (ENGELMANN, 1882) proposed that one of these varieties be elevated to specific rank as *P. reflexa*. Following that, SARGENT (1889) concluded that the Arizonan and Mexican specimens were drawn from the same population. He (SARGENT, 1889) first said they probably should be associated with *P. ayacahuite*, but then later (SARGENT, 1897) thought that the population deserved specific rank as *P. strobiformis* ENGELM. SHAW (1909, 1914) again subdivided the population and assigned members of the Mexican subpopulation to *P. ayacahuite* as variety *brachyptera* SHAW and those from Arizona, New Mexico, and Texas to *P. flexilis*. More recently, MARTÍNEZ (1948), in discussing the pines of Mexico, recognized both *P. ayacahuite* var. *brachyptera* and P. *reflexa*. A detailed review of the nomenclature and taxonomy of the complex has been presented by ANDRESEN and STEINHOFF (1971).

[1]) Information from the senior author's thesis submitted to Michigan State University in partial fulfillment of the Ph. D. requirements. The work was supported in part by National Science Foundation Grant G-15879 and a grant from the American Museum of Natural History to the junior author.

[2]) Research Geneticist, Forestry Sciences Laboratory, Intermountain Forest and Range Experiment Station, Moscow, Idaho, and Chairman, Department of Forestry, Southern Illinois University, Carbondale, Illinois, respectively. At the time the study was being conducted the authors were graduate assistant and associate professor, respectively, in the Forestry Department at Michigan State University, East Lansing, Michigan.

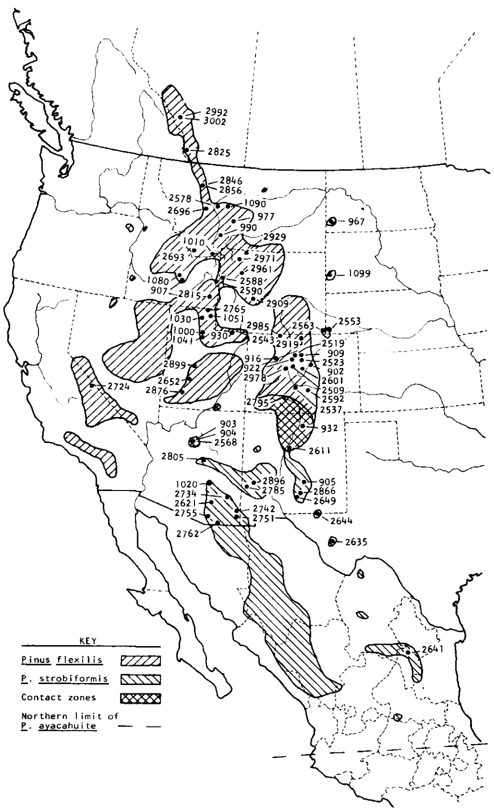


*Figure 1.* — Distribution of *Pinus flexilis* and *Pinus strobiformis* and location of collection areas.

Differences in taxonomic opinions and the varied botanical descriptions of *P. flexilis* and *P. strobiformis* indicate considerable variation in morphological traits, yet there has been almost no systematic investigation of that variation. Douglas and Douglas (1955) began a study of the variation in Colorado stands but illness forced discontinuation of the work.

One reason for the lack of interest is probably that these species have little commercial value. *Pinus flexilis* was used for lumber in the desert regions of Nevada in the days before railroad transportation (Jepson, 1910). However, because it usually grows in areas where moisture is limited, growth is slow and the trees are poorly formed and primarily important for watershed protection. *Pinus strobiformis* often grows on less exposed sites with more favorable moisture conditions than *P. flexilis*. In such areas the trees are often well formed and large enough to produce lumber but the species usually makes up only a small portion of the mixed stands in which it occurs.

The study on which this report is based had three primary objectives: (1) To study the extent of variation within *P. flexilis* and *P. strobiformis*, (2) to investigate differences between the taxa to see if their separate rank is justified, (3) to delineate the geographic boundaries of the species if they are distinct. Unfortunately, since we were able to obtain only one collection from Mexico, and that did not contain viable seed, the discussion of variation within *P. strobiformis* is essentially limited to the United States portion of its range.

We did not make any attempt to study the question of the separation between *P. strobiformis* and *P. ayacahuite*. If those taxa are not distinct, as indicated by Shaw's (1909) classification, then we should be discussing the separation of *P. flexilis* and *P. ayacahuite* rather than *P. strobiformis*.

## Materials and Methods

### *Acquisition and Handling of Materials*

A pilot study was initiated in 1959 by the junior author. Seed from several widely scattered areas throughout the species ranges was collected by cooperators. Seed from several trees in a stand was mixed and foliage specimens were not collected. Part of the seed was planted in 1960 to determine the best methods of handling the larger test which was to follow. Data from the preliminary test are not presented since seed from those collections were also planted for the study reported here.

Cones, seed, and foliage were collected in 1960 by U.S. Forest Service, provincial, and state employees. Where possible, each collection was to consist of cones and a foliage specimen from each of 10 trees in a stand. However, some stands did not contain 10 trees with cones and the cones from many trees contained no viable seed. Edaphic, ecologic, and geographic data pertinent to the collection areas were recorded. Michigan State Forest Genetics (MSFG) accession numbers were assigned to the collections. The seeds were stored at $45^0$ F. until sown about 6 months later. Foliage specimens were mounted on herbarium sheets for later measurements.

The seeds were planted in a randomized complete block design with four replications. Most plots within replicates consisted of progenies of individual trees. However, in seven of the 1959 collections, seed from several trees in each stand had been mixed.

Seeds were sown in late May in the Bogue Nursery at Michigan State University. The nursery soil, a sandy clay loam, had previously been fertilized and fumigated. The seed were planted at 4-cm. invervals in rows 100 cm. long and 15 cm. apart. After sowing, the seed were covered with a thin layer of sand. Soil moisture was maintained by sprinkler irrigation.

### *Parental Characters*

Data consisted of measurements of 11 characters on specimens from parental trees *(Tables 1 and 3)*. For each tree a character represented the mean value of measurements from five cones and five leaves removed from the central part of the growth produced in the year prior to collection. Methods of measurement of several characters need clarification:

*Character (5) Peduncle length:* Estimated because the point of attachment was often obscured by reflexed basal cone scales.

*Character (6) Cone width:* Measured at the widest point on open cones.

*Character (8) Length of cone scale apophyses:* Measured on the upper surface of five scales from the central portion of each cone.

*Characters (9) (10) (11) Cone scale reflexing:* Estimated from scales in the middle of the terminal, central, and basal portions of each cone as the exterior angle subtended by a line parallel to the upper surface of the cone scale and a line tangent to the terminal 5 mm. of the apophysis.

Two series of analyses of variance were performed. First, all of the collections from both taxa were included in a single analysis for each character. Secondly, the stands were assigned to two groups (taxa) based on the results of the first analyses. Form of the analyses and degrees of freedom for the parental traits were as follows:

| Source of variation | Degrees of freedom | | |
|---|---|---|---|
| | All stands | *P. flexilis* | *P. strobiformis* |
| Stands | 60 | 44 | 15 |
| Trees within stands | 412 | 324 | 87 |

### *Seedling Characters*

Twelve characters *(Tables 2 and 3)* represented by plot means of seedlings of individual maternal trees were recorded. Several characters need qualification:

*Character (15) Cotyledon length:* Length of the longest normal cotyledon.

*Characters (16) (17) Foliage color:* Scored in the fall on primary and secondary leaves for characters (16) and (17), respectively. Seedlings with the yellowest leaves were scored as Grade 1 and those with blue-green leaves as Grade 5.

