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ABSTRACT

THE CORRESPONDENCE BETWEEN GENETIC, MORPHOLOGICAL AND CLIMATIC VARIATION PATTERNS IN SCOTCH PINE

by John L. Ruby

Six hundred and eighty-nine cone, seed and leaf specimens of Scotch pine were collected from 39 stands in 10 regions of Europe and Asia by cooperators in those countries. Nineteen characters or ratios were measured on these. The individual tree measurements were grouped by stand and region, and then were subjected to analyses of variance.

Computations of the components of variance for the 8 most definitive characters showed that more than 85 per cent of the variance was attributable to between-region differences, and less than 3 per cent to stands-within-region.

Comparisons were made of the regional grouping based on the parental measurements and a regional grouping based on an associated 122-origin provenance study in a uniform environment in Michigan. The groupings were nearly identical. In other words, it is possible to delimit a race or variety nearly as well by studying parental specimens collected in Europe as by growing their progenies in this country. However, it was not possible to forecast a race's performance in Michigan from a study of the parental cones and leaves.

Character differences in juvenile performance were often related to the climate of the parent races. The fibrous shallow roots of the northernmost provenances were associated with an area where precipitation was not critical, while the tap roots of the Spanish origins reflected the affects of summer drought and high temperatures. Similarly the blue-green leaf coloration of the Spanish seedlings was due to the development of protective waxes in a dry climate.

The taxonomy of Scotch pine was reviewed for the last 60 years and summarized by geographic areas. The 10 geographic varieties defined in this study were compared and combined with other biometric and provenance results of Scotch pine studies and the varietal descriptions of previous authors and taxonomists. Based on this combined information 21 varieties of Scotch pine were named and their geographic location, taxonomic description and synonymy were detailed.

As regards stands within a region, there was little correspondence between variation patterns exhibited by the parents and seedlings grown in this country. In other words, two stands which differed markedly in some cone cr leaf trait might or might not differ appreciably in some seedling trait. This is thought to be so because the parental traits are subject to considerable environmental influences. Also it is likely that the genetic factors affecting mature cone or leaf traits and juvenile traits are different.

It was not possible to forecast which of several German-Czechoslovakian stands should have the tallest (or greenest or longest needled) offspring in Michigan from a study of the microclimates of the stands in Europe. This general lack of climate-progeny correlation was also true for the western Germany-eastern France regions. Apparently micro-evolution lags so that every stand is not perfectly adapted to its particular local climate.

In seven stands the parental data for growth rate, clear-stem length, crown size and length, and stem straightness, as well as for cone and leaf traits, were available for each parent tree. Two-year performance data for the offspring of those parents were also available. Coefficients of correlation were calculated between all parental characters and 20 juvenile characters in an effort to determine if any parental character could be used to predict juvenile performance in Michigan. Only 35 correlations were significant at the 5 per cent level out of a possible 1,260 combinations. There was little consistency from one stand to the next. The relative absence of correlations is thought to be due to genotype-environment interactions between Europe and America, and to the different ages at which parents and offspring were observed.

THE CORRESPONDENCE BETWEEN GENETIC, MORPHOLOGICAL AND CLIMATIC VARIATION PATTERNS IN SCOTCH PINE

By

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CHAPTER I

INTRODUCTION

The variation in phenotypic expression within a given species resulting from the interaction of genetic diversity and environment is receiving increased attention in studies of the range of variability within tree species. A thorough knowledge of this variability is a prerequisite to the intelligent use of tree species in silvicultural practice. The present common practice of utilizing only local seed sources or those from a narrowly restricted zone of similar environmental conditions seriously limits the development of our forest resources.

Scotch pine (*Pinus sylvestris* L.) is a species widely distributed throughout Europe and Asia. It has been greatly affected by the complex pattern of recent glaciation, particularly in Europe. The relatively recent changes in species distribution and in selection pressures brought about by glaciation in the northern part of the northern hemisphere has been described by Hulten (1937, 1949) and others. Changing environments have resulted in genetic differentiation among continuous populations as well as in the isolated remnant populations of southern Europe and central Asia.

Recently studies have been completed on phenotypic variation in the following pine species:

Lodgepole pine (Pinus contorta Dougl.), Critchfield (1957).

Black pine (Pinus nigra Arnold), Vidakovic (1960).

Scotch pine (Pinus sylvestris L.), Staszkiewicz (1960, 1961, 1962).

Jack pine (Pinus banksiana Lamb.), Schoenike et al. (1959), Rudolph et al. (1957).

Loblolly pine (Pinus taeda L.), Thor (1961), Zobel and Thorbjornsen (1961).

Virginia Pine (Pinus virginiana Mill.), Thor (1964).

Monterey pine (Pinus radiata D. Don), Fielding (1953).

Coulter pine (Pinus coulteri D. Don), Zobel (1952) (1953).

Sand pine (Pinus clausa (Chapm.) Vasey), Little and Dorman (1952).

The few studies that have been made of the natural variation in the genus Pinus have usually been limited in the coverage of the natural range of the species. Provenance tests to determine genetic differences in the same parental populations have been rare. Critchfield (1957) included both parental and seedling provenance studies in his study of geographic variation in lodgepole pine. The progeny provenance tests of jack pine made by Schantz-Hansen and Jensen (1954) were followed by a parental study of the same stands by Schoenike et al. (1959), and Rudolph et al. (1959). Rudolph's et al. (1957) study of jack pine parental variation in Minnesota was followed by vegetative propagation in a uniform environment. Thor (1964) has established a seedling provenance test in conjunction with his study of parental characteristics of Virginia pine.

The genetic variability in pine species has been widely studied through seedling provenance tests. Recent Scotch pine studies include those conducted by Weidemann (1930), Langlet (1934), Veen (1952), Vincent and Polnars (1953), Holst (1953), Baldwin (1955, 1956), Wright and Baldwin (1957), Rudolf and Slabaugh (1958), Langlet (1959) comment on Wright and Baldwin, Bolsinger (1958), Echols (1958), Gerhold (1959), Wettstein (1958, 1959), Sanikov (1959), Bouvarel (1959) comment on Langlet (1959), Vojcal (1961), Lazarescu et al. (1961), Troeger (1962), Rubner (1962), Wright (1963), Wright and Bull (1963), Dengler (1938).

Scotch pine is ideally suited to genetic and phenotypic study because of its great variability. It has been described as a complex by Semmler and Von Schiller (1927) and Mirov (1961). The utilization of this variability to improve the characteristics of stands planted under varying environments is a necessity. A knowledge of the genetic variability of the species and the parental phenotypic expression associated with the variability can materially improve and speed up the utilization of the best adapted races in a planting program.

The natural distribution of Scotch pine covers a greater area than that of any other pine. According to Elwes and Henry (1908):

> . . . It is by preference a tree of siliceous soils, but occurs on almost all geological formations; and in Scotland, Norway, and Sweden grows on peat bogs too wet for the spruce to exist on.
>
> The area of distribution includes almost all Europe and the greater part of Northern Asia. The northerly limit, commencing on the north-west coast of Norway at Alten (70° N. lat.), passes through Lapland, south of the Enara lake (68° 50'), and touches Pasvig Fjord on the arctic sea at 69°30'. Extending

through the Kola peninsula from Kola bay, it crosses the White sea at 66° 45' and in the Petchora territory goes as far north as 67° 15' and crosses the Ural at about 64°. In Siberia it never reaches quite as far north as the arctic circle, though it nearly touches it on the Ob and Yenisei rivers; east of the Lena river it descends to about 64°. It reaches its extreme easterly point (about 150° E. long.) in the Wercho-jansk Mountains. The eastern limit descends from there through the Stanovoi Mountains and the Seja territory to the upper Amur. According to Komarov (*Flora Manshuriae*, i. 175 (1901) it is a scarce tree on the banks of the rivers in Manchuria. Its southerly limit in Siberia is not well known; but it is known to occur in the mountains of Dahuria in the territory around Lake Baikal, and in the Altai Mountains. Its southern limit in European Russia is a very irregular line, which begins in the Ural south of Orenburg at about lat. 52°, is most to the north in the government of Tula (lat. 54° 30'), and descends from there to Kharkof (lat. 49°), passing into Galicia about lat. 50°. Far south of this line, and separated from it by the Russian Steppes, on which no pine trees grow, occurs an area of distribution, not yet well made out, which includes the Caucasus, the mountains of the Crimea, Asia Minor, and Northwest Persia. (*P. sylvestris* grows on the Armenian plateau, and has been described in *Linnaea*, xxii.296 (1849), as P. *armena*, Koch; P. *kochiana*, Klotzsch; and P. *pontica*, Koch. Cf. *Moniteur Jardin Botanique Tiflis*, ii.26 (1906). There is also an isolated area, in which the pine is found growing wild, in Macedonia, on Mount Nidjé. From Galicia the southern limit in Europe (exclusive of the last mentioned area) passes southward to the Transylvanian Alps; thence it extends along the mountains to Serbia where the tree grows on the Kopavnik mountain (about lat. 43°), continues through the mountains of Bosnia, Dalmatia, Illyria, Venetia, and through Lombardy to the Ligurian Appennines (about lat. 44°). It passes into France, across the Maritime Alps, into the Cevennes, and reaches the Eastern Pyrenees; in Spain it descends through the mountains of Catalonia, Aragon, and Valencia to the Sierra Nevada in Andalusia, which is its extreme southerly point in Europe (lat. 37°). The westerly limit beginning here, stretches northwest through the mountains of Avila to those of Leon in North Spain, and is continued through the mountains of Scotland to the northwest coast of Norway. In this vast area the pine is very irregularly distributed. The largest forests occur in the Baltic provinces of Russia, in Scandinavia, in Northern Germany, and in Poland. Towards the south it only occurs in mountains, and rarely forms pure forests of considerable extent. According to Huffel (*Forets de la Roumanie*, 6 (1890), it is rare in Roumania, where he saw it at the confluence of the Lotru and Oltu rivers at 1700 feet altitude, and in the valley of Bistritza (only on calcareous soils in Muscel region). See figures 1 and 2.

Scotch pine has been widely planted outside of its native range in Europe and Asia, particularly in the Northeast and North Central Regions of the United States, where it has propagated itself and exhibited rapid growth. Unfortunately many of the planted stands are of poor form, having originated from seed of doubtful origin or from areas known to produce trees of poor form.

Scotch pine has been widely planted on relatively sterile soils in sand dune and soil stabilization projects where its pioneer qualities of survival and growth under poor conditions of moisture and soil have been outstanding. Stands of good form and quality in Michigan attest to the potential of Scotch pine as a timber source.

Figure 1.--Natural distribution of Scotch pine in Europe (shaded) and provenances included in Wright and Bull (1963) test (numbered dots).

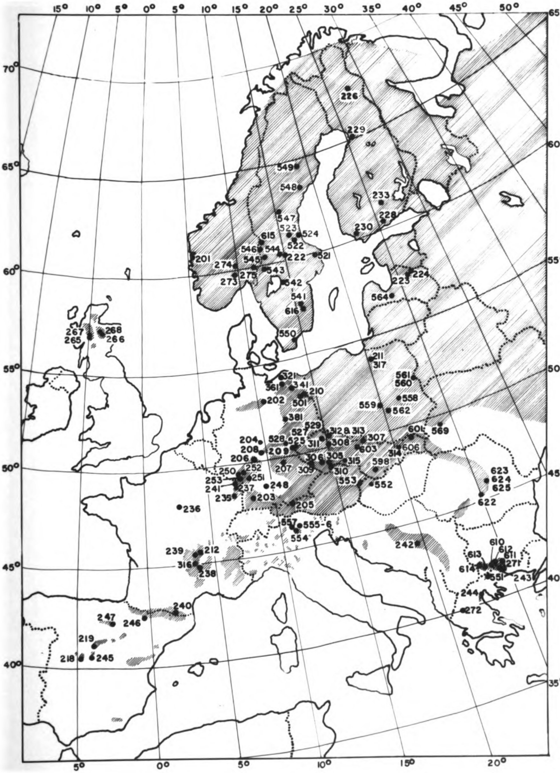
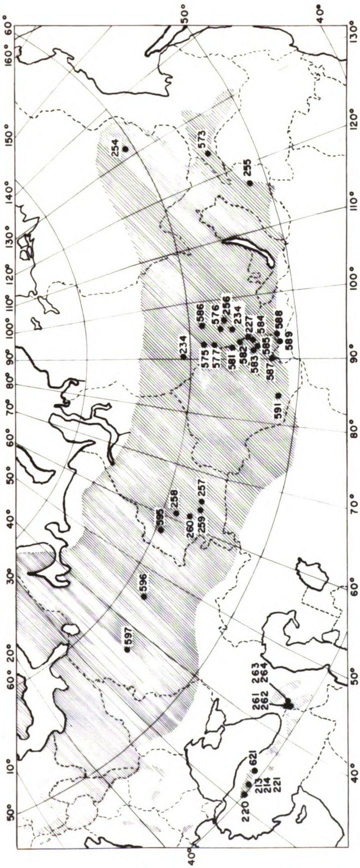


Figure 2.--Natural distribution of Scotch pine in Asia (shaded) and provenances included in Wright and Bull (1963) test (numbered dots).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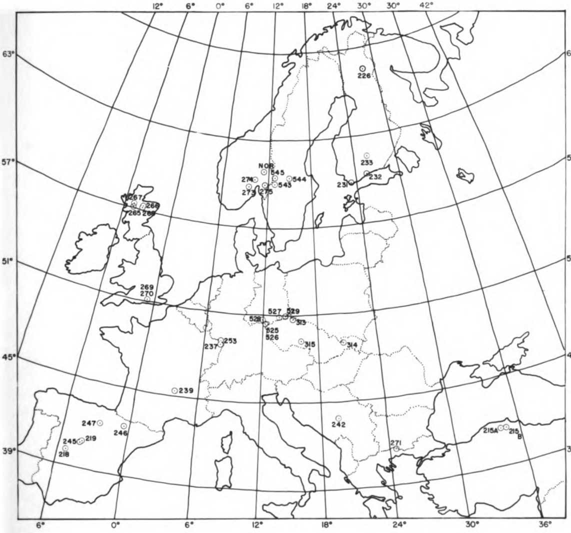


Figure 3.--Provenances included in this study of parental characters (numbered or lettered dots).

Figure 4.--Seventeen year old Scotch pine 20-25 feet high and 13 year old red pine (*Pinus resinosa* Ait.) 12-15 feet high in a wind erosion control plantation in Newaygo County, Michigan, June, 1960.

Figure 5.--Natural reproduction of Scotch pine averaging 18 inches in annual growth from 22 year old parent trees 25-35 feet high along U.S. Highway 2 near St. Ignace, Michigan.

Figure 4.

Figure 5.

Figure 6.--Thirty year old plantation of Scotch pine thinned in 1960 at Michigan State University's Kellogg Forest, in Kalamazoo County Michigan.

Figure 7.--General view of seedling beds in Bogue Forest Research Nursery, East Lansing, Michigan, containing four replicates of the Scotch pine 122 origin provenance test.

Figure 6.

Figure 7.

Figure 8.--View across seedling beds in Bogue Forest Research Nursery, East Lansing, Michigan, showing differences between 1-0 Scotch pine seedlings from Spain and Norway in provenance test in September, 1959. Each row represents a provenance.

Figure 9.--Scotch pine provenance test outplanting of 2-0 stock at Michigan State University's Russ Forest in Cass County, Michigan, one year after establishment in the spring of 1961. This 4 tree plot 10 replicate planting clearly shows color differences, particularly the winter yellowing of foliage, and height differences.

Figure 8.

Figure 9.

CHAPTER II

OBJECTIVES

This study is part of a long-range program directed toward the improvement of Scotch pine planted in the north central United States. The long-range program now includes a series of range-wide provenance tests to determine the best European origins. It also includes a series of 1-parent progeny tests to determine the role and the best methods of applying selection for the betterment of the best natural populations. Ultimately it will include the establishment of seed orchards and breeding for specified goals.

Broadly speaking, the objective of the present study was to determine the extent to which the performance of different Scotch pine genotypes when planted in Michigan could be forecast from the characteristics of these same genotypes in their native environments or the characteristics of those native environments. More specifically the objectives were (1) to determine the correspondence of the juvenile variation pattern found in the Michigan provenance tests with the temperature, precipitation, and daylength patterns of the localities of origin, (2) to determine the correspondence between the juvenile variation pattern found in Michigan and certain parental charcteristics such as the morphology of cone, seed, and leaf, (3) to determine the correspondence between juvenile performance in Michigan of the offspring of single trees and of the parents growing in Europe, and (4) to determine the extent to which genetic variation patterns as studied in uniform-environment growth tests are correlated with morphological variation patterns as studies in the field.

CHAPTER III

MATERIALS AND METHODS

Specimen Procurement

Cone and leaf specimens were collected in 1960, 1961, and 1962 by cooperators in Europe and Asia. Letters requesting the specimens were sent to forty-four cooperators who had previously furnished seed for the 122-origin provenance test initiated by Doctor Jonathan W. Wright at Michigan State University in 1958 (Wright (1963), Wright and Bull (1963)). The requests were for one cone and one leaf from ten to twenty trees per stand with sufficient spacing between trees to avoid inbred parents. The single needle was to be the largest 1960 needle from the south side of the tree and was to be placed in an envelope with the largest 1960 cone from the same tree. The initial request was for collections from open-grown trees 3 to 6 meters high. There was an additional request for specimens from the same trees from which seed had been originally collected for the provenance test.

Forty stand collections were received including eight individual tree collections from Norway, Belgium, and Germany matching those of the individual tree collection reported on by Wright (1963). The remaining collections were from the same stands as the original seed collections or from nearby stands.

One collection was too small to analyze so that the data for thirty-nine stands was used. The location of the stand collections is shown in Figure 3.

The cones and needles were catalogued and stored by tree and stand as they arrived. They were assigned the same MSFG (Michigan State Forest Genetics) number given the original stands that were included in the seed sampling for the provenance test.

Data Concerning Area of Origin

Meteorological data for the 122 stands represented in the provenance test of Wright (*ibid.*) were collected from the cooperators, weather services of the local governments, the United States Department of Commerce Weather Bureau, and from the Great Britain Meteorological Office (1958). The remote location of many of the stands permitted the collection of monthly and annual data only for use with the collection as a whole. In some instances, corrections for altitude were applied where the stands were far removed from the reporting meteorological stations. These corrections were made by the cooperators or with their advice.

The original request for specimens also were for data on the geographic location, political subdivision in which stand occurred (province, county, or town name), elevation of stand above sea level, type of soil, age of tree, the size of the collecting area, the date of collection and shipment, and the name of the collector.

Specimen Handling

All cone and needle specimens were packaged and identified by tree for each stand collection to preserve the identity of the trees. In eight stand collections these numbers also corresponded with the individual tree provenance test data (Wright, 1963).

The seeds were extracted and one typical seed with seed wing was attached to a card representing a stand collection. The remaining seeds were packaged by tree.

The needles were placed in vials and the cones in compartmented egg cartons.

Measurement Methods

Micrometer calipers were used for all length, width, and thickness measurements on cones, cone scales, and seeds. Needle length was measured on a flat scale. All measurements were in the metric scale to the nearest tenth of the unit of measure.

All specimens were stored in a constant environment for one month before measurement to equalize moisture content.

The open cones were measured for length and width of cone and length, width, and thickness of apophyses, then soaked in water for five minutes and placed under a polyethylene sheet for twenty-four hours before closed cone width was measured.

During the period in which the cones were drying to a constant moisture content they were stored in open egg cartons and studied for measurable morphological differences. Form factors of ratios of measurements were selected which would metrically describe the variability in shape.

The manner of making specific measurements and of analysing the data is discussed under the chapters concerned with the analysis of the data.

CHAPTER IV

VARIATION IN PARENTAL CHARACTERS WITHIN AND BETWEEN REGIONS

The choice of parental characters used in this study was influenced by four factors: review of literature, estimated influence of environment, availability and transportability of materials, and ease and rapidity of measurements.

Vidakovic (1958, 1960) studied the significance of seed, cone, and cone scale characters as taxonomic determinants in European black pine (Pinus nigra Arn.). The characters used were:

1. Seed color.
2. Seed mottling.
3. Color of scales.
4. Length, width, and thickness of seeds.
5. Length and width of cones.
6. Form of seed and cones.
7. Form of scales.
8. Weight of seed.

He found that the italicized characters, 1, 2, and 6, were most useful in differentiating between populations.

Staszkiewicz (1960, 1961, 1962) used the following cone characters in establishing morphological differences between Scotch pine populations:

1. Length of cones.
2. Width of cone.
3. Number of scales.
4. Length of apophysis.
5. Width of apophysis.
6. Thickness of apophysis.
7. Cone length/width ratio.
8. Relation of length of cone to number of scales.
9. Apophysis length/width ratio.
10. Apophysis length/thickness ratio.

He based his study on cones from Poland, Czechoslovakia, Switzerland, France, Scotland, Sweden and Finland. Staszkiewicz able to divide the material into 6 morphological types of cones, each type distinguished by some characteristic feature.

Renvall (1914) studied the variation in leaf length within mature individuals of Scotch pine and found that the average needle length declines with increasing branch order and branch age.

Gerhold (1959) studied the chloroplast pigments and nutrient elements in the needles of six geographic origins of Scotch pine growing in the New Hampshire IUFRO plantings. He found significant differences in needle color, total chlorophyll, magnesium, nitrogen, iron and calcium.

Cvrkal (1958) used Sutherland's methods to determine differences in the essential oils of Scotch pine from several European countries and checked the accuracy of the results by infra-red spectrums and chromatographic methods.

Fielding (1953) found distinct differences among three stands of Monterey pine (Pinus radiata D. Don) in cone and seed size, seed color, and needles per fascicle.

Critchfield (1957), in his study of geographic variation in lodgepole pine (P. contorta Dougl.), found that seven cone and leaf characters tended to follow a regional pattern while others conformed to elevation gradients. Resin canal number, leaf width, cone density, cone angle, cone symmetry, cone persistence, and apophysis form showed regional differences. He concluded that elevational variation was high in lodgepole pine, that each character studied had a unique variation pattern, and that there was no correlation with latitude in any characteristic.

Schoenike et al. (1959) reported in their study of cone variation in jack pine (P. banksiana Lamb) that cone closure and symmetry were useful in developing regional patterns.

Thor (1961) studied 18 stand samples from 10 southern and southeastern states in his investigation of variation patterns in loblolly pine (P. taeda L.). Within-stand variation accounted for a large proportion of the total variation. The majority of the 13 morphological characteristics, including seed-wing length, seed length, needle length, cone length, and frequency of serrations on the needle margin, did not show regional trends. However, seed form, seed coat thickness, cone weight, cotyledon numbers and stomatal frequencies showed regional trends but no evidence of discontinuity. Thor (1964) also studied natural variation in the wood properties of Virginia pine (P. virginiana Mill.). Basing his results on 13 stands in Tennessee and Kentucky he found highly significant differences within stands for radial growth, specific gravity based on green volume, and specific gravity after removal of extractives. He found regional differences in length of summer-wood tracheids of the 10th and 25th year. There was a geographic pattern to the specific gravity variation if based on fresh wood but not if based on extracted wood.

Wood characteristics, particularly tracheid length and specific gravity, have been studied by many researchers including Zobel (1961), Zobel and Rhodes (1955), Zobel and McElwee (1958), Zobel et al. (1961), Kramer (1957) and Echols (1958). The earlier studies in wood properties showed conflicting results. No geographic trend was found by Zobel and Rhodes in loblolly pine stands in east Texas, but a northerly and westerly trend was found by Zobel and McElwee in the southeastern states. In 1961 Zobel et al. reported their findings on the interrelationships of wood properties in loblolly pine.

Methods

The characters studied in the parental populations (Table 1) were principally those of the cone and seed because these have proven to be of value. Needle length and twist were also studied because they could be studied in the young progenies.

Thirty-nine stands from 13 countries were sampled. In each stand one cone or one needle fascicle was collected from each of a number of young trees growing in full sunlight. The location of the

Table 1.--Description of cone, seed, and leaf characteristics measured on parental specimens of Scotch pine.

Number	Characteristics	Unit of Measure
P6	Cone length.	cm.
P7	Cone width, closed.	cm.
P8	Cone width, open.	cm.
P9	Ratio, cone length/cone width, closed.	number
P10	Ratio, cone length/cone width, open.	number
P11	Basal angle of the open cone.	degrees (0 to 9 = 0° to 45°)
P12	Length of largest apophysis.	mm.
P13	Width of largest apophysis.	mm.
P14	Thickness of largest apophysis.	mm.
P15	Ratio, length/width of largest apophysis.	number
P16	Ratio, length/thickness of largest apophysis.	number
P17	Thickness of apophysis on opposite side of cone from largest apophysis.	mm.
P18	Asymmetry, ratio, thickness largest/ thickness of opposite apophysis.	number
P20	Ratio, cone length/length largest apophysis.	number
P28	Seed length.	mm.
P29	Seed width	mm.
P30	Ratio, seed length/seed width.	number
P35	Leaf length.	cm.
P38	Leaf twist.	grade (1 = straight, 17 = 360 degree twist)

sample on each tree was standardized. The number of trees sampled per stand was usually 20 trees but in a few cases was as low as 10 or as high as 34. The period of collection for all countries except Spain was from August, 1960 to March, 1961. Spanish collections were made during the period December, 1961 to February, 1962.

The 19 cone, seed, and needle measurements were subjected to analyses of variance using tree means, stand means and regional means to obtain a measure of variability within stand, between regions and within regions. The F-ratios are presented in Table 2. The components of variance are then determined from the same within-stand, within-region and between-region variances to determine the percentage of variability due to these variances. These percentages are shown in Table 3.

The individual tree data for each stand were processed through "MISTIC," Michigan State University's electronic computer, to obtain means, standard deviations, and variances. The combined analyses of variance for each character was completed by hand reprocessing the tree, stand and regional data output of MISTIC to obtain within-region and between-region variances for the species as a whole.

In addition to Tables 2 and 3 the data are presented graphically in Figures 11 to 18 for a biometric comparison of the regions.

Table 2.--Significance of the variation between stands in the same region and between regions for various parental characters.

	Character	F-Ratio	
		Between regions	Stands within regions
P6	Cone length	27.80**	1.53*
P7	Cone width, closed	15.20**	2.42**
P8	Cone width, open	8.30**	3.70**
P9	Cone length/width ratio, closed	3.49**	1.13
P10	Cone length/width ratio, open	3.87**	2.51**
P11	Cone basal angle, open	3.09*	3.26**
P12	Largest apophysis length	2.10	2.59**
P13	Largest apophysis width	9.73**	2.75**
P14	Largest apophysis thickness	9.76**	1.91**
P15	Apophysis length/width ratio	6.76**	1.85**
P16	Apophysis length/thickness ratio	6.51**	2.51**
P17	Apophysis thickness on concave side	5.09**	3.96**
P18	Index of cone asymmetry[a]	1.96	16.37**
P20	Ratio, cone length to length of largest apophysis	21.86**	13.95**
P28	Seed length	21.67**	---
P29	Seed width	42.09**	---
P30	Seed length/width ratio	5.76**	---
P35	Leaf length	15.00**	2.59**
P38	Leaf twist	1.41	---

[a] See Figure 10 for explanation of measurement.

*Significant at 5 per cent level. Greater than 2.27 or 1.50 for between-region and within-region comparisons respectively.

**Significant at 0.1 per cent level. Greater than 3.17 or 1.80 for between-region and within-region comparisons respectively.

Table 3.--Components of the variance in parental characters supplied by trees-within-stands, stands-within-region, and regions of origin.

	Character	Per cent of total variance attributable to		
		Trees within stands	Stands within region	Between regions
P6	Cone length	7.5	.4	92.1
P7	Cone width, closed	8.8	1.2	90.0
P8	Cone width, open	10.7	2.9	86.4
P9	cone length/width ratio, closed	54.0	.7	45.3
P10	Cone length/width ratio, open	30.8	4.7	64.5
P11	Cone basal angle	30.6	6.9	62.5
P12	Largest apophysis length	22.2	3.5	74.3
P13	Largest apophysis width	12.0	2.1	85.9
P14	Largest apophysis thickness	16.5	1.4	82.1
P15	Apophysis length/width ratio	23.4	2.0	74.6
P16	Apophysis length/thickness ratio	18.9	2.9	78.2
P17	Apophysis thickness on concave side	16.3	4.8	78.9
P18	Index of cone assymmetry[a]	13.8	21.3	64.9
P20	Ratio, cone length to length of largest apophysis	1.1	1.5	97.4
P35	Leaf length	8.4	1.3	90.3

[a]See Figure 10 for method of measurement.

Regional Variation Pattern--Parental Data

Eight of the 19 characters (Table 1) studied proved to be the most definitive in separating the various stands into natural groupings. These are:

P6. Cone length

P7. Cone width, closed.

P8. Cone width, open.

P13. Largest apophysis width.

P20. Ratio cone length to length of largest apophysis.

P28. Seed length.

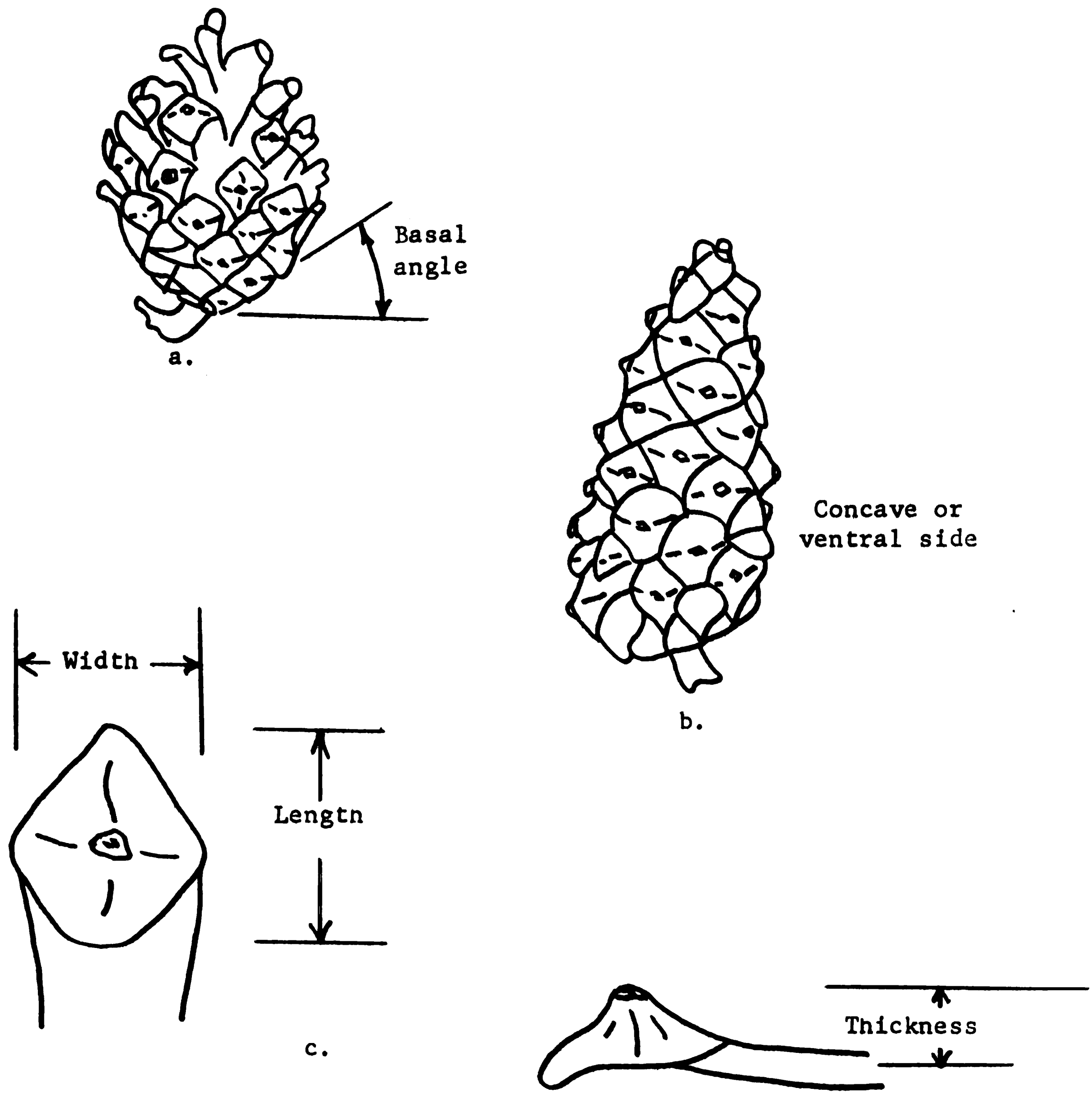
P29. Seed width.

P35. Leaf length.

Only one of six ratios computed was of particular value in defining differences between stands or regions. In other words, shape of the organs remained relatively constant. The one ratio which proved of value was that of cone length to length of the largest apophysis. This ratio is essentially a measure of the number of scales per cone and reflects the increased number of scales per cone from north to south. The ratio of thickness of the dorsal apophysis to the ventral apophysis was used as a measure of cone symmetry (Figure 10). It proved to be too variable within stand and within region to be of value.

The F-ratio for between-region variance in seed width was the largest of all the between-region ratios ($F = 42.09$, Table 2). Therefore seed width was one of the most definitive characters in developing regional patterns.

Figure 10.--Cone and cone scale measurements.



The method of measuring cones and cones scales on, a. open cone, b. closed cone, and c. cone scale. Basal angle is measured perpendicular to the cone axis. The largest apophysis on a reflexed cone is on the convex side of the cone and the opposite apophysis measured is on the concave side. The ratio of the two measurements is an index of asymmetry.

When seed width and length were plotted by regional group and latitude (Figure 11) there was a clear north to south pattern. Northern populations had the smallest seeds and the populations in Spain and Turkey had the largest. The two stands sampled in Surrey, England (Nos. 269 and 270), did not conform to the general pattern. They had larger seeds than expected for their latitude. They are known to be of planted origin. Historical and progeny-test evidence indicates that the Surrey population is hybrid, probably between Scottish and German types (Wright and Bull, 1963) (Edlin, 1962). Possibly the larger seed is a manifestation of hybrid vigor. The Greek stand, an isolated population, had smaller seeds than expected for its latitude.

The differences in seed width are sufficient to recognize a narrow-seeded Scandinavian population, a wide-seeded Spanish-Turkish-Yugoslavian population, and an intermediate French-German-Czechoslovakian population. Scotland is intermediate between the continental and Scandinavian groups.

Spain and Turkey are areas of relatively light precipitation, generally averaging between 30 and 40 millimeters per month on an annual basis. The precipitation tends to be heavier in the growing season than in the winter, reaching a high of 40 to 60 millimeters in four of the five stands sampled in Spain and 74 millimeters in Turkey. Natural selection would favor the survival of the larger seeds which would have the germinative capacity to get roots down deep enough into the soil to survive through the first growing season and the subsequent dry winter.

Seed length does not present the same pattern as seed width. The Scotch, German (No. 253), French, Yugoslavian, and Greek are different from the Finnish populations, but the East German (Nos. 525 to 529) are not significantly different from the Swedish or Norwegian populations. The Spanish seeds are longer than all other origins and appear to belong to the group including England, France (No. 239), Yugoslavia, and Turkey.