*Characters (19) (20) Degree of serrulation and number of dorsal surface stomatal rows:* Recorded for only a single replication.

*Character (21) First-year epicotyl growth:* Value used was the mean for the largest and smallest seedlings.

The criterion for selecting a character was either: (1) That considerable variation in the trait had been reported in the species descriptions (e. g., leaf length and serrulation) or (2) that it exhibited pronounced differences in the nursery trial.

*Table 1.* — Parental characters of *Pinus flexilis.*

| MSFG Number | State or Province | Number of Trees Sampled | North Latitude | West Longitude | Elevation | Seed Weight | Length of Secondary Leaves | Number of Dorsal Stomatal Rows | Degree of Leaf Serrulation | Length of Peduncle | Cone Length | Cone Width | Length of Apophysis | Degree of Cone Scale Reflexing: Terminal 1/3 of Cone | Central 1/3 of Cone | Basal 1/3 of Cone |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Characters | (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
| | | no. | ° ' | ° ' | feet | mg. | mm. | no. | grade[a] | mm. | mm. | mm. | mm. | ° | ° | ° |
| 2992 | Alta. | 9 | 51 00 | 115 10 | 4700 | 91 | 53 | 2.3 | 1.1 | 3 | 84 | 51 | 5 | 0 | 30 | 40 |
| 3002 | Alta. | 7 | 51 00 | 115 10 | 4200 | 77 | 58 | 2.4 | 1.0 | 3 | 84 | 46 | 3 | 0 | 30 | 50 |
| 2825 | Alta. | 10 | 49 20 | 114 20 | 5100 | 91 | 53 | 2.6 | 1.1 | 3 | 81 | 53 | 4 | 0 | 10 | 30 |
| 2846 | Mont. | 10 | 47 50 | 112 40 | 5800 | 91 | 46 | 2.4 | 1.0 | 3 | 76 | 48 | 4 | 0 | 20 | 40 |
| 2856 | Mont. | 10 | 47 50 | 112 40 | 5000 | 100 | 53 | 2.6 | 1.3 | 4 | 81 | 51 | 4 | 10 | 50 | 60 |
| 1090 | Mont. | 9 | 47 00 | 110 57 | 6700 | -- | 47 | 3.0 | 1.1 | 10 | 79 | 50 | 5 | 0 | 0 | 10 |
| 2578 | Mont. | 10 | 46 50 | 111 43 | 7800 | 83 | 51 | 2.3 | 1.0 | 5 | 81 | 51 | 4 | 0 | 0 | 10 |
| 2696 | Mont. | 6 | 46 36 | 112 20 | 7200 | 83 | 46 | 2.5 | 1.3 | 3 | 71 | 53 | 4 | 0 | 10 | 10 |
| 977 | Mont. | 10 | 46 15 | 110 15 | 6500 | 91 | 43 | 2.6 | 1.1 | 6 | 86 | 53 | 5 | 0 | 10 | 40 |
| 990 | Mont. | 9 | 45 28 | 111 02 | 7200 | 83 | 51 | 2.7 | 1.0 | 6 | 81 | 48 | 4 | 0 | 0 | 20 |
| 1010 | Mont. | 10 | 44 50 | 112 52 | 7500 | -- | 43 | 2.6 | 1.0 | 5 | 84 | 53 | 4 | 0 | 0 | 10 |
| 2693 | Mont. | 3 | 44 33 | 111 36 | 8300 | -- | 51 | 2.3 | 1.7 | 5 | 80 | 46 | 4 | 0 | 0 | 0 |
| 967 | N. Dak. | 10 | 46 28 | 104 00 | 2500 | 111 | 53 | 2.4 | 1.0 | 7 | 84 | 48 | 4 | 0 | 10 | 30 |
| 1099 | S. Dak. | 4 | 43 45 | 103 30 | 6400 | -- | 50 | 2.2 | 1.2 | 3 | 77 | 51 | 5 | 0 | 10 | 50 |
| 2929 | Wyo. | 9 | 44 45 | 109 20 | 6300 | 91 | 51 | 2.4 | 1.1 | 4 | 79 | 48 | 5 | 0 | 30 | 50 |
| 2971 | Wyo. | 6 | 44 29 | 109 49 | -- | 100 | 53 | 2.4 | 1.5 | 4 | 81 | 51 | 6 | 10 | 30 | 50 |
| 2961 | Wyo. | 9 | 43 48 | 109 35 | 6500 | 91 | 51 | 2.4 | 1.6 | 4 | 89 | 53 | 6 | 0 | 30 | 50 |
| 2909 | Wyo. | 10 | 42 33 | 108 45 | 8300 | 67 | 46 | 2.3 | 1.1 | 4 | 69 | 43 | 6 | 0 | 20 | 50 |
| 2588 | Wyo. | 2 | 43 40 | 110 50 | 8700 | -- | 55 | 2.5 | 1.0 | 3 | 89 | 50 | 5 | 0 | 50 | 50 |
| 2590 | Idaho | 2 | 43 18 | 111 05 | 6000 | 143 | 46 | 2.2 | 2.0 | 3 | 86 | 51 | 6 | 0 | 50 | 90 |
| 1080 | Idaho | 10 | 43 27 | 113 35 | 5800 | 111 | 51 | 2.2 | 1.0 | 5 | 89 | 53 | 7 | 0 | 20 | 50 |
| 907 | Idaho | --[b] | 43 20 | 113 30 | 5000 | 167 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2815 | Idaho | 10 | 42 25 | 111 31 | 8900 | 83 | 51 | 2.5 | 1.4 | 5 | 86 | 53 | 5 | 0 | 20 | 40 |
| 2765 | Utah | 4 | 41 58 | 111 30 | 7200 | 77 | 46 | 2.0 | 1.2 | 8 | 76 | 48 | 6 | 0 | 10 | 50 |
| 1051 | Utah | 4 | 41 35 | 111 20 | 8500 | 100 | 48 | 2.5 | 1.1 | 8 | 89 | 53 | 5 | 0 | 0 | 10 |
| 1030 | Utah | 10 | 41 22 | 112 02 | 9300 | 111 | 56 | 2.6 | 1.2 | 5 | 89 | 56 | 6 | 0 | 0 | 40 |
| 930 | Utah | --[b] | 40 55 | 110 08 | 7800 | 100 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 1000 | Utah | 10 | 40 40 | 111 40 | 9700 | 111 | 56 | 2.6 | 1.1 | 8 | 91 | 58 | 7 | 10 | 40 | 50 |
| 1041 | Utah | 6 | 40 31 | 111 41 | 9600 | 100 | 56 | 2.5 | 1.0 | 8 | 91 | 56 | 6 | 10 | 20 | 50 |
| 2985 | Colo. | 6 | 40 50 | 107 05 | 8300 | 83 | 53 | 2.6 | 1.2 | 6 | 71 | 48 | 6 | 0 | 10 | 40 |
| 2543 | Colo. | 4 | 40 50 | 106 58 | 8800 | 100 | 43 | 2.4 | 1.0 | 5 | 91 | 56 | 8 | 0 | 50 | 60 |
| 2919 | Colo. | 8 | 40 38 | 105 41 | 10200 | 91 | 53 | 2.9 | 1.0 | 3 | 71 | 53 | 5 | 0 | 0 | 30 |
| 2519 | Colo. | 4 | 39 40 | 106 08 | 9900 | 67 | 46 | 2.5 | 1.0 | 6 | 76 | 51 | 3 | 0 | 0 | 0 |
| 922 | Colo. | --[b] | 39 32 | 106 08 | 9900 | 83 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 909 | Colo. | --[b] | 39 40 | 105 36 | 10600 | 91 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2523 | Colo. | 10 | 39 36 | 105 36 | 10500 | 91 | 46 | 2.8 | 1.0 | 4 | 74 | 51 | 5 | 0 | 10 | 20 |
| 2509 | Colo. | 10 | 39 13 | 106 05 | 10900 | 83 | 53 | 3.2 | 1.0 | 4 | 81 | 53 | 4 | 0 | 0 | 10 |
| 2601 | Colo. | 10 | 39 05 | 105 33 | 10600 | 111 | 53 | 2.3 | 1.2 | 4 | 89 | 53 | 5 | 0 | 0 | 40 |
| 916 | Colo. | --[b] | 39 36 | 107 14 | 9300 | 100 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2978 | Colo. | 7 | 39 05 | 106 28 | 11000 | 111 | 53 | 2.5 | 1.3 | 3 | 79 | 53 | 4 | 0 | 20 | 40 |
| 2553 | Nebr. | 10 | 41 10 | 104 02 | 5200 | 111 | 58 | 2.2 | 1.7 | 7 | 91 | 53 | 6 | 0 | 20 | 40 |
| 2563 | Wyo. | 5 | 41 00 | 104 05 | 5300 | 125 | 64 | 2.7 | 1.8 | 8 | 102 | 56 | 8 | 20 | 50 | 80 |
| 902 | Colo. | --[b] | 39 20 | 105 00 | 8500 | 143 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2724 | Calif. | 10 | 37 30 | 118 10 | 10000 | 71 | 56 | 2.9 | 1.1 | 3 | 74 | 51 | 5 | 0 | 0 | 30 |
| 2899 | Utah | 10 | 39 00 | 112 08 | 9500 | 125 | 58 | 2.8 | 1.5 | 4 | 96 | 58 | 8 | 10 | 40 | 50 |
| 2652 | Utah | 10 | 38 31 | 112 31 | 8500 | 125 | -- | -- | -- | 5 | 91 | 56 | 5 | 0 | 30 | 50 |
| 2876 | Utah | 6 | 37 40 | 112 40 | 8600 | 111 | 56 | 2.2 | 1.1 | 7 | 89 | 56 | 6 | 0 | 10 | 20 |
| 2537 | Colo. | 3 | 38 23 | 106 09 | 9000 | -- | 52 | 2.6 | 1.0 | 7 | 88 | 47 | 7 | 0 | 10 | 10 |
| 2592 | Colo. | 4 | 38 00 | 105 10 | 9000 | 143 | 53 | 2.6 | 1.1 | 3 | 96 | 56 | 6 | 0 | 10 | 40 |
| 2795 | Colo. | 10 | 37 43 | 106 35 | 9800 | 125 | 58 | 2.2 | 1.1 | 5 | 102 | 61 | 7 | 0 | 30 | 40 |
| 2611 | N. Mex. | 10 | 35 12 | 106 27 | 10500 | 143 | 48 | 1.8 | 1.5 | 9 | 96 | 51 | 6 | 0 | 20 | 50 |
| Standard error of a stand mean | | | | | | 10.8 | 2.6 | 0.2 | 0.2 | 1.1 | 3.4 | 1.3 | 0.7 | 5.0 | 7.6 | 7.1 |
| $LSD_{.05}$ between means | | | | | | 35.6 | 8.6 | 0.7 | 0.7 | 3.6 | 11.2 | 4.3 | 2.3 | 16.5 | 25.1 | 23.4 |