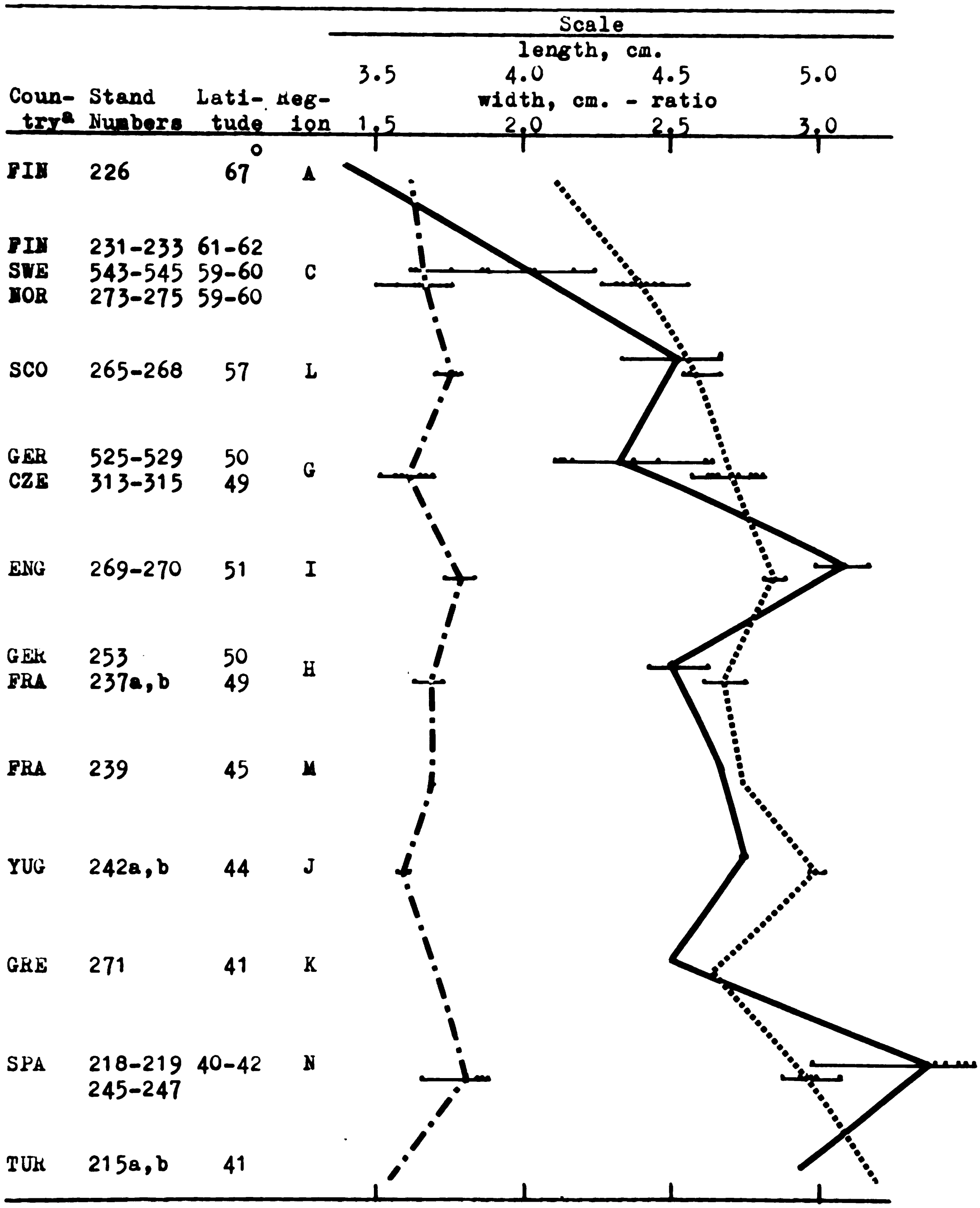
The patterns for the seed length/width ratio tends to parallel that for seed length, that is, the long-seeded Spanish and English samples also had the largest length/width ratios (Figure 11).

Cone length and width, and length/width ratios are presented graphically in Figures 12 and 13. Trees from north of the Arctic Circle had the smallest cones. Only one such stand was sampled. Hence it is not possible to say whether the northernmost population differs significantly from the more southerly ones but that is a possibility.

Also small-coned were the Greek and Yugoslavian parents, even though other trees from southern Europe (i.e., Turkey, southern France, and Spain) were large coned. The southern Scandinavian, German, Czechoslovakian, and Scottish parental populations were not separable on the basis of cone size.

The two collections made in Surrey, England (Nos. 269 and 270), had the largest cones of all. Those were from planted stands. As previously mentioned under seed dimensions these

Figure 11.--Regional variation pattern in length, width, and length-width ratio of Scotch pine seed.



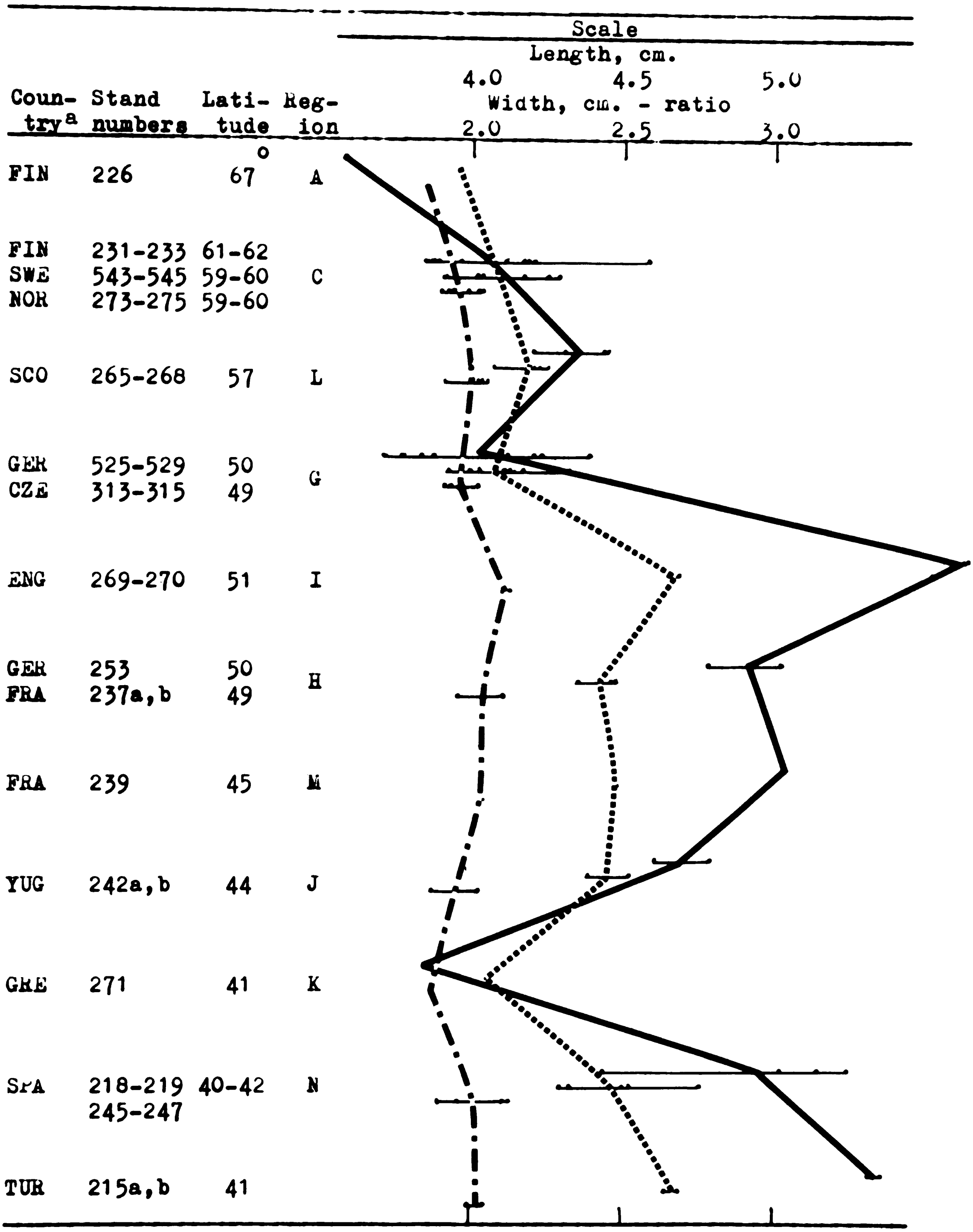
[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

———— Seed length.

·········· Seed width.

·–·–·– Seed length/width ratio.

Figure 12.--Regional variation pattern in cone length, width, and length/width ratio as determined from closed cones.

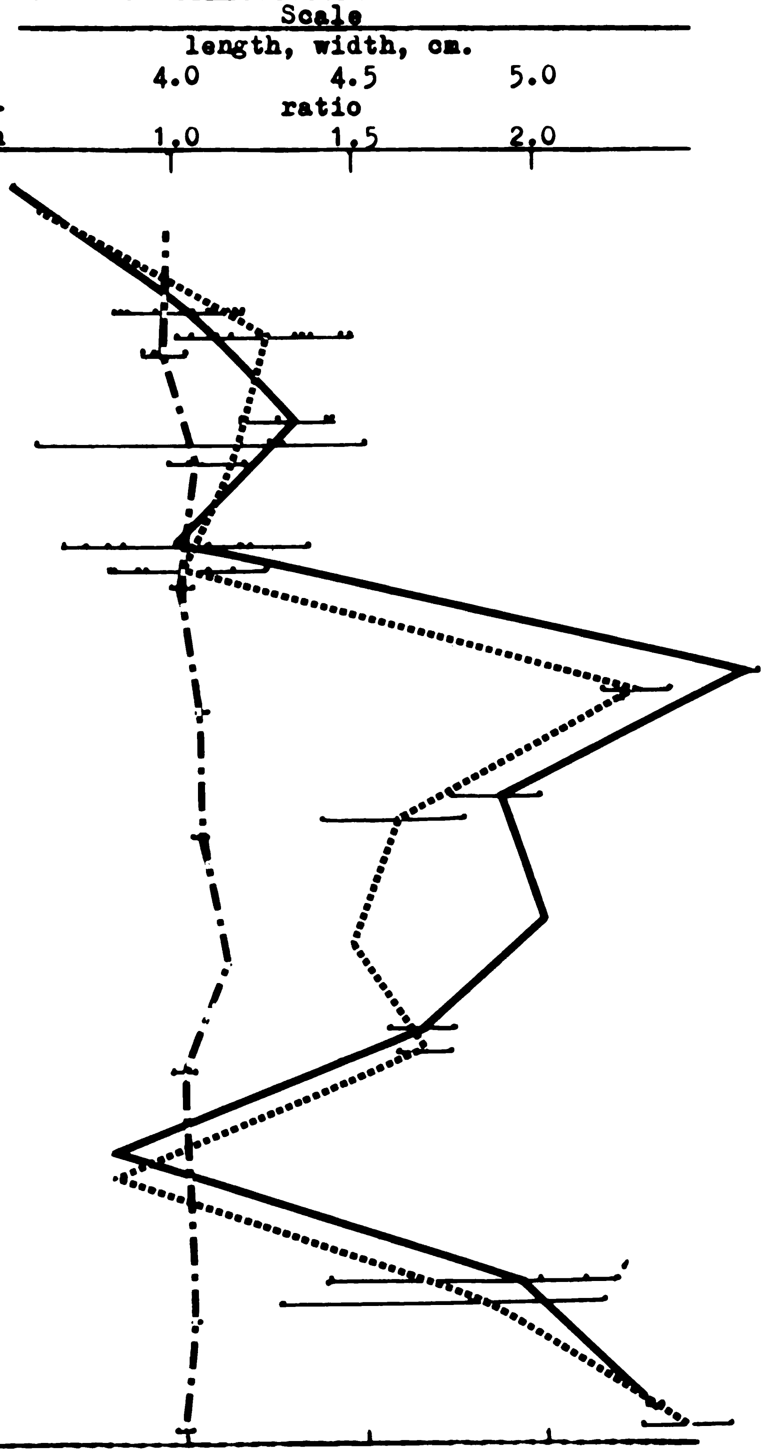


[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

Cone length.
Closed cone width.
Cone length/closed cone width ratio.

Figure 13.--Regional variation pattern in cone length, width, and length/width ratio as determined from open cones.

Country[a]	Stand numbers	Latitude	Region
		°	
FIN	226	67	A
FIN	231-233	61-62	
SWE	543-545	59-60	C
NOR	273-275	59-60	
SCO	265-268	57	L
GER	525-529	50	G
CZE	313-315	49	
ENG	269-270	51	I
GER	253	50	H
FRA	237a,b	49	
FRA	239	45	M
YUG	242a,b	44	J
GRE	271	41	K
SPA	218-219 245-247	40-42	N
TUR	215a,b	41	



[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

———— Cone length.
········ Open cone width.
—·—·— Cone length/open cone width ratio.

trees may be hybrids and the unusual cone size may be a manifestation of hybrid vigor.

A hybrid origin is also a possible explanation for the unusually long cones from stand 233 in southern Finland. There is nothing in the origin data to suggest that this is other than a native stand. But pollination by a planted stand of continental provenance could have introduced other genes into the native forest. The peculiar nature of stand 233 was also noted in the progeny test.

Large cones can either be an accommodation for more seeds or for larger seeds. The relatively large cones found in Turkey and Spain also contain the longest and heaviest seeds so that the adaptation is for larger seed in this case. Since the larger seeds have the best potential for survival, particularly in the semi-arid areas, this trend toward larger cones with larger seed in the Scotch pine endemic to these areas is possibly an answer to selection pressure.

Cone width was measured in both the open- and closed-cone condition (compare Figures 12 and 13). Except for the cones from stand 239 in south central France, the variation pattern was the same for the two measurement methods. The error variance was least for the measurements made on closed cones.

The ratio length/width of cone was of little value in the study of geographic variation. There was a tendency for the longer cones to be relatively narrower than the short cones.

The apophysis is the raised portion of the cone scale which is visible when the cone is closed (Figure 10). Within a single

Scotch pine cone the size and shape of the apophysis varies within wide limits. It was thought that this measurement would be most meaningful if confined to the scale with the largest apophysis in the case of length and width or to the scale with the thickest apophysis in the case of thickness.

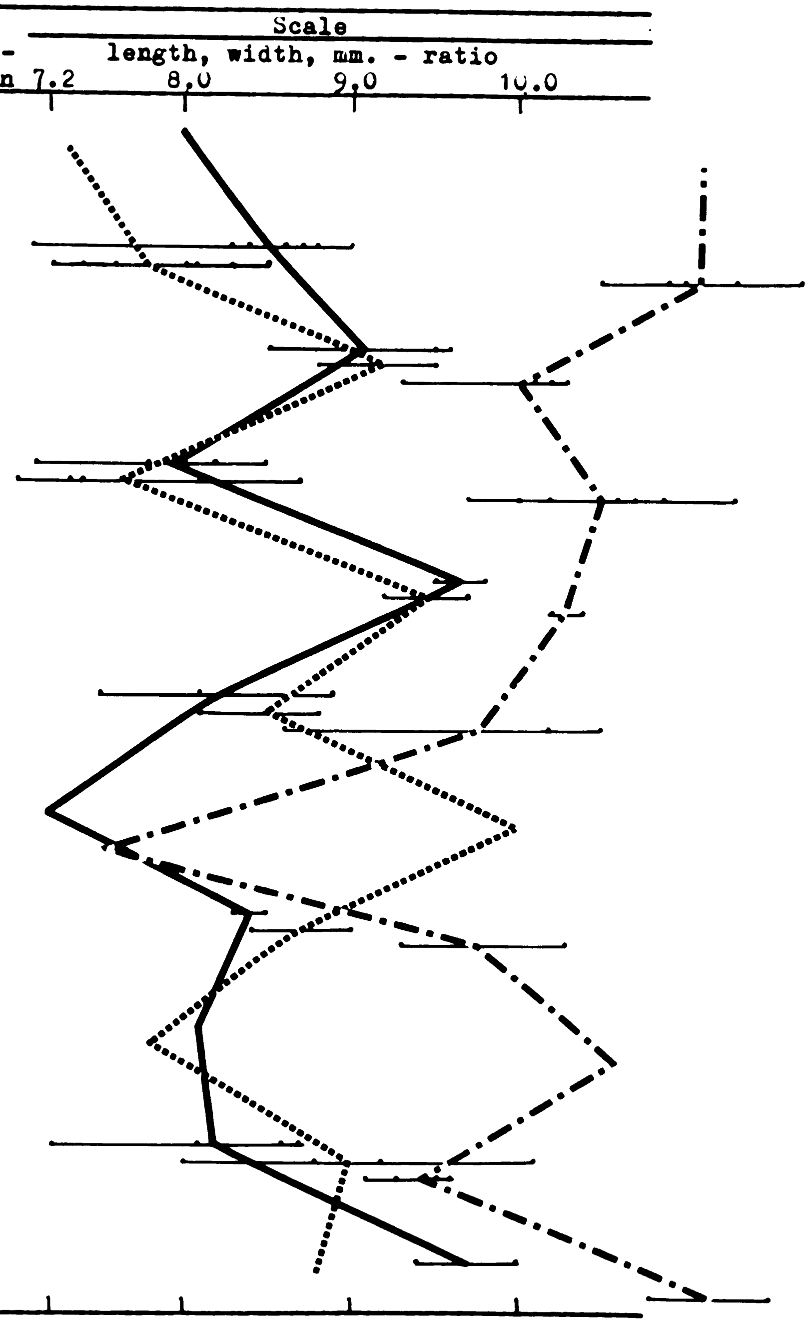
Among stands within the same region there were differences in apophysis length. But this character was of little value in identifying the region of origin of a sample (Tables 2 and 3, Figure 14).

The longer apophysis could be an indication of fewer seeds per cone if associated with greater apophysis width and short cones. However, apophysis length does not appear closely related to cone length or apophysis width throughout the range, suggesting a more complex evolutionary pattern for the apophyses from unknown factors, particularly in the highly variable southern limits of Scotch pine distribution. This may account for the lack of significance in the length of the apophysis when studied as a single factor.

The ratio of cone length/length of largest apophysis was, however, of geographic significance (Table 2). Of all the characters studied, the percentage of the total variance attributable to between-region differences was highest for the ratio (Table 3). It is an indirect measure of the number of scales per cone,--the higher the ratio the higher the number of scales per cone. When the regional means are plotted by latitude, as in Figure 15, the ratio is seen to increase from north to south

Figure 14.--Regional variation pattern in length and width of largest apophysis and the length/width ratio of the largest apophysis.

Country[a]	Stand numbers	Latitude °	Region
FIN	226	67	A
FIN	231-233	61-62	
SWE	543-545	59-60	C
NOR	273-275	59-60	
SCO	265-268	57	L
GER	525-529	50	G
CZE	313-315	49	
ENG	269-270	51	I
GER	253	50	H
FRA	237a,b	49	
FRA	239	45	M
YUG	242a,b	44	J
GRE	271	41	K
SPA	218-219 245-247	40-42	N
TUR	215a,b	41	



[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

Length of largest apophysis.
Width of largest apophysis.
Ratio length/width largest apophysis.

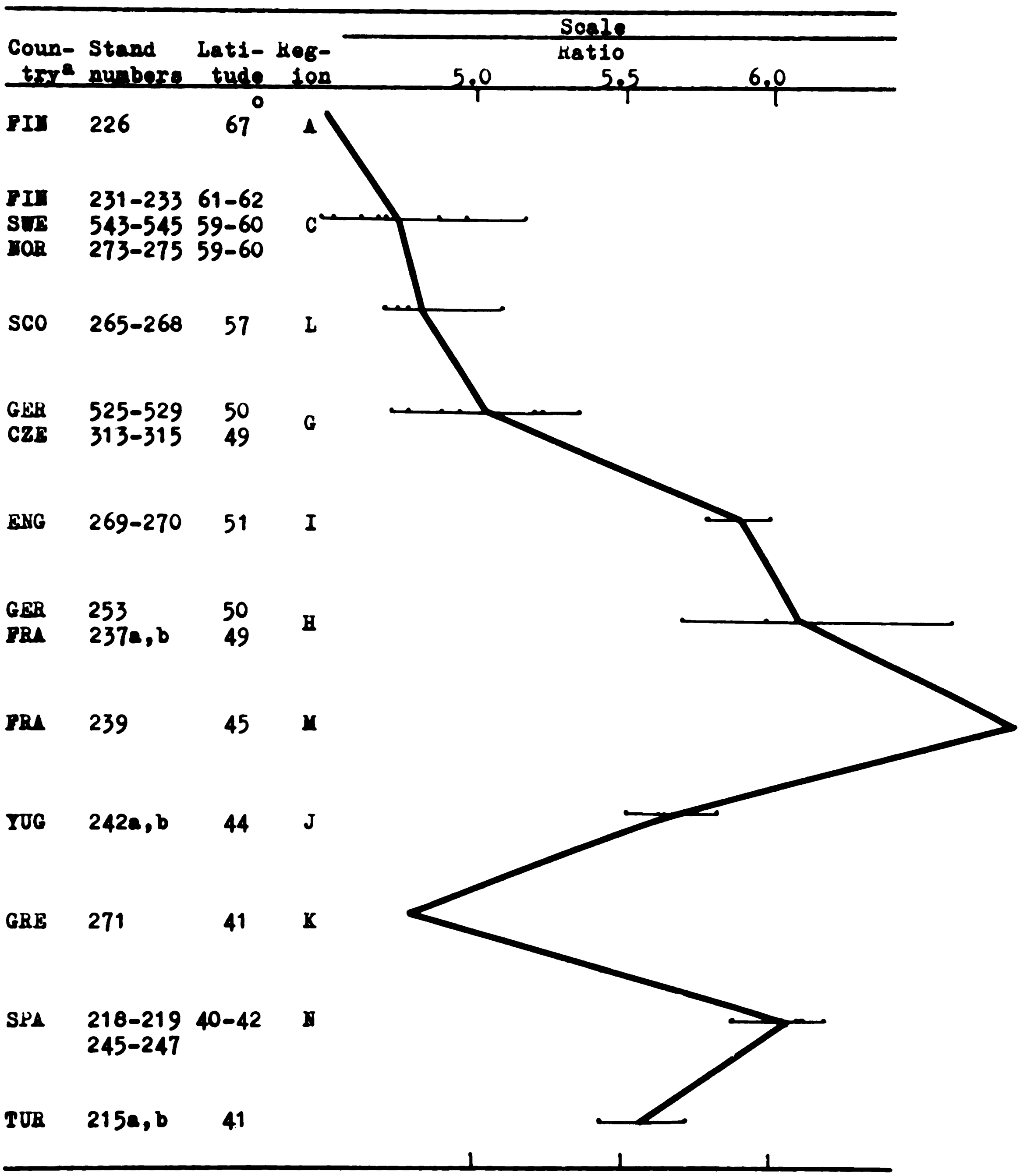
to a maximum in southern central France (Figure 15). Then it decreases and the southern populations (Spain, Turkey, Yugoslavia, and Greece) have values similar to those from Germany and Czechoslovakia. The major exceptions to the general latitudinal trends were furnished by the English (larger than expected ratio), Yugoslav (smaller than expected ratio), and Spanish (larger than expected ratio) populations. Also, the previously mentioned Finnish sample from stand number 233 had an abnormally high ratio for its geographic location.

The higher ratio of cone length to apophysis length would indicate that greater numbers of seed would be produced in England, West Germany, and France. This is an area of better soils and adequate moisture where survival of seedlings is not a problem but competition could be serious. Therefore greater seed quantities may be required. The decrease in the number of scales farther south would indicate more critical site conditions.

In contrast to apophysis length, apophysis width had geographic significance. So also did the length/width ratio for the apophyses. In neither trait, however, were there clear latitudinal or east-west trends. Perhaps the most noteworthy feature of the ratio was its small size for the south central French stand number 239, which had almost the widest apophysis of any sample.

Thickness of the apophysis is of evolutionary significance in the genus <u>Pinus</u> according to Shaw (1914). He considered species with thick apophyses to be more advanced. Within the single species, Scotch pine, however, this characteristic had less geographic

Figure 15.--Regional variation pattern in the cone length/ length of largest apophysis ratio.



[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

——— Cone length/length of largest apophysis ratio.

significance than did cone or seed size (Tables 2 and 3). There was a noticeable tendency for this trait to parallel cone width; that is, for wide cones to have thick apophyses (Figure 16).

Increased cone width and apophysis thickness could be a protective device that has developed in areas of more rigorous environments for Scotch pine.

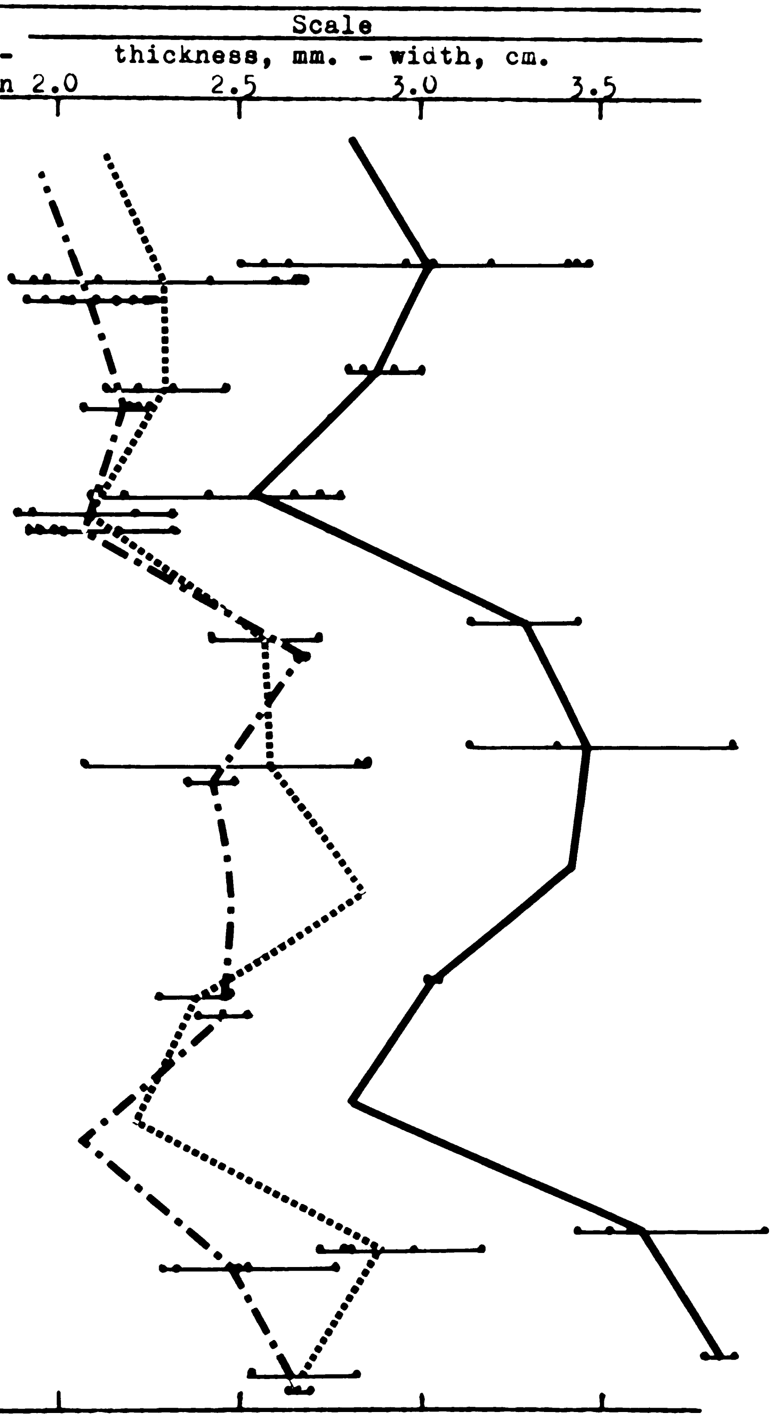
When the thickness of the largest apophysis was measured, an additional measurement was made of the thickness of the apophyses on the opposite side of the cone (character P17, thickness of opposite apophyses, Figure 10). This gave a ratio which was a measure of asymmetry (character P18). Thickness of the opposite apophyses, however, closely follows the pattern of thickness of the largest apophyses (Figure 16) and the ratio of the two measures showed that there were no significant differences in asymmetry (character P18, Table 2).

Another attempt to show cone scale variants was the use of the ratio of length of the largest apophyses over the thickness of the largest apophyses (Figure 17). Significant differences were obtained (Table 2). Shorter and thicker scales were found in the French, Turkish, and Spanish than in the other populations.

The basal angle of the open cones (character P11, Figure 17) closely approximated the pattern of the ratio of length to thickness of the largest apophyses. There was a tendency for the trees with large basal angles to have short, thick cone scales. The Scandinavian, Scotch, and Greek populations had the smallest basal angle and the Spanish and Turkish the largest.

Figure 16.--Regional variation pattern in thickness of the largest apophysis, thickness of the opposite apophysis (see Figure 10), and width of the open cone.

Country[a]	Stand numbers	Latitude °	Region
FIN	226	67	A
FIN	231-233	61-62	
SWE	543-545	59-60	C
NOR	273-275	59-60	
SCO	265-268	57	L
GER	525-529	50	G
CZE	313-315	49	
ENG	269-270	51	I
GER	253	50	H
FRA	237a,b	49	
FRA	239	45	M
YUG	242a,b	44	J
GRE	271	41	K
SPA	218-219 245-247	40-42	N
TUR	215a,b	41	

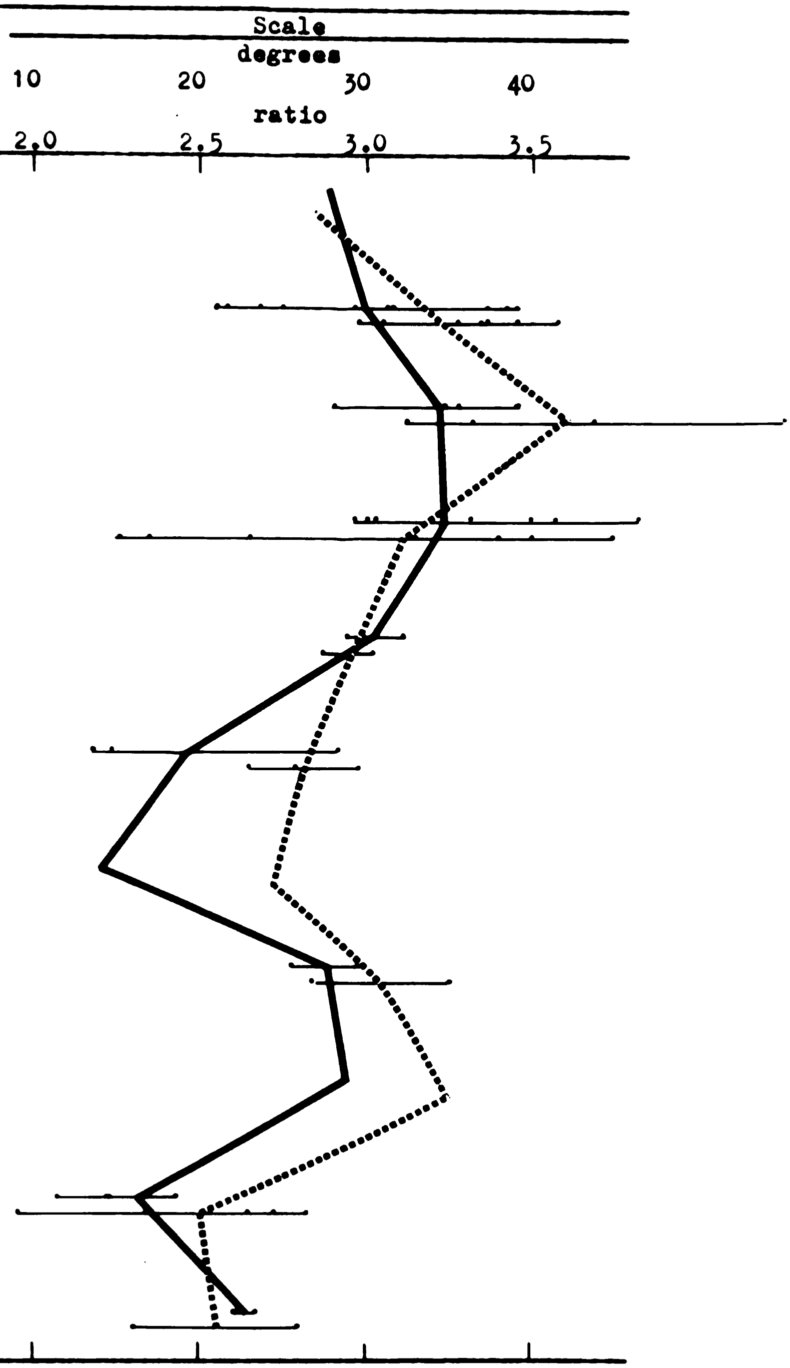


[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

Thickness of largest apophysis.
Thickness of opposite apophysis.
Closed cone width.

Figure 17.--Regional variation pattern in the basal angle of the cone, and the length/thickness ratio of the largest apophysis.

Country[a]	Stand numbers	Latitude °	Region
FIN	226	67	A
FIN	231-233	61-62	C
SWE	543-545	59-60	
NOR	273-275	59-60	
SCO	265-268	57	L
GER	525-529	50	G
CZE	313-315	49	
ENG	269-270	51	I
GER	253	50	H
FRA	237a,b	49	
FRA	239	45	M
YUG	242a,b	44	J
GRE	271	41	K
SPA	218-219 245-247	40-42	N
TUR	215a,b	41	



[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

——— Length of largest apophysis/width of largest apophysis.

·········· Basal angle of cone.