[a] Leaf serrulation grades:

Grade 1 - Serrulations absent or extremely minute and very few in number.
Grade 2 - Serrulations few in number and small but readily discernible.
Grade 3 - Serrulations prominent or numerous or both.

[b] Collected for the pilot study. Cones and foliage not available for measurement.

Statistical analyses followed the general procedure used for characters of parental trees, but was of the following form:

| Source of variation | Degrees of freedom | | |
|---|---|---|---|
| | All stands | *P. flexilis* | *P. strobiformis* |
| Replicates | 3 | 3 | 3 |
| Stands | 59 | 44 | 14 |
| Trees within stands | 216 | 185 | 31 |
| Pooled interactions (error) | 830 | 687 | 140 |

## Results

### *Variation Within Pinus flexilis*

*Parental characters:*

In preparing the distribution map *(Figure 1)* we have generalized the distributional patterns. In actuality, the distribution of *P. flexilis* is mostly restricted to individual mountain ranges separated by valleys where the species is absent (c. f. Critchfield and Little, 1966, Map 8). On a single mountain range the distribution is often further divided into narrow belts at lower and upper timberlines. In *Table 1* we have grouped and arranged the data by the location of the collections *(Figure 1)* from north to south within broad general areas.

The first group of collections represents the area from southwestern Alberta to west central Wyoming and the area north of the Snake River in southeastern Idaho. We have also included the isolated stands in western North and South Dakota with the group because the specimens from those collections are very similar to those from the broader area. Within the area there appear to be no geographically associated patterns or trends in the various characters studied. Differences between stands were usually limited to one or two characters; e. g., collections 2856 from Montana and 2590 from Idaho had cones with more reflexed scales and the seeds from collections 2590 and 907 from Idaho were heavier than those of the other collections. In general, the leaves from most of the collections were short (50 mm.), lacked serrations or were only minutely serrate, and commonly had about 2.5 rows of stomata on the dorsal leaf surface. The cones were short (75—80 mm.), and bore lightweight (80—100 mg.) seeds. The apophyses of the cone scales were short (3—6 mm.) and straight or only slightly reflexed (0—30°) in the terminal and central portions of the cones and only moderately (30—50°) reflexed in the basal portion of the cone.

The next more southerly area extends from the Snake River in southeastern Idaho south and east into northeastern Utah. Within that area there were some north to south patterns of variation but the differences were small. Cones from the southern collections are slightly (6 mm.) longer and wider than those from the northern collections; leaves of the southern collections were also about 8 mm. longer. While the cones and leaves of the Idaho-Utah group of collections were larger, on the average, than those of the Alberta-Montana-Woyming group they differed only slightly from the larger specimens of the latter.

Collections from northern and central Colorado (north of the east-west portion of the Arkansas River) represent a third group. Although this area is separated from both of the previous ones by about 100 miles, specimens from this group were quite similar to those from collections in both of the other areas, although they appeared to resemble the northern ones more closely. There were differences between stands within this group with regard to one or two characters but, as with the northern group, no geographically related patterns were apparent. The cones of collection 2543 were silghtly longer and wider, the apophyses of the cone scales were somewhat longer and more reflexed, and the leaves were shorter than those of other collections.

Two collections were made in the small isolated population that is found near the town of Pine Bluffs in southeastern Wyoming and adjacent areas in Nebraska and Colorado. Specimens from both of the collections had slightly longer and more serrate leaves than collections farther west and north. Cones of collection 2563 from Wyoming also were longer and had more reflexed cone scales than most of the others already mentioned. We are grouping collection 902, which came from that part of the Colorado Front Range which lies east of the South Platte River, with the two collections mentioned above on the basis of seedling characters which will be discussed later. All three collections had heavy seeds.

We were able to obtain only a single collection from the western part of the species range, number 2724 from the White Mountains in east central California. Seeds from the collection were light and the cones were short and had only slightly reflexed scales. The collection was similar to others from the northern part of the species range and to those from northern and central Colorado.

Specimens of the three collections from central and southwestern Utah were similar to those from northern Utah but had slightly heavier seeds. Longer leaves, larger cones, and heavier seeds differentiated this group from the more northern groups and from the central and northern Colorado group.

In the southern Rocky Mountains we are grouping collections from Colorado south of the Arkansas River and a single collection (2611) from the Sandia Mountains in north central New Mexico. Another collection (932) from northern New Mexico is included in the *P. strobiformis* materials. The collections from the area had longer and wider cones and heavier seeds than those from collections made in central and northern Colorado. However, the cones were no longer or wider than some more northern collections such as 2563 from southeastern Wyoming. Leaf length, number of dorsal stomatal rows, and leaf serrulation were similar to those of most collections from other groups.

The variability of trees within stands was not analyzed because techniques of cone and foliage sampling were not standard.

*Seedling characters:*

Pattern of geographic variation exhibited by seedling characters *(Table 2)* essentially paralleled that found in the parental specimens although the range of variation was larger. Seedlings from Alberta, Montana, North Dakota, Wyoming, Idaho, Utah, California, and northern Colorado generally had from 8 to 9 short (23—27 mm.) cotyledons, had short secondary leaves, and tended to be yellow-green. Epicotyl growth in the first year ranged from 8 to 13 mm. and total height at the end of the second year was slightly greater for seedlings from the south than from the north. Seedlings of collection 2590 from southeastern Idaho were taller at the end of the second year than those of all but the most southern collections. Western Colorado collections 2985, 916, and 2978 had seedlings which grew slightly faster

*Table 2.* — Seedling characters of *Pinus flexilis*.

| MSFG Number | State or Province | Number of Parent Trees Sampled | Mean date of germination | Period of Active Growth | Cotyledon Number | Cotyledon Length | 1-year Foliage Color | 2-year Foliage Color | Length of Second Year Secondary Leaves | Degree of Leaf Serrulation | Number of Dorsal Stomatal Rows | First-Year Epicotyl Growth | 2-year Height | Amount of Lammas Growth in Second Year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Characters | (12) | (13) | (14) | (15) | (16) | (17) | (18) | (19) | (20) | (21) | (22) | (23) |
| | | no. | days after June 1 | days | no. | mm. | grade[a] | | mm. | grade[a] | no. | ------mm.------ | | |
| 2992 | Alta. | 7 | 49 | 50 | 8.4 | 26 | 2.4 | 3.6 | 30 | 1.0 | 1.8 | 10 | 43 | 5 |
| 3002 | Alta. | 7 | 15 | 63 | 8.0 | 25 | 1.7 | 3.1 | 25 | 1.0 | 1.6 | 10 | 43 | 3 |
| 2825 | Alta. | 9 | 21 | 64 | 8.8 | 25 | 2.1 | 3.6 | 25 | 1.2 | 1.5 | 11 | 43 | 2 |
| 2846 | Mont. | 10 | 61 | 31 | 8.6 | 25 | 1.9 | 3.3 | 23 | 1.1 | 1.6 | 10 | 43 | 3 |
| 2856 | Mont. | 8 | 65 | 34 | 8.8 | 26 | 1.8 | 3.0 | 25 | 1.1 | 1.5 | 9 | 41 | 3 |
| 2578 | Mont. | 1 | 30 | 48 | 8.4 | 20 | 3.0 | 3.2 | 30 | 1.0 | 1.5 | 11 | 48 | 8 |
| 2696 | Mont. | 4 | 63 | 43 | 9.0 | 23 | 1.9 | 3.2 | 23 | 1.2 | 1.4 | 8 | 41 | 3 |
| 977 | Mont. | 8 | 54 | 31 | 9.0 | 26 | 1.6 | 3.2 | 25 | 1.5 | 1.5 | 10 | 43 | 2 |
| 990 | Mont. | 2 | 66 | 33 | 9.0 | 23 | 1.5 | 3.1 | 25 | 1.0 | 1.5 | 10 | 48 | 5 |
| 967 | N. Dak. | 5 | 60 | 53 | 9.0 | 27 | 2.0 | 3.3 | 28 | 1.1 | 1.6 | 12 | 48 | 5 |
| 2929 | Wyo. | 10 | 37 | 55 | 9.2 | 28 | 1.8 | 3.4 | 30 | 1.3 | 1.4 | 12 | 53 | 8 |
| 2971 | Wyo. | 3 | 24 | 75 | 9.8 | 24 | 2.0 | 3.0 | 30 | 2.0 | 2.0 | 12 | 56 | 10 |
| 2961 | Wyo. | 3 | 29 | 49 | 8.4 | 26 | 1.4 | 3.2 | 28 | 1.7 | 1.8 | 12 | 51 | 8 |
| 2909 | Wyo. | 10 | 38 | 47 | 8.0 | 24 | 1.6 | 3.2 | 25 | 1.1 | 1.7 | 11 | 46 | 5 |
| 2590 | Idaho | 2 | 66 | 33 | 8.8 | 33 | 1.5 | 3.8 | 33 | 1.5 | 2.0 | 14 | 66 | 13 |
| 1080 | Idaho | 4 | 58 | 41 | 9.2 | 28 | 1.6 | 3.2 | 30 | 2.0 | 2.0 | 12 | 53 | 8 |
| 907 | Idaho | --[b] | 47 | 59 | 9.8 | 32 | 2.5 | 3.2 | 36 | 1.0 | 2.5 | 12 | 53 | 8 |
| 2815 | Idaho | 1 | 61 | 38 | 8.8 | 26 | 2.0 | 3.8 | 30 | 2.0 | 1.5 | 12 | 58 | 13 |
| 2765 | Utah | 3 | 42 | 50 | 9.0 | 26 | 2.1 | 3.3 | 30 | 1.0 | 1.6 | 10 | 53 | 10 |
| 1051 | Utah | 1 | 49 | 50 | 8.4 | 27 | 1.2 | 4.0 | 30 | 1.0 | 2.0 | 10 | 51 | 5 |
| 1030 | Utah | 7 | 49 | 36 | 9.2 | 28 | 1.7 | 3.1 | 28 | 1.0 | 1.6 | 12 | 48 | 5 |
| 930 | Utah | --[b] | 39 | 53 | 7.8 | 27 | 1.0 | 2.2 | 30 | 1.0 | 1.5 | 14 | 56 | 13 |
| 1000 | Utah | 3 | 51 | 48 | 9.8 | 30 | 1.8 | 3.2 | 36 | 2.0 | 1.0 | 15 | 58 | 10 |
| 1041 | Utah | 2 | 43 | 39 | 8.6 | 28 | 1.8 | 3.1 | 28 | 1.5 | 2.2 | 10 | 46 | 8 |
| 2985 | Colo. | 2 | 24 | 61 | 8.6 | 27 | 1.6 | 3.2 | 28 | 1.2 | 1.7 | 12 | 64 | 13 |
| 2543 | Colo. | 4 | 62 | 51 | 8.2 | 29 | 1.7 | 3.2 | 33 | 1.2 | 2.0 | 11 | 48 | 8 |
| 2919 | Colo. | 2 | 20 | 79 | 9.2 | 24 | 1.6 | 3.8 | 28 | 1.0 | 2.0 | 8 | 41 | 5 |
| 2519 | Colo. | 1 | 47 | 52 | 8.2 | 24 | 1.8 | 3.0 | 20 | 1.0 | 2.0 | 10 | 41 | 0 |
| 922 | Colo. | 7 | 20 | 65 | 8.0 | 26 | 1.6 | 3.4 | 28 | 1.1 | 1.6 | 11 | 46 | 5 |
| 909 | Colo. | 7 | 15 | 70 | 7.8 | 27 | 1.6 | 3.3 | 28 | 1.0 | 1.7 | 11 | 48 | 8 |
| 2523 | Colo. | 6 | 39 | 53 | 8.2 | 25 | 1.7 | 3.6 | 25 | 1.1 | 1.8 | 10 | 46 | 5 |
| 2509 | Colo. | 10 | 22 | 63 | 8.2 | 25 | 1.5 | 3.6 | 30 | 1.3 | 2.0 | 11 | 46 | 5 |
| 2601 | Colo. | 10 | 36 | 63 | 8.6 | 27 | 1.9 | 3.6 | 28 | 1.1 | 1.8 | 11 | 48 | 8 |
| 916 | Colo. | 5 | 58 | 48 | 8.4 | 29 | 1.8 | 3.4 | 33 | 2.0 | 2.0 | 12 | 56 | 10 |
| 2978 | Colo. | 6 | 12 | 73 | 8.6 | 28 | 2.0 | 3.5 | 33 | 1.2 | 1.9 | 13 | 56 | 10 |
| 2553 | Nebr. | 10 | 37 | 83 | 10.0 | 27 | 2.3 | 4.2 | 38 | 1.2 | 2.1 | 15 | 61 | 10 |
| 2563 | Wyo. | 5 | 28 | 85 | 9.6 | 32 | 2.8 | 4.2 | 43 | 1.4 | 2.0 | 16 | 58 | 5 |
| 902 | Colo. | --[b] | 15 | 77 | 9.6 | 28 | 2.2 | 4.0 | 36 | 1.0 | 2.0 | 15 | 64 | 15 |
| 2724 | Calif. | 10 | 36 | 49 | 7.2 | 24 | 1.9 | 3.4 | 25 | 1.2 | 1.6 | 9 | 43 | 5 |
| 2899 | Utah | 9 | 59 | 40 | 9.4 | 30 | 2.4 | 3.5 | 33 | 1.4 | 1.7 | 13 | 61 | 13 |
| 2652 | Utah | 10 | 49 | 50 | 9.8 | 29 | 2.3 | 3.4 | 36 | 1.3 | 1.8 | 16 | 69 | 13 |
| 2876 | Utah | 3 | 16 | 69 | 9.4 | 30 | 2.0 | 3.5 | 33 | 1.0 | 2.0 | 16 | 66 | 13 |
| 2592 | Colo. | 2 | 16 | 83 | 9.2 | 31 | 2.6 | 4.1 | 30 | 1.0 | 2.0 | 16 | 66 | 10 |
| 2795 | Colo. | 5 | 18 | 81 | 9.4 | 32 | 3.2 | 4.0 | 36 | 1.0 | 1.7 | 17 | 74 | 18 |
| 2611 | N. Mex. | 3 | 16 | 97 | 10.4 | 28 | 3.2 | 4.6 | 33 | 1.8 | 1.9 | 17 | 74 | 13 |
| Standard error of a stand mean | | | 5.8 | 4.3 | 0.3 | 1.0 | 0.2 | 0.1 | 1.3 | 0.4 | 0.4 | 0.8 | 2.8 | 1.5 |
| $LSD_{.05}$ between means | | | 19.1 | 14.2 | 1.0 | 3.3 | 0.7 | 0.3 | 4.3 | 1.3 | 1.3 | 2.6 | 9.2 | 5.0 |