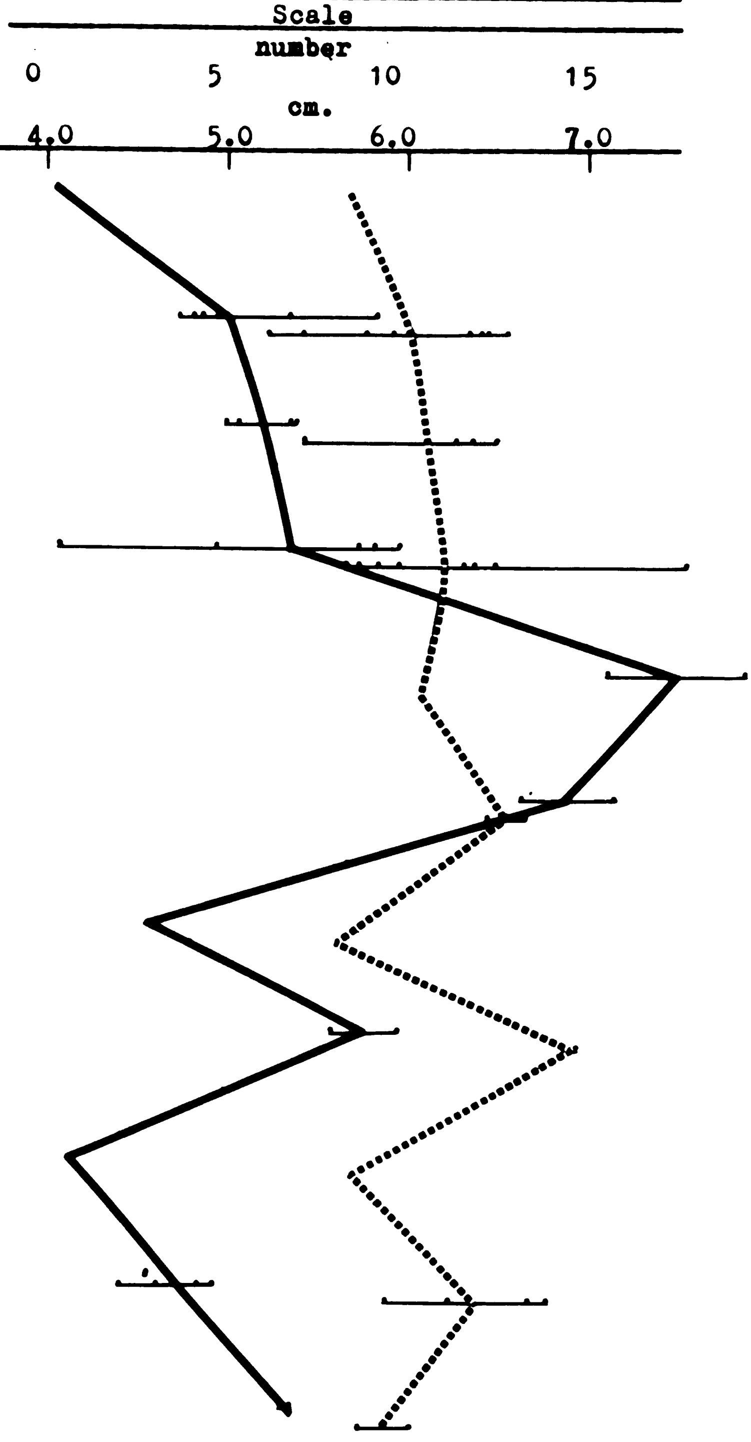
In extracting seed from the cones it was quite noticeable that the cones which opened the widest (small basal angle) also permitted the seed to be extracted more easily and quickly. Cones with large basal angles retained the seed in the lower half of the cone. The heavier scale and larger cone with the greater opening of the scales was more efficient in seed dispersal. This condition coincides with less favorable environmental conditions for seedling development. Shaw (1914) states that the heavier cone and scale is a higher evolutionary development. However, it was also noted in some of the northern stands, particularly in Norway, that there was an occasional serotinous or partially serotinous cone, also an indication of a higher development.

Leaf length (character P35, Figure 18) increased from the Arctic Circle to England, West Germany, and eastern France. Then it decreased and was short in trees from Greece and south central France.

Stover (1944) stated that leaf length in conifers was longest under mesic habitat and shortest under xeric conditions. Since growth would also be greatest under mesic conditions leaf length should be a measure of growth rate of the tree. The general pattern of leaf length does follow the growth rate of Scotch pine. The Scotch pine of the palatinate region of Germany has been noted for the quantity of wood which it produces. The English population is the result of natural reseeding by what appears to be hybrids showing hybrid vigor. If the above premise is correct, the English population should also have a

Figure 18.--Regional variation pattern in leaf length and twist.

Country[a]	Stand numbers	Latitude °	Region
FIN	226	67	A
FIN SWE NOR	231-233 543-545 273-275	61-62 59-60 59-60	C
SCO	265-268	57	L
GER CZE	525-529 313-315	50 49	G
ENG	269-270	51	I
GER FRA	253 237a,b	50 49	H
FRA	239	45	M
YUG	242a,b	44	J
GRE	271	41	K
SPA	218-219 245-247	40-42	N
TUR	215a,b	41	



[a] FINland, SWEden, NORway, SCOtland, GERmany, CZEchoslovakia, ENGland, FRAnce, YUGoslavia, GREece, SPAin, TURkey.

Leaf length.

Leaf twist.

high growth rate in comparison to other geographical races of Scotch pine.

The measurement of leaf twist (character P38, Figure 18) proved to be of little value except to indicate that leaves from English and Turkish populations have less twist per unit length than other populations.

The Naturalness of the Regional Grouping

One of the initial objectives of the study of parental characteristics was to determine if population discontinuities existed, where they occurred, and which characters would prove most valuable in defining populations.

The original parental data were grouped by natural region of origin in such a manner that the regions were as homogeneous as possible with regard to morphological characteristics. The final grouping is very similar to that used by Wright and Bull (1963) for progeny test data, the major exceptions being the separation of the Czechoslovakian from the German and the Turkish from the Greek populations. For the analysis of variance the data for stand 226 in Finland (region A) and stand 271 in Greece (region K) were discarded because there was only one stand per region. Data from 10 trees in each stand were used. The degrees of freedom for the analyses were as follows: between regions--8, between stands within regions--30, between trees within stands--351, total--389.

When grouped in this manner, between-region variances accounted for 62 to 97 per cent of the total variances in the various characteristics. Stands-within-region variances generally accounted for less than 5 per cent of the total variances, the exception being the index of cone symmetry (character P18 in Tables 1, 2, and 3).

The large between-region differences indicate that the regional grouping was natural. Furthermore, they indicate that it is possible to tell the region of origin from cone and leaf specimens. Perhaps the variation is too great to permit this on the basis of cones or needles from a single tree, such as might be found on an ordinary herbarium specimen. But, if mass collections are made from several trees in a stand, the stand as a whole can be characterized sufficiently to identify its place of origin.

Turesson (1922) stated that an ecotype is one of a series of relatively discrete, genetically differentiated, natural entities whose limits coincide with the distribution of some environmental effect. Huxley (1939) said that a cline is a geographical gradient in a phenotypic character with continuity and a genetic gradient implied. Langlet (1959) reviewed the concept of continuous variability in his discussion of Wright and Baldwin's (1957) report on New Hampshire plantings of the 1938 IUFRO Scotch pine provenance test. He stated that "Discontinuity may thus very well occur--where the conditional ecological factors vary discontinuously."

Stebbins (1950) in discussing geographical races stated "There is no doubt that in plants, as in animals, many species may be divided into races or groups of genetic types which are adapted to the different parts of their ranges, and that these sub-divisions are separated from each other by partial discontinuities in the variation pattern."

Mayr (1942) was less flexible in his definition of a geographical race stating that such a race was "A complex of interbreeding and completely fertile individuals which are morphologically identical or vary only within the limits of individual ecological and seasonal variability. The typical characters of this group are genetically fixed and no other geographical race of the same species occurs within the range."

The analyses of variance based on the sample of 39 stands indicates that regional discontinuities exist after removal of the within-stand or within-region variability. The use of the word ecotype has been avoided as being applicable to a certain situation and the term geographical variety has been used to describe a population which is different although there may be a continuity in the characteristic as it merges with another geographical area. Ecotypes, as defined by Turesson, do exist in Scotch pine where there are sharp breaks in the factors which have produced them. Glaciation disrupted the original continuity of Scotch pine during the complex patterns of glaciation in Europe and Asia according to Hulten (1937, 1949). The movement of Scotch pine back into areas of original distribution following the shrinking of the glaciers once more established continuity in distribution but not genetic continuity. Certain populations have remained isolated, particularly along the south and east of the area of distribution of Scotch pine.

Langlet's insistence that the variability of Scotch pine can be called only clinal is well authenticated by other authors who have studied the species. The concept of continuity is not disputed in the case of continuous populations under continuous meteorological or edaphic conditions. The sampling upon which this study is based is too meager to prove discontinuities over such a wide range as that covered by Scotch pine. It does prove that if population samples are taken at discrete locations within the range that there are identifiable geographic races which predominate at the location that also are genetically different from other samples taken at other locales.

The range of Scotch pine covers a wide area of complex geographical and meteorological conditions that are often quite well defined. Even in the less well defined and less abrupt gradients differences have been found between populations which are of significant importance to a tree breeder, much as a superior tree within a given stand. However, there is an important difference, a superior tree in a stand represents an improvement in some desirable character or combination of characters that are identified with an individual tree, an ideal situation only if vegetative propagation is planned.

Selection of a segment of a population permits the acquisition of sufficient breeding material without seriously restricting the gene pool required for a breeding program.

Many authors who have reported their observations of Scotch pine have pointed out that although there are recognizably different varieties of Scotch pine these are contained in highly variable populations in which they predominate. In this meaning, a geographical variety is recognized here by the predominance of a characteristic which arose in answer to selection pressures based on local environmental conditions.

The between-region differences have been summarized by character in Table 4.

Finland north of the Arctic Circle (region A) is represented by a single stand which is significantly different at the one per cent level from the southern Finland, Sweden, and Norway population (region C) in open-cone width, and seed and leaf length. The regions are significantly different at the five per cent level in cone length, and the cone length/length of largest apophysis ratio.

Southern Finland, Sweden, and Norway are significantly different from the population of Scotland (region L) at the one per cent level in the open cone length/cone width ratio, width of the largest apophysis, and the length and width of seed. The regions are significantly different at the five per cent level in cone length and the cone length/length of largest apophysis ratio.

Table 4.--Summary of significant parental character differences between regions.[1]

Re-gion	Country	N. Scand. A	C	L	G	I	H	M	J	K	N
C	Finland, Sweden, Norway	6,8,20,29,35									
L	Scotland	6,8,9,20,28, 29,35	6,10,13,20, 28,29								
G	Ne.Germany, Czechoslovakia	6,8,11,13,18, 20,28,29,35	14,17,18,20 28,29	6,10,11,13, 17,18,20,30							
I	England	6,7,8,9,13, 17,20,28,29, 35	6,7,8,9,10, 13,17,20,28, 29,35	6,7,8,11,14, 17,20,28,29, 35	6,7,8,9,10, 13,14,17,18, 20,28,30,35						
H	W.Germany, NE. France	6,7,8,9,10, 13,14,16,17, 20,28,29,35	6,7,8,10,11, 13,16,17,20, 28,29,35	6,7,8,11,13, 14,16,17,18, 20,35	6,7,8,10,13, 14,16,17,18, 20,35	6,7,8,13,16, 18,20,28,29, 35					
M	S.central France	6,7,8,9,10, 13,14,15,16, 17,18,20,28, 29	6,7,10,11,13, 15,16,17,18, 20,28,29	6,7,8,10,11, 13,14,16,17, 20	6,7,10,13,14, 16,17,20,35	6,7,8,16,18, 20,35	13,18,20,35				
J	Yugoslavia	6,7,8,13,16, 20,28,29,35	6,7,8,13,20, 28,29,35	6,7,8,10,11, 20,29,30,35	6,7,8,13,14, 17,18,20,29	6,8,9,13,20 30,35	10,14,16,20 29,35	10,13,16,17 18,20,35			
K	NE.Greece	20,28,29	8,28,29,35	6,9,13,35	20,35	6,7,8,9,13, 14,17,20,28, 35	6,7,8,9,14 16,17,18,20, 35	6,7,8,9,10, 13,14,16,17, 20	6,7,8,13,20, 29,35		
N	Central Spain	6,7,8,9,13, 14,16,17,20 28,29,35	6,7,8,11,13, 14,16,17,18, 20,29,30,35	6,7,8,11,14, 16,17,20,28 29	6,7,8,11,13, 14,16,17,20, 28,29,30,35	6,7,8,11,16, 17,20,28,35	10,17,18,28, 28,29,35	10,13,20,28, 29	11,14,16,17, 20,28,30,35	6,7,8,9,11, 13,14,16,17, 20,28,29,35	
T	Turkey	6,7,8,9,13, 14,17,18,20 28,29,35	6,7,8,11,13, 14,16,17,18, 20,28,29	6,7,8,10,11, 14,17,18,20, 29,30	6,7,8,11,13, 14,17,18,20, 28,29	13,14,16,18, 20,29,30,35	6,7,8,10,18 20,29,30,35	7,8,10,13,15 18,20,29,35	6,7,8,11,14, 18	6,7,8,9,11, 13,14,18,20, 29,30,35	6,7,8,18,20, 28,29,30,35

[1] See Table 1 for description of characters.
Underlined characters significant at 1 per cent level, others at 5 per cent level of significance.

Scotland is significantly different from the East German--Czechoslovakian population (region G) at the one per cent level in the open-cone length/width ratio, basal angle of the open cone, width of the largest apophysis, asymmetry, and the seed length/width ratio. These regions are significantly different at the five per cent level in cone length, thickness of opposite apophysis, and the cone length/length of largest apophysis ratio. The Scottish population is intermediate between regions C and G but not different in cone width, leaf length, and leaf twist.

The cones, leaves, and seed of the Surrey, England, population (region I) exceeded the length of all others except for the Spanish seed. The English population was significantly different from that of the East Germany and Czechoslovakia in 13 characters and from the West German, eastern France in 10 characters.

The population in eastern France and West Germany (region H) differed significantly from that in East Germany and Czechoslovakia in 10 characters and from the Central Massif of France in 4 characters, all at the one per cent level of significance.

Region M, the Central Massif of France, represented by a single stand, differed from the Spanish (region N) population in the open cone length/width ratio, width of the largest apophysis, and the cone length/length of largest apophysis ratio at the one per cent level of significance, and in seed length and width at the five per cent level.

The Greek population, represented by a single stand in the mountains northeast of Drama near the Bulgarian border, was different from the Turkish population, represented by two stands from the mountains of north central Turkey near the Black Sea, in 12 characters, and from the Yugoslavian population represented by two stands, in 7 characters. The Greek population, however, differed in only two characters, cone length/length of largest apophysis ratio and leaf length, from the East German, Czechoslovakian. The Greek stand differed in only four characters from region C and L, and in three characters from region A.

The differences between regions outlined in Table 4, combined with the data presented in Figures 11 to 18, not only define the variability of the Scotch pine in Europe and Asia Minor, but permits comparative analysis of herbarium specimens and placement in the region of origin. The eleven regions defined are all separated by significant differences in their cones, seeds, and leaves except for regions C, L, and G, where there were no differences in leaf length. The parental data supports the regional patterns based on total similarities in juvenile characters reported by Wright and Bull (1963) except for the Turkish population. However, the data presented by Wright and Bull in their table of similarities and differences for region K does indicate a possible separation of the Turkish-Georgian populations from that of Greece.

Staszkiewicz (1960, 1961, 1962) studied the cones of Scotch pine populations from Finland, Sweden, Scotland, Czechoslavakia, Hungary, Poland, Switzerland, and the Central Massif of France. He separated the populations on the basis of ten cone measurements into seven regional varieties having different types of cones as following:

var. lapponica, northern Finland.

var. suecica, Sweden.

var. scotica, Scotland.

var. polonica, Poland.

var. subcarpatica, northeastern Czechoslovakia.

var. meridionalis, Czechoslovakia, Switzerland, and Central Massif of France.

Comparisons between his and my data show general agreement with regard to the first five varieties. They are separable in both cases. On the other hand, the population which he regards as var. meridionalis and as homogeneous, is very heterogeneous according to the present study.

In a later chapter, these data on phenotypic varability patterns will be coordinated with past taxonomic treatments to give a recommended series of varietal names.

Sample Size

The specific question of how small a sample can be measured without appreciably changing the results is important. Staszkiewicz (1960) reported that his original sample size was 100 cones picked under 100 trees, or one cone per tree from 100 trees per stand. In some instances he collected 2 cones per tree. Since the measurement of so many samples was laborious he halved some of his samples and found that the data obtained from sample sizes of 50 did not exceed the permissible error. Critchfield (1957) used a sample size of 5 cones and 5 needles per tree for 12 trees per stand. Thor (1961) used 20 sound and mature cones and 5 twigs from 15 trees in his study of variation patterns in natural stands of loblolly pine. Thor (1964) took two core samples from each of 15 trees per stand in his wood property study in Virginia pine.

In the course of analysing the 19 characters utilized in this study correlations were run between the standard deviations of each sample and the size of that sample. The samples ranged in size from 10 to 34 cones (1 cone per tree). There was no correlation between size of sample and of the standard deviations. This shows that the disparity in sample sizes was unimportant and that one cone per tree from each of 10 trees would have been sufficient.

If, in the present study, cone length and needle length are used to determine the actual size of an acceptable sample, the following procedure can be used: Stand 226 (Finland) was represented by a collection of 29 cones taken from 29 different trees. The analysis of variance for cone length produced the following information:

$\bar{X} = 3.567$ centimeters (cone length)

$S^2 = .268$

$S = .517$

$S_{\bar{X}} = .096$

The 95% confidence interval for the mean $= \pm (t_{.95})\ (S_{\bar{X}})$

$= (2.048)\ (.096) = .1966$

$$\text{Sampling error} \quad \frac{100\ (t_{.95})\ (S_{\bar{X}})}{\bar{X}} = \frac{100(2.048)\ (.096)}{3.567} = 5.5\%$$

Assuming that the permissible error is 10 per cent of the mean, the confidence interval is:

$.10\ (\bar{X}) = .10\ (3.567) = .3567$

Since the confidence interval (.3567) is equal to $(t_{.95})(S_{\bar{X}})$ we can solve for $S_{\bar{X}} = \frac{.3567}{2.26} = .158$

The number of sample plots needed can be computed using the formula:

$$S_{\bar{X}} = \frac{S}{\sqrt{n}} \qquad \text{or } n = \frac{S^2}{S_{\bar{X}}^2} = \frac{.268}{(.158)^2} = \frac{.268}{.0249} = 11\text{cones.}$$

Based on the cone-length data, sample size ranged from 3 to 14 cones for 9 different stands. The computed sample sizes for these 9 stands were 11, 7, 6, 4, 10, 3, 5, 14, and 11 cones. Therefore cones from 10 trees is not only a good average sample, but a sample sufficient for nearly any stand.