[a] Character grades:

| Character | (16 & 17) | (19) |
|---|---|---|
| | Foliage Color | Degree of Leaf Serrulation |
| Grade 1 | Yellow-green | Serrulations absent or extremely minute and very few in number. |
| Grade 2 | Light green | Serrulations few in number and small but readily discernible |
| Grade 3 | Green | Serrulations prominent or numerous or both. |
| Grade 4 | Dark green | |
| Grade 5 | Blue-green | |

[b] Collected for the pilot study--cones from a variable number of trees within the stand grouped at time of collection.

than those from more eastern collections whereas parental materials from the two areas showed no differences.

Seedlings from the Pine Bluffs area of Wyoming and Nebraska (stands 2553 and 2563) and from stand 902 in east-central Colorado had longer and darker green leaves, had more cotyledons, and were taller than seedlings from stands farther north and west.

Central and southern Utah seedlings were faster growing (average 65 mm. vs. 53 mm. at age 2) than those from northern Utah, but differences among stands of these groups for other traits appeared to be associated with stand to stand variation rather than fitting a geographic pattern.

Seedlings from the stands in southern Colorado and north-central New Mexico were the tallest and had the darkest green leaves. They also continued to grow for a longer period during the first year than most others. With regard to other traits, they were similar to the majority of seedlings from other stands.

In addition to the differences between seedlings among geographic areas and among the stands within an area, there were also significant differences attributable to the individual female parents within stands. Tree to tree differences in the number of cotyledons per seedlings were apparent in over half of the stands and differences in cotyledon length were apparent in nearly all stands. Differences among trees within stands for epicotyl growth were detected in nearly all stands but second-year height differences appeared in less than half of the stands. In approximately one third of the stands length of secondary leaves varied significantly among the progenies.

### *Variation Within Pinus strobiformis*

*Parental characters:*

Our sampling of the northern part of the distribution of *P. strobiformis* was very limited. Although four collections were made (one in New Mexico and three in Arizona) three of these were made for the pilot study so we obtained only the seed. While collection 932 from New Mexico was classified as *P. strobiformis* primarily on the basis of seedling characters, subsequent field observations of trees in the area indicated that the cones and foliage were simalar to those from other parts of New Mexico and Arizona.

Of the three collections (903, 904, 2568) obtained from the San Francisco Mountains of north central Arizona we received only seed from 903 and 904. The leaves from the remaining collection (2568) were the shortest and had the most dorsal stomata of any from the species *(Table 3A)*. They were also less serrate than most others from collections made in more southern Arizona. Cones from the collections were the shortest of the species and the cone scales exhibited almost no reflexing. On the basis of later observations in the field we feel that the cones of collection 2568 were not representative of most of those which would be found in the general area in most years. Whether they

*Table 3.* — Parental and seedling characters of *Pinus strobiformis*.

A. Parental Characters.

| MSFG Number | State or Province | Number of Trees Sampled | North Latitude | West Longitude | Elevation | Seed Weight | Length of Secondary Leaves | Number of Dorsal Stomatal Rows | Degree of Leaf Serrulation | Length of Peduncle | Cone Length | Cone Width | Length of Apophysis | Degree of Cone Scale Reflexing: Terminal 1/3 of Cone | Degree of Cone Scale Reflexing: Central 1/3 of Cone | Degree of Cone Scale Reflexing: Basal 1/3 of Cone |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Characters | (1) | (2) | (3) | (4) | (5) | (6) | (7) | (8) | (9) | (10) | (11) |
| | | no. | ° ' | ° ' | feet | mg. | mm. | no. | grade[a] | mm. | mm. | mm. | mm. | ° | ° | ° |
| 932 | N. Mex. | --[b] | 36 20 | 105 40 | 7000 | 143 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 903 | Ariz. | --[b] | 35 20 | 111 40 | 9600 | 200 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 904 | Ariz. | --[b] | 35 20 | 111 40 | 9100 | 167 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2568 | Ariz. | 9 | 35 20 | 111 42 | 8800 | 200 | 69 | 1.8 | 1.9 | 9 | 99 | 58 | 5 | 0 | 0 | 20 |
| 2805 | Ariz. | 10 | 34 26 | 111 11 | 7400 | 143 | 71 | 1.1 | 2.3 | 8 | 137 | 64 | 8 | 30 | 50 | 80 |
| 1020 | Ariz. | 5 | 33 18 | 110 50 | 7700 | 167 | 71 | 0.5 | 2.6 | 13 | 117 | 61 | 9 | 20 | 70 | 90 |
| 2734 | Ariz. | 8 | 32 40 | 109 55 | 8400 | 250 | 76 | 1.6 | 2.5 | 11 | 132 | 61 | 8 | 30 | 60 | 90 |
| 2621 | Ariz. | 14 | 32 26 | 110 46 | 8000 | 250 | 79 | 0.3 | 1.9 | 9 | 125 | 61 | 9 | 30 | 80 | 90 |
| 2742 | Ariz. | 9 | 31 55 | 109 15 | 7600 | 200 | 81 | 0.7 | 2.4 | 14 | 130 | 58 | 12 | 50 | 100 | 130 |
| 2755 | Ariz. | 4 | 31 41 | 110 51 | 6500 | 200 | 84 | 0.7 | 2.0 | 9 | 120 | 58 | 12 | 70 | 120 | 130 |
| 2751 | Ariz. | 4 | 31 46 | 109 15 | 8000 | 200 | 96 | 0.8 | 2.2 | 9 | 112 | 56 | 10 | 50 | 90 | 110 |
| 2762 | Ariz. | 3 | 31 24 | 110 18 | 7200 | 250 | 86 | 0.0 | 2.0 | 14 | 122 | 56 | 13 | 50 | 100 | 100 |
| 2896 | N. Mex. | 2 | 33 20 | 108 10 | 9000 | -- | 60 | 1.0 | 2.0 | 13 | 147 | 62 | 10 | 20 | 50 | 70 |
| 2785 | N. Mex. | 10 | 33 13 | 108 46 | 6800 | -- | 76 | 1.4 | 2.2 | 14 | 123 | 57 | 8 | 20 | 60 | 60 |
| 905 | N. Mex. | --[b] | 33 33 | 105 34 | 8000 | 250 | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 2866 | N. Mex. | 8 | 32 58 | 105 31 | 8500 | -- | 67 | 1.2 | 1.7 | 9 | 138 | 64 | 8 | 20 | 60 | 80 |
| 2649 | N. Mex. | 4 | 32 57 | 105 44 | 8700 | 250 | 75 | 1.4 | 1.8 | 6 | 110 | 54 | 7 | 30 | 60 | 80 |
| 2644 | Texas | 3 | 31 51 | 104 50 | 7700 | 143 | 79 | 1.0 | 1.8 | 9 | 114 | 53 | 8 | 60 | 80 | 100 |
| 2635 | Texas | 4 | 30 35 | 104 10 | 6500 | -- | 87 | 1.6 | 2.4 | 11 | 107 | 51 | 8 | 50 | 80 | 80 |
| 2641 | Nuevo Leon | 3 | 24 30 | 100 20 | 11250 | -- | 75 | 0.0 | 2.1 | 10 | 139 | 68 | 7 | 30 | 50 | 50 |
| Standard error of a stand mean | | | | | | 20.9 | 3.2 | 0.2 | 0.2 | 1.4 | 4.3 | 1.3 | 0.9 | 7.5 | 10.2 | 8.3 |
| $LSD_{.05}$ between means | | | | | | 69.0 | 10.6 | 0.7 | 0.7 | 4.6 | 14.2 | 4.3 | 3.0 | 24.8 | 33.7 | 27.4 |

B. Seedling Characters.

| MSFG Number | State or Province | Number of Parent Trees Sampled | Mean date of germination | Period of Active Growth | Cotyledon Number | Cotyledon Length | 1-year Foliage Color | 2-year Foliage Color | Length of Second Year Secondary Leaves | Degree of Leaf Serrulation | Number of Dorsal Stomatal Rows | First-Year Epicotyl Growth | 2-year Height | Amount of Lammas Growth in Second Year |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Characters | (12) | (13) | (14) | (15) | (16) | (17) | (18) | (19) | (20) | (21) | (22) | (23) |
| | | no. | days after June 1 | days | no. | mm. | grade[a] | grade[a] | mm. | grade[a] | no. | mm. | mm. | mm. |
| 932 | N. Mex. | --[b] | 20 | 93 | 11.6 | 30 | 4.2 | 4.8 | 61 | 2.0 | 2.5 | 30 | 124 | 28 |
| 903 | Ariz. | --[b] | 20 | 93 | 11.2 | 31 | 3.2 | 4.5 | 56 | 1.0 | 2.0 | 25 | 117 | 37 |
| 904 | Ariz. | --[b] | 19 | 101 | 11.0 | 29 | 3.8 | 4.8 | 51 | 2.0 | 1.5 | 27 | 99 | 25 |
| 2568 | Ariz. | 5 | 14 | 99 | 11.4 | 36 | 3.6 | 4.4 | 53 | 1.8 | 1.4 | 30 | 142 | 36 |
| 2805 | Ariz. | 7 | 15 | 105 | 10.8 | 35 | 4.2 | 5.0 | 69 | 2.6 | 0.6 | 27 | 127 | 33 |
| 1020 | Ariz. | 5 | 24 | 103 | 11.2 | 37 | 4.7 | 5.0 | 76 | 2.3 | 1.0 | 30 | 130 | 31 |
| 2734 | Ariz. | 2 | 12 | 108 | 13.2 | 37 | 4.9 | 5.0 | 69 | 2.0 | 1.8 | 37 | 150 | 28 |
| 2621 | Ariz. | 7 | 34 | 100 | 11.4 | 38 | 4.6 | 5.0 | 71 | 2.4 | 0.3 | 28 | 135 | 43 |
| 2742 | Ariz. | 5 | 27 | 107 | 12.0 | 37 | 4.1 | 4.7 | 66 | 2.4 | 1.0 | 28 | 109 | 15 |
| 2755 | Ariz. | 3 | 19 | 108 | 12.4 | 34 | 4.0 | 5.0 | 58 | 2.0 | 1.5 | 30 | 128 | 25 |
| 2751 | Ariz. | 3 | 16 | 118 | 14.0 | 40 | 3.4 | 4.4 | 74 | 2.1 | 1.0 | 26 | 117 | 20 |
| 2762 | Ariz. | 1 | 12 | 129 | 12.0 | 36 | 5.0 | 5.0 | 86 | 3.0 | 0.2 | 36 | 135 | 18 |
| 905 | N. Mex. | --[b] | 25 | 109 | 11.8 | 37 | 4.5 | 4.8 | 61 | 3.0 | 1.5 | 29 | 127 | 28 |
| 2649 | N. Mex. | 4 | 10 | 110 | 12.2 | 38 | 4.4 | 5.0 | 61 | 1.8 | 1.8 | 29 | 145 | 44 |
| 2644 | Texas | 2 | 19 | 115 | 12.6 | 39 | 4.5 | 5.0 | 69 | 2.5 | 1.8 | 35 | 119 | 23 |
| Standard error of a stand mean | | | 6.4 | 5.6 | 0.4 | 1.7 | 0.2 | 0.1 | 3.5 | 0.6 | 0.3 | 2.0 | 9.1 | 5.6 |
| $LSD_{.05}$ between means | | | 21.1 | 18.5 | 1.3 | 5.6 | 0.7 | 0.3 | 11.6 | 2.0 | 1.0 | 6.6 | 30.0 | 18.5 |

[a] Character grades:

| Character | (16 & 17) | (4 & 19) |
|---|---|---|
| | Foliage Color | Degree of Leaf Serrulation |
| Grade 1 | Yellow-green | Serrulations absent or extremely minute and very few in number |
| Grade 2 | Light green | Serrulations few in number and small but readily discernible |
| Grade 3 | Green | Serrulations prominent or numerous or both |
| Grade 4 | Dark green | |
| Grade 5 | Blue-green | |

[b] Collected for the pilot study--cones from a variable number of trees within the stand grouped at time of collection. Cones and foliage not available for measurement.

were representative of the particular trees sampled or whether they were representative of the cones produced in that particular year we do not know.