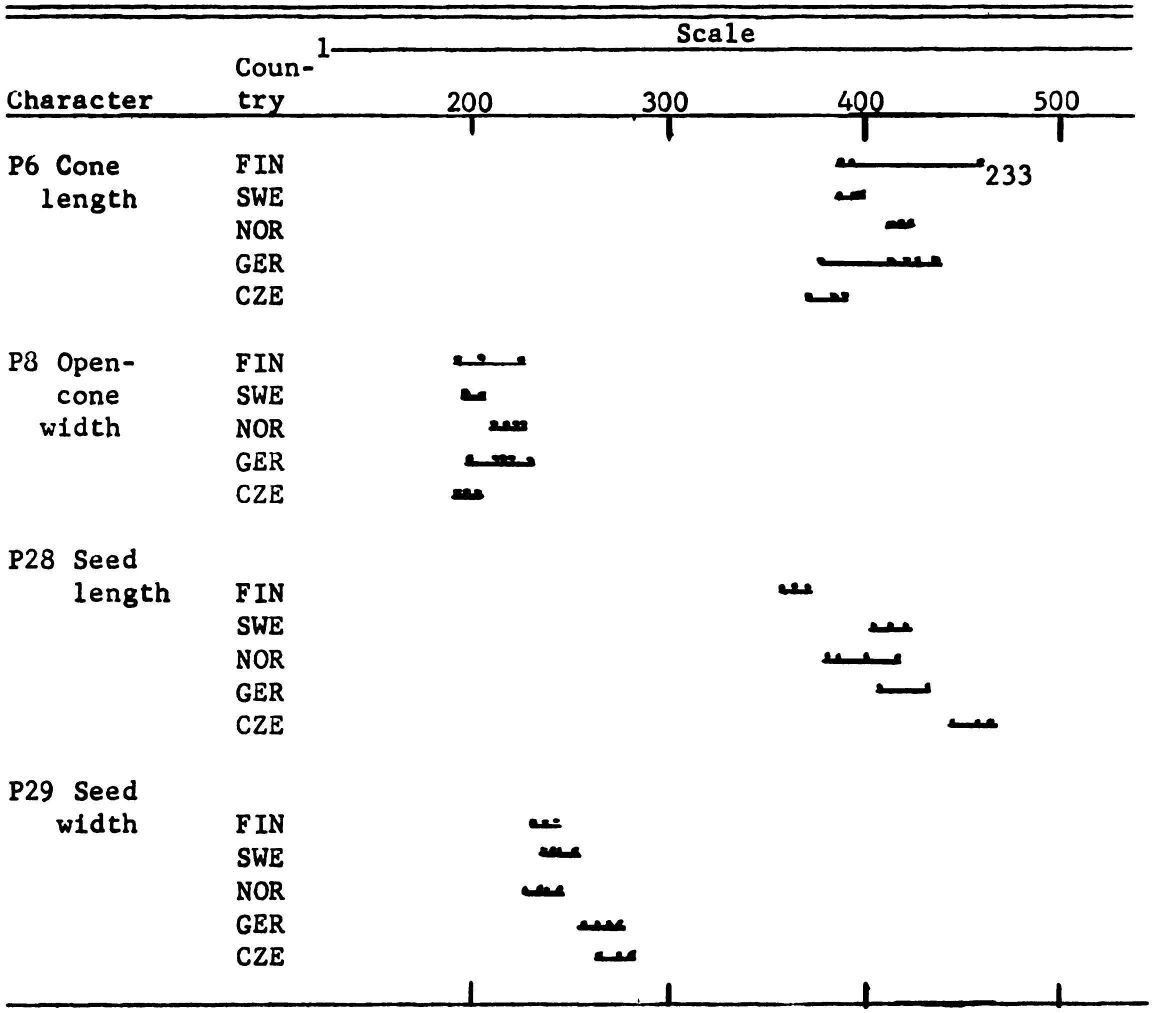
At the 95 per cent confidence limit, the sampling error with regard to needle length was 10.4 per cent from a 15-tree sample. In other words, needles from 16 or 17 trees would have been required to give the desired 10 per cent sampling error. Using the formulas given previously on needle length data, the numbers of needles needed to give that sampling error for eight different stands were found to be 30, 9, 18, 19, 7, 12, 15, and 4.

In other words, needles from 15 or 20 trees would be needed to give the same accuracy as can be achieved with cones from 10 trees per stand.

The specifications for needle and cone samples for the study called for one needle and one cone per tree from 10 to 20 trees per stand over an area which would minimize the chances of obtaining seed from two trees that had been pollenated by a single parent. Some cooperators sent in two cones and two needle fascicles per tree. A comparison of the results of measuring two cones and four needles per tree and one cone and one needle revealed no significant difference between the sampling. Samples based on single cones and leaves had sampling errors of the same magnitude as samples based on two cones and two needles. In other words, if cones or leaves are collected in a standard manner, within-tree variation can be disregarded.

There were some intra-regional differences which should be noted, particularly in region G which included northeast Germany and Czechoslovakia. The north to south variation pattern here is apparently complicated by an east to west difference due to geographical and meteorological differences. Seed length and width, and needle length follow the established trend of small to large from north to south but open cone length and width of the Czechoslovakian populations are smaller than that of the northeast German (Figure 19). Although the Czechoslovakian material falls within the range of the German it does not show the high variability of the German and is centered at the low end of the scale. Origin 233 in east Finland represents another stand sample which is materially out of line with the remaining populations sampled in southern Finland. The cones of 233 are of significantly larger size but the seeds are normal to that region (Figure 18).

Figure 19.--Intra-regional variation pattern for region C, southern Finland, Sweden, and Norway, and region G, northeast Germany and Czechoslovakia.



[1] FINland, SWEden, NORway, GERmany (northeast Germany), CZEchoslovakia.

CHAPTER V

RELATIONS INVOLVING SINGLE PARENTS AND THEIR PROGENY

Materials and Methods

A series of half-sib progeny tests was started in 1959 with Scotch pine seed received from eight stands in northern Europe (Table 5). Two of these stands are in Belgium and were sampled through the courtesy of Dr. Alain de Jamblinne (parents 285-304), Chief, Section of Genetics, Centrum voor Bosbiologisch Onderzoek, Bokrijk-Genk, Belgium. In addition to the stand data the collectors sent parental data on height, age, and diameter for nine trees which were progeny tested in Belgium.

A stand in southern Norway was sampled by Dr. Tollef Ruden, Norwegian Forest Research Institute, Vollebekk, Norway, who also furnished information on the site characteristics and age and height of the parent trees.

The sampling of the East German stands was done by Dr. Otto Schröck, Director of the Branch for Forest Research at Waldsievers-dorf of the German Academy of Agricultural Science of Berlin, Institute for Forest Science, Eberswalde. Dr. Schröck furnished data on many characteristics of the parental trees including age, height, diameter breast high, stem form, crown length, length of clear stem, crown diameter, flatness, and form, and foliage condition.

In each of the eight stands open-pollinated seeds were collected from either 10 or 20 randomly selected dominant trees. In general, the parents in any one stand were 100 feet or more distant from each other. Thus they probably did not have common female parents although they may have had common grandparents.

After receipt in late 1958, the seeds were weighed and placed in cold storage. They were sown in the Bogue Forest Research Nursery on May 13 and 14, 1958. A variation of a randomized complete block design was used. The 10 or 20 seed-lots from each stand were randomized and grouped together. These progeny-groups were then randomly distributed (along with the stand-progenies from the geographic origin test) through each of the four replicates. This arrangement resulted in greater precision for the detection of within-stand than between-stand differences.

The seedlings were grown for two years at an approximate spacing of 50 per linear foot (25 per square foot). Then they were thinned to an approximate spacing of 20 per linear foot (10 per square foot). They were partially lifted at the start of the third year and completely outplanted by the start of the fourth year.

The European cooperators measured metric characters (height, etc.) to an accuracy of approximately one-twentieth of the range between extremes. They described other traits in words which were translated to numerical codes for purposes of analysis (Table 6). The linearity of these translated numerical grades is not known.

Table 5.--Description of parent stands

Stand No.	North Lat. °	'	East Long. °	'	Country and locality	Elev. meters	Stand age years	Trees sampled number	Soil type	Remarks
275-284	59	50	11	34	NORWAY, N. Holland	220	130-160	10	---	Natural stand
285-294	51	17	5	30	BELGIUM, Achel Limberg	35	38	10	Half-bog, sandy subsoil	Planted stand, unknown origin
295-304	51	07	5	21	BELGIUM, Hechtel, Limburg	65	35-50	10	Iron podzol on sand	Seedlings from a nearby 100-year-old plantation
321-340	54	11	12	15	E. GERMANY, Rövershagen, Meyershausstelle For. Dist.	9	104	20	---	Natural stand
341-360	53	22	13	05	E. GERMANY , Neustrelitz, Wilhelminenhof d. Oberförsterei, Zinnow For. Dist. (Cpts. 27d and 28d)	80-90	110	20	Coarse sand at base of terminal morain	Natural stand
361-380	53	48	12	11	E. GERMANY, Güstrow, Kluess For. Dist. (Sect. 20)	20	97	20	Coarse sand	Natural stand
381-400	52	05	12	15	E. GERMANY, Nedlitz, Dobritz For. Dist. (Cpt. 539b)	94	97	20	---	Planted, unknown origin
501-520	52	58	13	46	E. GERMANY, Joachimsthal, Hubertusstock Dist. (Cpts. 18 and 19)	45	110	20	---	Natural stand

Table 6.--Description of parental characters and grades

Character and number	Unit of Measurement	Lowest value assigned to	Highest value assigned to
40 Total height	Meter	Slow growth	Fast growth
41 Diameter breast high	Centimeter	Small diameter	Large diameter
42 Stem form	Grades 1 to 8	Many curves	Straight stem
43 Live crown length	Meter	Great length	Short length
44 Length of clear stem	Meter	Short length	Long length
45 Crown diameter	Meter	Narrow crown	Wide crown
46 Crown flattening	Grades 1 to 5	Pointed crown	Flat crown
47 Crown shape	Grades 1 to 8	One-sided crown	Round crown
48 Foliage condition	Grades 1 to 5	Thin foliage	Heavy foliage
49 Age	Years		
50 Growth rate	Ratio $\frac{\text{height in meters}}{\text{age in years}}$	Slow growth	Fast growth

The seedlings were measured or scored periodically for all macroscopic traits in which preliminary examination showed the probable presence of between-progeny differences (Table 7). Measurements were made to an accuracy of approximately one-twentieth of the range between extremes. Non-metric characters were scored by numerical grades. In order to avoid the need for transformation the grades were so defined as to result in normal distributions and linearity.

The details of progeny performance were described by Wright (1963) who performed an analysis of variance for each trait and each group of progenies from a single stand. In those analyses plot means were used as items.

For the present paper all possible simple (product-moment) correlations were calculated among parental and progeny characters. Values applicable to single parents or to progeny means were used as items. When analyzed in this manner, the word-interpretation of a significant relationship such as reported between parental character No. 44 and progeny character No. 22 is as follows: the offspring of trees with long clear boles had fewer lateral buds in May, 1960, than did the off-spring of trees with short clear boles.

Because of the relatively small number of significant parent-progeny correlations it was deemed inadvisable to use multiple correlation or factor analysis.

The correlations were calculated by MISTIC, the former Michigan State Integral Computer.

Table 7.--Description of juvenile characteristics and grades used in scoring Scotch pine progeny study

Character and number		Date	Unit of measure	Range	Lowest value assigned to	Highest value assigned to
5	Seed weight	11/58	mg.	2.9-12.2	Light seed	Heavy seed
6	Seed length	11/58	mm.	3.4-5.9	Short seed	Long seed
7	Height, age 1	10/59	mm.	37-131	Short tree	Tall tree
8	Height, age 2	7/60	mm.	57-387	Short tree	Tall tree
9	Foliage color	6/59	Grade	4-8	Yellow-green	Green
11	Foliage color	9/59	Grade	8-20	Red-maroon	Green
12	Foliage color	10/59	Grade	8-20	Maroon	Green
13	Foliage color	8/60	Grade	8-16	Green	Dark-green
15	Foliage color	11/60	Grade	4-32	Yellow-green	Dark-green
16	Foliage color	12/60	Grade	4-32	Yellow-green	Dark-green
18	Bud color	5/60	Grade	4-24	Bright-green	Brown
19	Time of bud set	9/59	Day of year	200-269	Early set	Late set
21	Bud diameter	4/60	mm.	1.5-6.4	Small bud	Large bud
22	Branched buds	5/60	Per cent of trees	0-13	Small number	Large number
23	Branched buds	10/60	Per cent of trees	0-5	Small number	Large number
26	Presence of primary lvs.	5/60	Grade	0-12	None present	Present on 3" of stem
27	Presence of secondary lvs.	9/59	Grade	0-4	None present	Present on 50% of seedlings
28	Presence of secondary lvs.	10/59	Grade	0-24	None present	Present on 90% of seedlings
29	Leaf length	8/60	cm.	25-43	Short needle	Long needle
7/5	Ratio 1-yr.ht. / seed wt.	5/60	Number	8-26	Low ratio	High ratio

Parent-Parent Correlations

The simple correlations among the parental characters in the five German stands are presented in Table 8. Because the stands were even-aged, total height and height growth rate are identical; relations involving one also involve the other.

For the 9 traits and 5 German stands, a total of 180 simple correlations were calculated. Actual and expected numbers of correlations significant at various levels were as follows:

Significance level	0.1 per cent	1 per cent	5 per cent
r needed for significance	.68	.56	.44
Number of r's exceeding amount needed for significance			
Actual	7	19	36
Expected	.18	1.8	9.0

Approximately 25 per cent of the total significant correlations and 50 per cent of those for which $.05 > P > .01$ are presumed to be meaningless. Presumably the six correlations significant at only the 5 per cent level and for only one stand have little meaning. Thus clear-stem length, crown form (one-sided or round), and foliage condition were essentially uncorrelated with the other variables.

The 36 correlations, which were above the level needed for significance at the 5 per cent level were distributed among the five stands as follows.

Table 8.--Correlations between parental characters in five East German stands. With 18 degrees of freedom for each stand the value of r needed for significance at the 5, 1, and 0.1 levels was .444, .561, and .679 respectively.

Character		Stand	40. Ht.	41. Diameter breast high	42. Stem form	43. Crown length	44. Clear stem length	45. Crown diameter	46. Crown flattening	47. Crown shape
41.	Diameter breast high	Rövershagen	*							
		Neustrelitz	*							
		Güstrow	NS							
		Nedlitz	NS							
		Joachimsthal	NS							
42.	Stem form	Rövershagen	NS	**						
		Neustrelitz	NS	NS						
		Güstrow	NS	NS						
		Nedlitz	NS	NS						
		Joachimsthal	NS	NS						
43.	Crown length	Rövershagen	NS	NS	**					
		Neustrelitz	NS	*	NS					
		Güstrow	NS	NS	NS					
		Nedlitz	***	*	NS					
		Joachimsthal	***	NS	NS					
44.	Clear-stem length	Rövershagen	NS	-*	NS	NS				
		Neustrelitz	NS	NS	NS	NS				
		Güstrow	NS	NS	NS	NS				
		Nedlitz	NS	NS	NS	NS				
		Joachimsthal	NS	NS	NS	NS				
45.	Crown diameter	Rövershagen	NS	***	**	*	-**			
		Neustrelitz	NS	**	NS	NS	NS			
		Güstrow	NS	*	NS	NS	NS			
		Nedlitz	NS	**	NS	NS	NS			
		Joachimsthal	NS	*	NS	NS	-*			
46.	Crown flattening	Rövershagen	NS	**	NS	**	-*	***		
		Neustrelitz	NS	NS	NS	NS	NS	***		
		Güstrow	NS	**	NS	NS	NS	***		
		Nedlitz	NS	**	NS	NS	NS	***		
		Joachimsthal	NS	**	NS	NS	NS	**		
47.	Crown shape	Rövershagen	NS	NS	NS	*	-*	NS	*	
		Neustrelitz	NS	NS	NS	*	-*	NS	*	
		Güstrow	NS	NS	NS	NS	NS	NS	NS	
		Nedlitz	NS	NS	NS	NS	NS	NS	NS	
		Joachimsthal	NS	NS	NS	NS	NS	NS	NS	
48.	Foliage condition	Rövershagen	NS	NS	NS	NS	NS	NS	NS	NS
		Neustrelitz	NS	NS	NS	NS	NS	NS	NS	NS
		Güstrow	NS	NS	NS	NS	NS	NS	NS	NS
		Nedlitz	NS	NS	NS	*	NS	NS	NS	NS
		Joachimsthal	NS	NS	NS	NS	NS	NS	NS	NS

Stand	Correlations greater than r = .444
Rövershagen	15
Neustrelitz	7
Güstrow	3
Nedlitz	6
Joachimsthal	5
Total	36

There was nothing in the origin data to account for the greater amount of intercorrelation in the Rövershagen stand. Nor was it accounted for by a greater range of variability in the measured traits; the other stands were just as variable.

Bole diameter, crown diameter, and crown flattening were strongly inter-correlated in each of the five stands. Trees with large boles had large-diameter crowns which tended to be flat rather than pointed. These relations probably reflect cause-and-effect relationships. The large crowns are needed for rapid diameter growth. Also, large crowns are a sign of approaching maturity which is heralded by a flattening of the crown.

Crown length was strongly correlated with total height in two stands. It was weakly correlated with bole and crown diameter, stem form, crown flattening, crown shape, and foliage condition in one or two stands.

In the Rövershagen stand, length of clear stem was inversely correlated with bole and crown diameter, crown pointedness, and greater crown growth on one side than on the other.

Total height and diameter were weakly correlated in two stands, and were not correlated in the other three. This is contrary to what would normally be expected. It indicates that the seed collectors may have tried to select unusual trees which departed from the normal behavior pattern.

These results for the five German stands are in partial agreement with the results of previous investigators. Zieger (1928) (cited in Spurr (1948)), working with Scotch pine, found bole and crown diameter to be strongly correlated. Ilvessala (1950) (cited in Spurr (1960)), also working with Scotch pine, found that bole diameter could be estimated from crown length and total height. The standard error of estimate was about 10 per cent, less than if only one variable was used in the regression. Willingham (1951), working with longleaf pine (*P. palustris* Mill.) found a significant simple correlation ($r = .51$) between total height and bole diameter. The correlation was much stronger ($r = .82$) if bole diameter was treated as a function of two independent variables--total height and crown diameter.

Data from 9 parent trees in two Belgian stands and from 10 parent trees in the Norwegian stand were available for analysis. In each case, the trees were of differing ages so that the ratio $\frac{\text{total height}}{\text{age}}$ (character 50) was considered as a measure of height growth rate. Correlations were calculated between total height, height growth rate, bole diameter, and age for the Belgian material; between total height, length of clear stem, age, and height growth rate for the Norwegian material. None were significant, probably because of the smallness of the samples.

What do these correlations mean in terms of plus-tree selection? Most of the answers must, of course, be applicable to the German stands for which the most data are available. First, there was a high loading of bole diameter, crown diameter, and crown flattening with a common diameter-growth or maturity factor. Selection for any one of the three characters would mean selection for that factor and the other two characters. In these five stands it would not be advisable to select for large diameters and pointed crowns. Second, there were several inter-correlations in the Rövershagen stand so that selection for greater bole diameter would be accompanied by selection for greater total height and less clear bole length. Selection for greater crown diameter would also be accompanied by selection for greater bole diameter, fewer stem crooks, greater live-crown length, less clear stem length, and greater crown flattening. Regardless of whether or not these relationships had a common causal factor, they are present in that particular stand. Attempts to reverse the selection trend against one of the associated characters would be successful only if a very large number of trees were sampled.

Third, in the other four stands there were relatively few inter-correlations. This means that in them selection for one trait will have relatively little effect on other characters.

The presence of significant correlations is sometimes interpreted as favoring indirect selection, for example selection for large diameter to achieve a gain in height growth. When practicing such selection, the rate of progress in the correlated character is r^2 (r^2 = coefficient of determination) as great in the correlated character as in the character for which selection is practiced. For the five German stands, the frequency of coefficients of determination was a follows:

Number of correlations	Range of r^2
145	below .2
11	.2 to .3
10	.3 to .4
6	.4 to .5
3	.5 to .6
3	.6 to .7
2	.7 to .8
0	.8 to 1.0

Thus there were 7 cases in which 50 per cent as much progress could be expected by indirect as direct selection. Progress by indirect selection would be very slow (less than 20 per cent of maximum) in 145 cases.

Parent-Progeny Correlations

The most impressive fact obtained from this portion of the individual tree study is the exceptionally low number of correlations between parental and progeny characters and the complete lack of a pattern in the correlations. In considering the 11 parental characters (only 4 for the Belgian and Norwegian stands) and the 20 progeny characters for the 7 stands under consideration there were 1,260 possible simple correlations (Tables 9-15). The actual and expected correlations significant at various levels were as shown on page 90.

Table 9.--Parent-progeny and progeny-progeny correlations for nine Belgian trees from two stands. Only characters involved in one or more significant correlations are included. [a]

	PROGENY CHARACTERS													
	5 Seed weight	6 Seed length	7 Height age 1	8 Height age 2	9 Leaf color 6/59	15 Leaf color 11/60	16 Leaf color 12/60	18 Bud color	19 Time of bud set	21 Bud diam. 5/60	23 Branched buds 10/60	26 Primary lvs. 5/60	27 Presence secondary lvs. 9/59	28 Presence secondary lvs. 10/59
PARENTAL CHARACTER														
40. Total height	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS
PROGENY CHARACTERS														
6. Seed length	**	--	--	--	--	--	--	--	--	--	--	--	--	--
12. Leaf color 10/59	NS	NS	NS	NS	*	--	--	--	--	--	--	--	--	--
15. Leaf color 11/60	*	NS	NS	NS	NS	--	--	--	--	--	--	--	--	--
16. Leaf color 12/60	*	NS	NS	NS	NS	*	--	--	--	--	--	--	--	--
18. Bud color 9/59	NS	NS	*	NS	NS	NS	-*	--	--	--	--	--	--	--
19. Time of bud set	NS	NS	NS	NS	NS	NS	NS	**	--	--	--	--	--	--
21. Bud diameter 5/60	NS	NS	*	NS	NS	NS	NS	NS	NS					
22. Br. buds 5/60	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	--	--	--	--
23. Br. buds 10/60	NS	*	NS	*	NS	NS	NS	NS	NS	NS	--	--	--	--
27. Sec. lvs. 9/59	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	--	--
28. Sec. lvs. 10/59	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-*	**	--
29. Leaf length	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
7/5. Height age 1 / Seed weight	-*	NS	*	NS	NS	NS	-*	*	-*	NS	NS	NS	NS	*

* r = greater than 0.67 needed for significance at 5 per cent level.

** r = greater than 0.80 needed for significance at 1 per cent level.

NS Correlation not significant

[a] Parents and progenies analyzed were numbers 286, 288, 292, 294, 297, 298, 301, 303, and 304.

Table 10.--Parent-progeny and progeny-progeny correlations for eight Norwegian trees from a natural stand in southern Norway. Only characters involved in one or more significant correlations are included.[(a)]

	PROGENY CHARACTERS											
	Seed weight	Seed length	Height age 1	Leaf color 9/59	Leaf color 10/59	Leaf color 8/60	Leaf color 11/60	Bud set 9/59	Bud diameter winter 59-60	Lateral buds 5/60	Presence secondary leaves 9/59	Presence secondary leaves 10/59
	5	6	7	11	12	13	15	19	21	22	27	28
PARENTAL CHARACTERS												
44. Clear length	NS	NS	NS	NS	NS	NS	NS	NS	NS	-**	NS	NS
50. Av. annual growth	NS	NS	NS	NS	NS	NS	NS	NS	NS	-*	NS	NS
PROGENY CHARACTERS												
6. Seed length	**	--	--	--	--	--	--	--	--	--	--	--
7. Height age 1	*	NS										
8. Height age 2	NS	NS	**	--	--	--	--	--	--	--	--	--
11. Leaf color 9/59	NS	NS	*	--	--	--	--	--	--	--	--	--
12. Leaf color 10/59	NS	NS	*	***	--	--	--	--	--	--	--	--
13. Leaf color 8/60	NS	NS	NS	*	NS	--	--	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	***	***	*	NS	--	--	--	--	--
27. Sec. lvs. 9/59	-*	-*	NS	NS	NS	NS	NS	NS	NS	NS	--	--
28. Sec. lvs. 10/59	NS	-*	NS	NS	NS	NS	NS	NS	-*	NS	*	--
29. Leaf length 8/60	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS
7/5. Height age 1 / Seed weight	-*	-**	NS	NS	NS	NS	-*	NS	NS	NS	*	*

* r = greater than 0.707 needed for significance at 5 per cent level.
** r = greater than 0.834 needed for significance at 1 per cent level.
*** r = greater than 0.925 needed for significance at 0.1 per cent level.
NS correlation not significant.

(a) Parents and progenies analyzed were numbers 275,276 and 278 through 283.

Table 11.--Parent-progeny and progeny-progeny correlations for 20 trees (Nos. 321 to 340) from an even-aged stand near Rövershagen, East Germany. Only characters involved in one or more significant correlations are included.

	PROGENY CHARACTERS										
	Seed weight	Seed length	Height age 1	Height age 2	Leaf color 6/59	Leaf color 8/60	Leaf color 11/60	Bud set 9/59	Bud diameter winter 59-60	Lateral Buds 5/60	Presence primary leaves 5/60
	5	6	7	8	9	13	15	19	21	22	26
PARENTAL CHARACTERS											
40. Total height	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS
44. Clear length	NS	NS	NS	NS	NS	NS	NS	-**	NS	**	-*
47. Crown form	NS	-*	NS	NS	NS	NS	NS	NS	NS	NS	NS
PROGENY CHARACTERS											
6. Seed length	**	--	--	--	--	--	--	--	--	--	--
7. Height age 1	***	NS	--	--	--	--	--	--	--	--	--
8. Height age 2	**	NS	*	--	--	--	--	--	--	--	--
13. Leaf color 8/60	NS	NS	NS	*	NS	--	--	--	--	--	--
15. Leaf color 11/60	NS	NS	NS	NS	NS	**	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	NS	NS	*	***	--	--	--	--
21. Bud diam. 5/60	NS	NS	*	NS	NS	NS	NS	NS	--	--	--
22. Br. buds 5/60	NS	NS	*	NS	NS	NS	NS	-**	*	--	--
23. Br. buds 10/60	NS	NS	NS	NS	**	NS	NS	NS	NS	NS	--
26. Primary lvs. 5/60	NS	NS	NS	NS	NS	NS	NS	**	NS	-*	--
28. Sec. lvs. 10/59	NS	NS	NS	NS	NS	NS	NS	-*	NS	NS	-**
7/5. Height age 1 / Seed weight	-***	-*	NS	NS	NS	NS	NS	NS	NS	NS	NS

* r = greater than 0.44 needed for significance at 5 per cent level.
** r = greater than 0.56 needed for significance at 1 per cent level.
*** r = greater than 0.68 needed for significance at 0.1 per cent level.
NS Correlation not significant.

Table 12.--Parent-progeny and progeny-progeny correlations for 20 trees (Nos. 341 to 360) from an even-aged natural stand near Neustrelitz, East Germany. Only characters involved in one or more significant correlations are included.

	PROGENY CHARACTERS														
	Seed weight	Seed length	Height age 1	Height age 2	Leaf color 6/59	Leaf color 9/59	Leaf color 10/59	Leaf color 11/60	Bud set 9/59	Bud diameter winter 59-60	Lateral buds 5/60	Branched buds 10/60	Presence primary leaves 5/60	Presence secondary leaves 9/59	Presence secondary leaves 10/59
	5	6	7	8	9	11	12	15	19	21	22	23	26	27	28
PARENTAL CHARACTERS															
40. Total height	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-***	NS
41. Diameter	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	*	NS
42. Stem form	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-*
43. Crown length	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
44. Clear length	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	*	NS	NS	NS
47. Crown form	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS
48. Foliage condition	NS	NS	NS	NS	NS	NS	NS	-*	NS	NS	NS	NS	NS	NS	NS
PROGENY CHARACTERS															
7. Height age 1	*	NS	--	--	--	--	--	--	--	--	--	--	--	--	--
8. Height age 2	NS	NS	**	--	--	--	--	--	--	--	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	NS	NS	NS	NS	***	--	--	--	--	--	--	--
18. Bud color 5/60	NS	NS	NS	NS	-*	NS	NS	NS	--	--	--	--	--	--	--
19. Bud set 9/59	NS	NS	*	NS	NS	NS	NS	NS	--	--	--	--	--	--	--
21. Bud diam. 5/60	NS	NS	NS	*	NS	NS	NS	NS	NS	--	--	--	--	--	--
22. Br. buds 5/60	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	--	--	--	--	--
26. Prim. lvs. 5/60	-*	NS	NS	NS	NS	NS	NS	-*	*	-*	-*	NS	--	--	--
27. Sec. lvs. 9/59	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	--	--
28. Sec. lvs. 10/59	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS	-*	NS	--
7/5 Height age 1 / Seed weight	-***	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS	NS	NS	NS

*, **, *** = r greater than .44, .56, and .68 needed for significance at the 5, 1, and 0.1 levels respectively.

Table 13.--Parent-progeny and progeny-progeny correlations for 20 trees (Nos. 361-380) from an even-aged stand near Güstrow, East Germany. Only characters involved in one or more significant correlations are included.

	PROGENY CHARACTERS										
	Seed weight	Seed length	Height age 1	Height age 2	Leaf color 9/59	Leaf color 10/59	Leaf color 11/60	Leaf color 12/60	Bud set 9/59	Presence primary leaves 5/60	Presence secondary leaves 10/59
	5	6	7	8	11	12	15	16	19	26	28
PARENTAL CHARACTERS											
44. Clear length	NS	NS	NS	NS	NS	NS	NS	**	NS	NS	NS
45. Crown diameter	NS	NS	NS	NS	NS	NS	NS	NS	*	**	NS
PROGENY CHARACTERS											
6. Seed length	***	--	--	--	--	--	--	--	--	--	--
7. Height age 1	***	**	--	--	--	--	--	--	--	--	--
8. Height age 2	*	*	**	--	--	--	--	--	--	--	--
11. Leaf color 9/59	NS	-**	-**	NS	--	--	--	--	--	--	--
12. Leaf color 10/59	-*	-*	NS	NS	**	--	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	-**	NS	NS	NS	--	--	--	--
19. Bud set 9/59	-*	-***	-***	NS	***	*	NS	NS	--	--	--
22. Br. buds 5/60	NS	NS	NS	NS	NS	NS	NS	NS	-*	--	--
26. Prim. lvs. 5/60	NS	NS	NS	NS	**	NS	NS	NS	***	--	--
27. Sec. lvs. 9/59	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	--
28. Sec. lvs. 10/59	NS	NS	NS	NS	NS	NS	NS	NS	NS	-*	--
29. Leaf length 8/60	NS	NS	NS	NS	NS	**	NS	NS	NS	NS	NS
7/5. Height age 1 / Seed weight	-***	-**	NS	NS	NS	NS	NS	NS	NS	NS	*

* r = greater than 0.44 needed for significance at 5 per cent level.
** r = greater than 0.56 needed for significance at 1 per cent level.
*** r = greater than 0.68 needed for significance at 0.1 per cent level.
NS correlation not significant.

Table 14.--Parent-progeny and progeny-progeny correlations for 20 trees (Nos. 381 to 400) from an even-aged stand near Nedlitz, East Germany. Only characters involved in one or more significant correlations are included.

	PROGENY CHARACTERS								
	Seed weight	Height age 1	Leaf color 9/59	Leaf color 11/60	Leaf color 12/60	Bud set 9/59	Presence secondary leaves 9/59	Presence secondary leaves 10/59	Height age 1 / Seed weight
	5	7	11	15	16	19	27	28	7/5
PARENTAL CHARACTERS									
41. Diameter	NS	NS	NS	NS	NS	NS	NS	*	NS
43. Crown length	NS	NS	-*	NS	NS	NS	*	NS	NS
45. Crown diameter	NS	*	NS	NS	NS	NS	NS	NS	NS
46. Crown flattening	NS	NS	NS	NS	NS	NS	NS	NS	-*
PROGENY CHARACTERS									
6. Seed length	*	--	--	--	--	--	--	--	--
8. Height age 2	NS	NS	***	--	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	**	--	--	--	--	--
19. Bud set 9/59	NS	NS	NS	*	NS	--	--	--	--
22. Br. buds 5/60	NS	*	NS	NS	-*	NS	--	--	--
28. Sec. lvs. 10/59	NS	NS	NS	NS	NS	-**	*	--	--
29. Leaf length 8/60	NS	*	NS	NS	NS	NS	NS	NS	--
7/5. Height age 1 / Seed weight	-***	**	NS	NS	NS	NS	NS	NS	--

* r = greater than 0.44 needed for significance at 5 per cent level.
** r = greater than 0.56 needed for significance at 1 per cent level.
*** r = greater than 0.68 needed for significance at 0.1 per cent level.
NS Correlations not significant.

Table 15.--Parent-progeny and progeny-progeny correlations for 20 trees (Nos. 501 to 520) from an even-aged stand near Joachimsthal, East Germany. Only characters involved in one or more significant correlations are included.

	PROGENY CHARACTERS											
	Seed weight	Seed length	Height age 1	Leaf color 9/59	Leaf color 10/59	Leaf color 11/60	Leaf color 12/60	Bud set 9/59	Lateral buds 5/60	Presence secondary leaves 9/59	Presence secondary leaves 10/59	Height age 1 / Seed weight
	5	6	7	11	12	15	16	19	22	27	28	7/5
PARENTAL CHARACTERS												
43. Crown length	**	NS	NS	NS	NS	-*	NS	NS	NS	NS	NS	-**
47. Crown form	NS	NS	NS	NS	NS	NS	NS	NS	-*	NS	NS	NS
48. Foliage condition	NS	NS	NS	NS	NS	NS	-*	NS	NS	NS	NS	NS
PROGENY CHARACTERS												
6. Seed length	**	--	--	--	--	--	--	--	--	--	--	--
8. Height age 2	NS	NS	***	--	--	--	--	--	--	--	--	--
15. Leaf color 11/60	NS	-*	NS	NS	NS	--	--	--	--	--	--	--
16. Leaf color 12/60	NS	NS	NS	*	NS	**	--	--	--	--	--	--
19. Bud set 9/59	NS	NS	NS	**	NS	*	NS	--	--	--	--	--
22. Br. buds 5/60	NS	NS	NS	NS	*	NS	NS	NS	--	--	--	--
26. Pri. Lvs. 5/60	NS	NS	NS	NS	NS	NS	NS	*	NS	--	--	--
29. Leaf length 8/60	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	--
7/5. Height age 1 / Seed weight	-***	-*	NS	NS	NS	NS	NS	NS	NS	NS	NS	--

* r = greater than 0.44 needed for significance at 5 per cent level.
** r = greater than 0.56 needed for significance at 1 per cent level.
*** r = greater than 0.68 needed for significance at 0.1 per cent level.
NS Correlation not significnat.

Significance level	0.1 per cent	1 per cent	5 per cent
Number of r's exceeding amount needed for significance			
Actual	1	7	35
Expected	1.26	12.6	63

Thus the actual numbers were considerably below expected numbers. In only one case (clear stem length of parent and lateral bud precence in progeny) were the same two characters significantly correlated in two stands. Even in this instance the direction of the correlation was reversed from one stand to the other.