The collections from central and southern Arizona form a loose, variable group. Length of secondary leaves increased sharply from north to south while the number of dorsal stomatal rows declined. Cone length remained relatively constant but cone width decreased from north to south. The scales of cones from the most southern collections were more reflexed and had longer apophyses than ones from slightly farther north.

The materials from southern New Mexico and western Texas were also loosely grouped. There were differences among the stands but most of the variation did not suggest a geographic pattern. However, leaf length increased from north to south for the collections east of the Rio Grande River in New Mexico and Texas.

The cones and leaves of our only collection from Mexico were similar to those from southern Arizona, southern New Mexico, and western Texas even though the areas are 500 or more miles apart.

*Seedling Characters:*

Seedlings from northern New Mexico and Arizona had fewer and shorter cotyledons, shorter leaves, and more rows of stomata on the dorsal leaf surface than more southern origins *(Table 3B)*. They also had the shortest period of growth in the first year, the least serrulate leaves, and were most yellow in color. One of the northern Arizona collections (904) had the shortest seedlings at the end of the second year while those of another one (2568) were third tallest.

The progenies of central and southern Arizona trees generally had the longest secondary leaves. The leaves from these progenies also had the most pronounced serrulations and the fewest dorsal stomata. Seedlings from this area were generally tall but there were some stand to stand differences. Moreover, they also had many (often 12 or more), long, cotyledons and their foliage was dark green to blue-green in color.

Seedlings from southern New Mexico and western Texas were similar to those from southern Arizona with regard to most characters.

Significant differences among the progenies from trees within a single stand were common for cotyledon length, secondary leaf length, and first- and second-year height measures. Few differences were found among trees for the other characters.

*Differences Between P. flexilis and P. strobiformis*

*Parental Characters:*

The values for the various characters presented in *Tables 2 and 3* show that the *P. flexilis* and *P. strobiformis* specimens collected at a distance from the areas where their distributions are sympatric differ in most respects. Of more importance, however, is the question of how the taxa differ in and near the sympatric areas. To better illustrate the variation patterns the data for two characters, leaf length and cone length, are presented graphically in *Figure 2.*

The leaves of specimens of *P. flexilis* collected nearer the contact zone were progressively longer than those slightly farther away. However, they were no longer than the leaves of some of the most distant collections, and the leaves of the most southern collection, 2611 from the Sandia Mountains, were shorter than the majority of the others. A trend of increasing cone length for more southerly collections was more apparent. Both of these characters showed sharper gradients from northern to southern Colorado than were found for the whole geographic range.

Within the specimens we classified as *P. strobiformis* there was a steep gradient of increasing length of leaves from north to south. Leaf length of southern *P. flexilis* stands differed from those of the northern *P. strobiformis* stands by 12 to 15 mm. When individual tree means were compared there was considerable overlap; *P. flexilis* leaves ranged from 38 to 71 mm. and *P. strobiformis* from 53 to

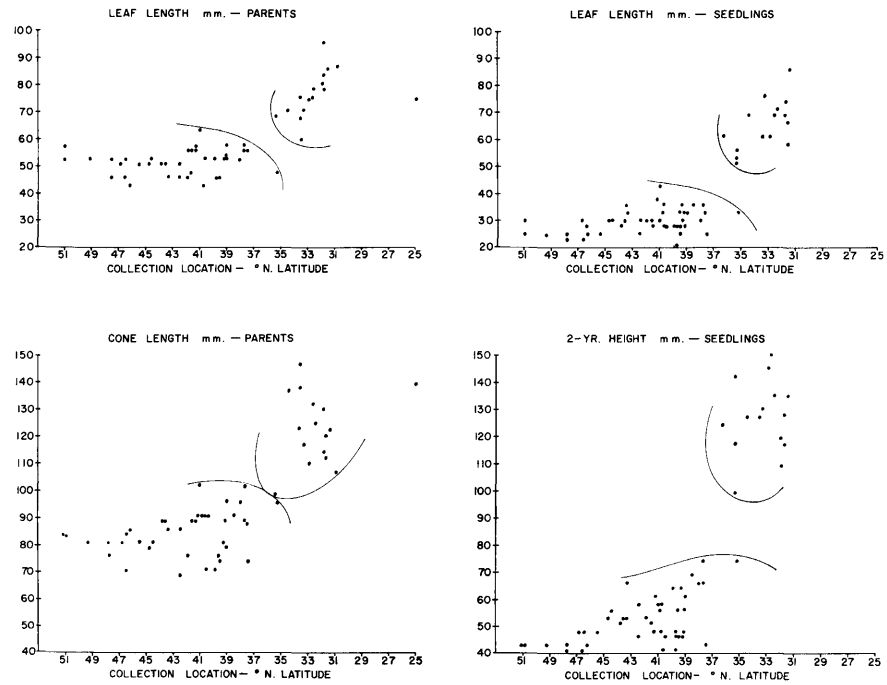


*Figure 2.* — Variation patterns for representative seedling and parental characters. *Pinus flexilis* stands in the lower left and *P. strobiformis* in the upper right on each chart.

84 mm. For other leaf traits, serrulation and dorsal stomata, the specimens of collection 2568 from the San Francisco Mountains in north central Arizona were nearly intermediate between those of most *P. flexilis* and *P. strobiformis* collections.

No pattern of variation in cone length of *P. strobiformis* was observed. Almost all collections except 2568 could be readily distinguished from *P. flexilis*. The cones of collection 2568 were similar to those of the southern *P. flexilis* collections in length and in the degree to which their scales were reflexed. Scale reflexing was a good diagnostic character for assigning the other collections to their respective taxa. Peduncle length and apophysis length were of little value in distinguishing between the taxa for specimens near the contact zones.

In terms of parental characteristics, stand 2568 apparently is intermediate between *P. flexilis* and *P. strobiformis*.

*Seedling characters:*

North to south gradients for traits of *P. flexilis* were all of gentle slope (*Table 2* and *Figure 2*). By contrast, consistent differences in cotyledon length, secondary leaf length, and foliage color were found between northern and southern *P. strobiformis* seedlings (*Table 3* and *Figure 2*). Moreover, the differences between northern *P. strobiformis* stands and southern *P. flexilis* stands were of greater magnitude than for parental characters.

An additional series of analyses were performed to evaluate the differences between the southern *P. flexilis* and northern *P. strobiformis* seedlings. In these analyses the data for seedlings of collections 2899, 2652, and 2876 from Utah; 2592 and 2795 from Colorado; and 2611 from New Mexico were compared with those of collection 932 from New Mexico and 903, 904, and 2568 from Arizona. The mean values applicable to the seedlings from all the trees in a stand collection were used as items in the analyses (*Table 4*). Significant differences between the species were evident for most seedling characters. For many of the characters there was no overlap between species when stand means were compared. Moreover, values for second-year height did not overlap even for comparisons of progeny means from single trees; values for *P. flexilis* ranged from 56 to 81 mm. and those for *P. strobiformis* from 96 to 162 mm. For first-year epicotyl growth and secondary leaf length single tree progeny means did not overlap, but the distribution for leaf length was essentially continuous.

*Table 4.* — Results of analysis of variance to test the differences between the most southern *Pinus flexilis* and the most northern *Pinus strobiformis* seedlings.

| Character | | Value of F resulting from the comparison of variation attributable to differences between and within species[1]) |
|---|---|---|
| (12) | Mean germination date | 1 |
| (13) | Period of active growth | 11*[2]) |
| (14) | Cotyledon number | 48*** |
| (15) | Cotyledon length | 1 |
| (16) | 1-year foliage color | 13** |
| (17) | 2-year foliage color | 9* |
| (18) | Length of secondary leaves | 110*** |
| (19) | Degree of leaf serrulation | 9* |
| (20) | Number of dorsal stomatal rows | 0 |
| (21) | First-year epicotyl growth | 104*** |
| (22) | 2-year height | 48*** |
| (23) | Amount of lammas growth in second year | 37*** |

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

[2]) *, **, and *** indicate significance at the 5, 1, and 0.1 percent levels respectively.

Although the parental specimens of collection 2568 from northern Arizona were like *P. flexilis* in cone traits and somewhat intermediate in leaf traits, seedlings from the collection grew nearly as tall as the tallest *P. strobiformis* seedlings. Seedling leaf length and foliage color were intermediate to slightly more like *P. strobiformis*. Seedlings from another collection (904) made in the same general area were the shortest classified as *P. strobiformis*.

On the basis of seedling characteristics there were no problems in species identification, i. e., seedlings could readily be assigned to one or the other.

## Discussion

The *Pinus flexilis* materials exhibited gradation in some characters that followed a north to south pattern but, for the geographic range involved, the variation was small. For a comparable geographic range Wells (1964) described two major and one minor subdivisions within *P. ponderosa*. Critchfield (1957) found several differences between Rocky Mountain and Sierra Nevada forms of *P. contorta* but our single California collection (2724) was similar to many from the Rockies. Much of the variation, other than that due to north-south trends, was related to collections from isolated areas. The isolated areas were usually considerably lower in elevation than other areas where *P. flexilis* grows at the same latitude. For example, the collections from the vicinity of Pien Buffs, Wyoming (2553 and 2563), were made at 5200—5300 feet while others from the same latitude were made at 7800 feet or more. Specimens and seedlings from the isolated collections often were more similar to those from more southern collections than to collections from the same latitude. However, isolated collections did not always follow that pattern as the materials collected in North Dakota at 2500 feet (collection 967) were similar to those from Montana collections from comparable latitude but higher elevation.

In contrast, when the fact that samples of *P. strobiformis* included only 5° of latitude (*P. flexilis* covered 16°) is taken into consideration the *P. strobiformis* materials appeared quite variable. Although we were not able to study a large part of the distribution of the taxa, the single Mexico collection and field observations indicated that the range of values for parental characters may have been nearly covered.

Part of the variation in materials tentatively classified as *P. strobiformis* appeared to be related to an intergradation between the taxa. Intergradation was evident primarily in materials from the San Francisco Mountains of north central Arizona. Cones from the area were very similar to those of *P. flexilis* but parental and seedling leaves were somewhat intermediate while the seedlings grew nearly as tall as the tallest *P. strobiformis*.

Materials of collection 2611 from the Sandia Mountains in north central New Mexico, although primarily like *P. flexilis*, also gave some evidence of intergradation. Immature cones of a number of trees in the area were purple colored, a condition commonly found among *P. strobiformis* trees but, as far as we know, not typical of *P. flexilis*. The number of cotyledons on seedlings from this collection was intermediate between that for most *P. flexilis* and *P. strobiformis* seedlings.

Although the ranges of the two taxa apparently overlap in northern New Mexico and southern Colorado, there may be an elevational separation. Parental specimens and seedlings of collection 2611 from 10,500 feet in elevation were primarily like *P. flexilis* while the seedlings of collection 932, made some 60 miles to the north but at only 7000 feet, were most like *P. strobiformis*. Some additional collections have been made in the area of contact or intergradation but more collections and field work are needed.

The occurrence of trees which are more or less intermediate suggests that the two taxa, although once separated, have since come together and hybridized. The variable nature of the materials collected in the San Francisco Mountains and the presence of purple cones on what otherwise appear to be *P. flexilis* trees also indicate that the taxa were previously isolated and have since come into contact rather than having differentiated while in contact (MAYR, 1963: 380). A probable time for the contact to have occurred would have been during the Pleistocene period when the distributions of many plants shifted. Hybridization may still be occurring in northern New Mexico and may also be possible in the San Francisco Mountains if typical *P. flexilis* occurs there at higher elevations. It seems unlikely that *P. flexilis* presently occurs south of the San Francisco Mountains in Arizona or more than a few miles south of the Sandia Mountains in New Mexico because the mountains to the south are not high enough. It is noteworthy that these locations also mark the southern limits of the distribution of *Pinus aristata* ENGELM., a species which is commonly associated with *P. flexilis* in Colorado, Utah, and Nevada.

Despite the occurrence of intermediate forms in the zone where the taxa are sympatric, we believe that they are sufficiently distinct to warrant equal rank as species, i. e., *Pinus flexilis* JAMES and *Pinus strobiformis* ENGELM. As an aid to identification of specimens of the two species the following guidelines are offered:

*P. flexilis* — leaves, usually less than 55 mm. long, lacking serrations or minutely and sparsely serrate with two or more rows of stomata on the dorsal surface; cones, usually less than 100 mm. long, commonly 75—90 mm., terminal scales straight, central and basal scales slightly to moderately reflexed, apophyses 4—7 mm. long; seeds, usually weighing less than 140 mg. commonly 80—110 mg., embryos (and seedlings) usually have less than 10 cotyledons.

*P. strobiformis* — leaves, usually more than 70 mm. long, serrations readily discernible, dorsal stomata limited to one row or a few partial rows; cones, usually more than 110 mm. long occasionally ranging to 235 mm., terminal scales slightly to moderately reflexed, central and basal scales strongly reflexed, apophyses 8—12 mm. long; seeds usually weighing more than 140 mg., often 200 mg., embryos usually have 11 or more cotyledons. The seeds of both species occasionally have short (2—6 mm.) wings but they are perhaps a little more common for *P. strobiformis*.

Further work is needed in the contact zone as our sample from the area was very limited. In addition study of the Mexican distribution of *P. strobiformis* should be undertaken and the question of the *P. strobiformis* — *P. ayacahuite* relationship should be investigated.

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**Summary**

Foliage and cones were collected and studied from several native stands of *Pinus flexilis* and *P. strobiformis*, mostly from within the United States portions of their distributions. Seeds from the cones were sown in a replicated, randomized nursery test in East Lansing, Michigan. The resulting seedlings were observed and measured for two years. Data from the measurements of the parental specimens and the seedlings were subjected to analyses of variance to evaluate the variation within and between the taxa.

Within *P. flexilis* some north-south variation patterns were observed but the range of values for any one trait was small. Materials from isolated stands often were more like those from stands of southern origin than from stands of comparable latitude.

*Pinus strobiformis* parental specimens and seedlings were more variable but, except for leaf length which increased from north to south, geographic patterns were very weak or absent. Within both taxa there were differences between trees within some stands that equalled or exceeded the differences between stands.

In contrast to the gently sloping character gradients in *P. flexilis* the transition to *P. strobiformis* was very steep or abrupt for most characters. The distinction was stronger for seedling than parental characters. Materials from northern Arizona and New Mexico collections exhibited some characteristics which indicated that hybridization has occurred. The distributions of the taxa overlap latitudinally in northern New Mexico and probably do so in southern Colorado and northern Arizona but they appear to be separated elevationally. We believe the taxa deserve the separate and equal rank of species.

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