The lack of a pattern in the parent-progeny correlations is due in part to the lack of comparable parental and progeny characters. For example, there was no <u>a priori</u> reason to believe that such mature-tree traits as crown length or crown diameter would be associated with the various juvenile traits which were measured. On the other hand, correlations were expected between parental growth rate (as measured by height or diameter) and progeny growth rate or between foliage condition in parents and leaf length in progeny.

Genotype-environmental interactions also explain part of the lack of correlations. The parents were grown in Europe under different conditions than those prevailing in the Michigan nursery where the progeny tests were conducted. Admittedly the range of genetic variability within a single stand is relatively small when compared with that in the species as a whole. It may be that this range is just about the same as that of the range of interaction between single genes and diverse environments.

Still a third factor may explain part of the lack of correlation. The parental stands had been managed from the silvicultural standpoint but contained a relatively large amount of environmentally induced variability. This fact, combined with the low selection differential which can be practiced within a single stand usually results in a low realized heritability.

This lack of correlations between parental growth characters and juvenile characters indicates that under the conditions of this test the use of such characters would be of little value in predicting the performance of the progeny. While this may be true for juvenile characters based on two years growth it is not necessarily true of characters based on later growth over a broader base of environmental reactions such as will be obtained from outplanting observations as the test progresses. There is also the possibility of a conscious or unintended bias in the selection of the parent trees. However, this would seem unlikely considering the paucity of correlations. A continuing study of environmental interactions in both parental and progeny stands may provide an answer to the value of parental observations in predicting juvenile performance.

Basically, this lack of parent-progeny correlations means that progeny testing in areas of intended introduction is a necessity if definitive results are to be obtained.

Past and recent research concerned with possible phenotypic correlations between single parents and their open-pollinated and grafted progeny has produced both negative and positive results as shown in the following literature review which has been grouped by species for convenience:

Scotch pine (Pinus sylvestris L.)--Rohmeder (1961) reviewed progeny tests made by the München Institut für Forstsamenkunde und Pflanzenzüchtung. The tests were designed to determine whether selection of Scotch pine mother trees having the highest volume content can lead to an increase in growth in the following generation. In no case was there a relation between the growth of the progeny groups and that of the mother-tree groups.

Schröck (1957) tested the open-pollinated progeny of a 19-year-old Scotch pine with "cone disease". He found great variation in vigor, growth habit, increment, foliage, form and size of cones, fertility and germination of seeds and cone production.

Ilmurzynski (1961) tested the open-pollinated offspring of three crown-habit forms of Scotch pine. The parents included 15 wolf trees, 16 slower growing trees and 15 fast growing trees with narrow compact crowns. He found that rapid growth is not necessarily connected with excessive branchiness.

Nilsson (1958) reported on 10- to 50-year-old progeny and clonal tests of Scotch pine in south central Sweden (Tatle 16). In test number 32 there were significant positive correlations ($r = .56$, $r = .58$) between the height-diameter ratios of 85-year-old Scotch pine mother trees and progeny height at ages 10 and 20 respectively, and a significant negative correlation ($r = -.43$) between mother tree volume and progeny height. Other correlations were not significant.

Rohmeder (1962) reported a test of smoke resistance (industrial waste gases) involving scions of 17 Scotch pines and 36 Norway spruces. The scions of selected Norway spruces could tolerate much higher smoke concentrations than could the controls. In Scotch pine the difference between selected and control scions was less.

Ericson (1962) reported a test of 60 selected Scotch pine trees and 441 of their grafted progeny in 2 clonal collections in Sweden. A significant correlation between wood density of the parent trees and the progeny was found. He concluded that it was possible to select trees with hereditary capacity for producing heavy wood.

Schütt (1957) found significant differences in the degree of attack among grafted progeny of Scotch pine parents selected for severe needle cast attack and progeny of parents selected for slight attack.

Simak and Gustafsson (1954) reported that in Scotch pine seed shape and seed details were distinct genotype properties unchanged by environment or stock material (for grafts) but that seed and seed wing color were not reliable. Their results were based on grafts from 6 selected mother trees in central and northern Sweden grown in one location.

Nilsson (1956) reported 1954 measurements of a Scotch pine experiment grafted in 1947. There was a slight positive ortet-ramet correlation for branch angle, branch thickness, height at the same

Table 16.--Parent-progeny and parent-ramet correlations reported by Nilsson (1958) for Scotch pine and Norway spruce tests in south-central Sweden.

Species	Test No.	Parent trees	Age of Parents	Age of Progeny	Correlations of progeny height with Parental volume r	Parental volume P	Parental Ht./Diam. ratio r	Parental Ht./Diam. ratio P.
		number	--years--		r	P	r	P.
CORRELATIONS BETWEEN PARENTS AND OPEN-POLLINATED PROGENIES								
Scotch pine	32	19	85	10	-.43	.05	.56	.01
	32	19	85	20	-.38	.2	.58	.01
	9	13	170	13	-.01	1.0	.14	.4
Norway spruce	25	25	110	10	.08	.7	.15	.7
	25	25	110	20	.05	.8	.20	.4
	25	25	110	50	.17	.5	.23	.3
	8	25	114	13	-.24	.3	.35	.05
	19	22	112	12	-.11	.6	.18	.4
	18	14	112	12	-.11	.7	.49	.05
CORRELATIONS BETWEEN ORTETS AND RAMETS								
Scotch pine	28	19	104	7	--	--	.44	.1
	28	19	104	7	-.25	.3	.36	.2

P = probability that r does not differ from zero.

diameter, and height in relation to branch angle and a slight non-significant negative correlation for volume between clone material and parent tree.

Western white pine (Pinus monticola Dougl.)--Bingham et al. (1960) found that the correlation between open-pollinated progenies and parents was not significant in a replicated test for blister rust resistance. They suggested that the greater variability found in open-pollinated progenies requires that tests include 3 or 4 times as many progenies as were used.

Loblolly pine (Pinus taeda L.)--Van Buijtenen (1962) assessed a 5-year-old, 17-parent, open-pollinated progeny replicated test in Texas and found no significant correlations in height or diameter. However, he did find a significant correlation (r = .84) in wood specific gravity.

Minckler (1942), in summarizing the results of a replicated progeny test of 200 loblolly pine trees selected from 33 stands in South Carolina, reported no correlation between height growth or survival and any observable characteristic of mother trees including the growth of parents in the last 5 and 10 years. However, highly significant differences were found between progenies of different mother trees.

Slash pine (Pinus elliottii Engelm.)--Jackson and Greene (1957) made an analysis of tracheid length for 7 slash pine parents and ten 1-year-old seedlings of each. There was a slight positive parent-progeny correlation which was not significant statistically. Echols (1955) also studied tracheid length. He found large differences among control-pollinated progenies but slight differences among open-pollinated progenies. Barber et al. (1955) studied crown width in Georgia. The ratio $\frac{\text{crown width}}{\text{total height}}$ for the progeny of five narrow-crowned, two broad-crowned, and unselected mother trees was .42, .55, and .52 respectively. Barber (1961) found that bulk progenies of crooked parents had a higher-than-average per cent of crooked stems.

Zobel et al. (1962) reported in a study of wood properties based on samples from a 1955 slash pine grafted clone seed orchard with cuttings made in 1961. The original scions were from parent trees in South Carolina, southern Georgia and northern Florida. An r of .276 was obtained for parent-graft specific gravity. The values of r were .064 and .117 respectively for the tracheid lengths from the third annual ring of the grafts compared with the 15th and 30th annual ring of the parent trees. All of these are non-significant.

McWilliams and Florence (1955) summarized tests started in 1942 and 1946 in the Beerwah District of Queensland. By restricting seed collections to trees selected for vigor and straightness a 100 per cent increase in the number of acceptable stems per acre was obtained. In a companion 2-parent test the number of acceptable stems and plus stems obtained were respectively 4 and 25 times as great as from unselected parents.

Eastern white pine (Pinus strobus L.)--Riker et al. (1943) reported no significant difference between open-pollinated off-spring of 163 parents which had been carefully selected for blister rust resistance and the offspring of average parents.

Norway spruce (Picea abies (L.) Karst.)--Ruden (1963) tested seeds from 83 selected Norway spruce trees in southeastern and western Norway and 5 commercial sources in a replicated nursery and outplanting experiment. At the end of 11 years the offspring of selected trees were 30 per cent taller than the commercial sources. Nilsson (1958) in reporting on 10- to 50-year-old 1-parent progeny tests in south central Sweden (Table 16) found significant correlations (r = .49 and r = .35) between the height-diameter ratio of parents and height of progenies in 2 of 6 cases. Rohmeder (1962) reported that the scions of 36 smoke-resistant trees were more resistant than the scions of controls.

Black wattle (Acacia mearnsii De Wild.)--Moffet and Nixon (1963) evaluated diameter, bark thickness, and tannin in two open-pollinated replicated progeny trials in the Union of South Africa. One test was started in 1952 with 21 parents; the other in 1955 with 49 parents. Only in the per cent tannin could phenotypic selection produce enough gain to be economically worthwhile.

Chamaecyparis obtusa Endl.--Miyajima (1962) found that parental diameter growth was the best but not totally reliable criterion of clonal performance.

Monterey pine (Pinus radiata D. Don)--Fielding and Brown (1960) found no connection between wood density and any morphological characteristic of the tree in a test involving 6-year-old progeny of 14 parents.

In general the literature cited indicates that previous attempts to find correlations between characteristics of single-parents and their progeny have been largely unsuccessful when concerned with such favorable characteristics of trees as growth rate, volume, survival, resistance to disease and pollution, and wood properties. In most instances some morphological or anatomical character or group of characters was studied in an effort to find a means of predicting progeny performance in either the same or a supposedly related characteristic as in this study. Too little is known at this time of the dependence or independence of the various characteristics studied or of the effects of genotype-environment interactions.

In a breeding program involving single-tree selection one should presumably treat each character independently and not expect selection for one trait to give a response in another. The present data indicates that little can be done to better juvenile performance in Michigan by rigorous parental selection in Europe. Although the review of literature shows several significant parent-progeny correlations there were even more cases in which such correlations did not seem to be present. Evidently they are not to be assumed in any specific case without experimental evidence. In other words a breeding program should be based on progeny testing.

Progeny-Progeny Correlations

A total of 1330 (=20·19·7/2) simple correlations were computed among the characters studied in progeny from seven stands;

the correlations were calculated separately from each stand. Those which were statistically significant at the 5 per cent level or greater are shown in Tables 9 to 15. The actual and expected numbers of cases which were significant at the various levels are as follows:

	Significance Level		
	0.1 per cent	1 per cent	5 per cent
Value of r needed	.68	.56	.44
Number of r's exceeding amount needed			
Actual	18	49	128
Expected	1.3	13.3	66.5

It can be seen that about half of the "statistically significant" correlations are biolobically meaningless. Presumably these include the many instances in which a relationship was evident in only one stand or in which the direction of the relationship was reversed between stands.

The most consistent trends involved measurement of the same character at different times or in different ways. They are therefore to be considered as measures of repeatability or experimental procedure. Among them are:

Seed weight and seed length (significant for 6 of 7 stands).

Seed weight and 1-year height (4 of 7 stands).

Seed weight and 2-year height (2 of 7 stands).

1-year height and 2-year height (6 of 7 stands).

Color in November and December, 1960 (6 of 7 stands).

Early bud set and continued presence of primary leaves (4 of 7 stands).

Late absence of primary leaves and early presence of secondary leaves (4 of 7 stands).

Presence of secondary leaves in two successive months (3 of 7 stands).

Ratio $\frac{\text{1-year height}}{\text{seed weight}}$ and 1-year height or seed weight (4 of 7 stands and 7 of 7 stands).

The relationship between more secondary leaves late the first season, and a high ratio $\frac{\text{1-year height}}{\text{seed weight}}$ deserves more attention. This high ratio presumably means a rapid mid-season or late season growth rate. A high late-season growth rate does not fit with early maturity. Hence a high ratio may be inferred as indicative of a high mid-season rate.

The two summer color scoring (characters 9 and 13) were not correlated with each other or with scorings made in late autumn, indicating that different genes are involved. First-year autumn color was not correlated with autumn color in the second-year and succeeding-years. During the first year trees change from green to maroon with the onset of winter, presumably as the result of development of anthocyanins. In later years a yellow color develops, partly as a result of loss of chlorophyll and partly as a result of the development of carotenoids (Gerhold, 1959). The lack of within-stand correlation indicates that the reddening and yellowing are basically different processes.

Several inferences may be made from the relative lack of correlation. First, such traits as color, height, and time of bud set seem to have basically different physiological mechanisms. Second, there seems to have been little or no linkage between these physiologically different traits. If there were linkage, we should expect instances in which a relationship was evident in several stands and reversed in others. Third, in stand 361-380 from Güstrow, there was an unexpectedly large number of unexplained "significant" correlations. This could happen if several parents were traceable to a common maternal grandparent and if others were traceable to another maternal grandparent. This phenomenon was not noticeable in the other stands, indicating that the parents were random samples of the entire stands and that there was panmixia within each stand.

CHAPTER VI

CORRELATIONS INVOLVING PARENTAL CHARACTERISTICS

Materials and Methods

The 19 parental characters measured (Table 6) on the cone, seed, and leaf specimens of the 39 parental stands of Scotch pine sampled were analyzed to determine the correlations existing within the stands, between stands, between regions, and within major area groupings of regions.

The individual tree means, stand means, regional means, and area means were entered on punch cards and processed through the Controlled Data Corporation 3600 computer on a correlation program as individual problems designed to arrive at the correlations applicable to the various means.

The analysis of the 39 stand means resulted in a considerable number of nonsense correlations. There were 46 correlations significant at the 0.1 per cent level of significance out of a total of 171 combinations when the all stand means were analysed without stratification. In order to reduce the number of false correlations the stands were grouped into a northern area, regions A through G, and a southern area, regions J, K, M, N, and Turkey. The English and Scotch stands were grouped as a distinctive climatic area apart from the other two areas. While grouping by areas resulted in a reduction of the degrees of freedom the correlations obtained have a greater validity. The Great Britain area contained too few stands and their correlations are not included in this discussion. Further breakdown of the northern group would be desirable but impractical in view of the limited number of stands sampled. The southern area is essentially Mediterranean with some exceptions.

Correlations Within Stands

The within stand correlations were computed for all 39 stands. The results were combined and expressed as a percentage of the total number of possible correlations (39) that were significant at the five per cent level of significance (Table 17). In this analysis the actual and expected number of correlations were as follows:

	Significance Level 5 per cent
Value of r needed (37 d.f.)	.332
Number of r's exceeding amount needed	
Actual	1181.
Expected (5,051 combinations, all characters not measured in all stands)	253.

It can be seen that approximately 21 per cent of the correlations are probably biologically meaningless.

Expected high percentages of correlations were found between cone length and closed-cone width (90 per cent of the stands sampled), cone length and open-cone width (92 per cent), closed-cone width and apophysis width (64 per cent) and closed-cone width and apophysis thickness (67 per cent).

Characters P6 through P18 and P20 are physiologically related single measurements or ratios having to do with cone shape or size. A large number of significant correlations would be expected, and were obtained in most cases. The most noteworthy exceptions are furnished by apophysis width and the ratio cone length/closed-cone width. The percentage of stands in which those and other cone traits were correlated were relatively low, indicating that shape varied considerably.

Seed length and width might also be expected to vary consistently with cone or cone-scale size, as the result of nutrition. However, this was not usually the case. The highest seed-cone correlation (seed length-open-cone width) was significant in only 46 per cent of the stands sampled. Most other seed-cone correlations were evident in less than 25 per cent of the stands.

Leaf length was correlated with cone size in from 27 to 55 per cent of the stands. This is possibly the result of nutrition, the most vigorous trees tending to have large leaves as well as large cones. Correlations between leaf length and apophysis thickness were also large in a number of stands but were reversed in some cases. For the most part, other leaf and cone relationships were not significant.

These data indicate that in general it is best to consider leaf and cone traits which are not obviously related physiologically as separate entities when classifying or selecting individual trees within a stand. It is not wise to attempt to define a particular type of tree which can be recognized on the basis of one trait and have a definite combination of other traits. Nor would it be wise to rely heavily on strong correlation to effect improvement in a cone trait by indirect selection in another trait.

Correlations Between Widely Distributed Stands and Between Regions

Between-stand correlations in parental characters are presented in Table 18 for the species as a whole. For the analysis on which that table is based, the means for all 39 parental stands were used as items.

Of the 171 possible correlations, 48 or 27 per cent were significant at the 0.1 per cent level. Before discussing their biological significance, it is well to present the results of other analyses in which the data were grouped differently.

Table 19 is similar to Table 18 except that the data for the 39 stands were grouped into 10 regions of origin, and the regional means were used as items. Whereas the high correlation between cone length and closed-cone width (characters P6 and P7) in Table 18 should be interpreted as saying that "A stand with long cones also tends to have wide cones," the same high correlation in Table 19 should be interpreted as meaning "If a large region is characterized by long cones, trees from that region will also have broad cones."

The actual and expected numbers of significant correlations in Table 19 are as follows. The actual exceed the expected by large amounts, indicating that most of the correlations are real.

	Significance Level		
	0.1 Per cent	1 Per cent	2 Per cent
Value of r needed (8 d.f.)	.972	.765	.715
Number of r's exceeding amount needed			
Actual	6	35	57
Expected (171 combinations)	0.2	1.7	3.4

There is a similarity in general pattern between Tables 18 and 19. In approximately 82 per cent of the comparisons the significance relations are the same in both Tables. For example, cone length is strongly correlated with most other traits in both.

This similarity raised the possibility that many of the seemingly significant relations among stands were due to between-region differences and were not necessarily indicative of gradual trends or cause and effect relationships. That possibility was also suggested by the many discrepancies between the between-stand and within-stand correlation data presented in Table 17. For example, within two-thirds of the individual stands there was little relation between seed length and seed width, but Tables 18 and 19 indicate that stands or regions having long seeds also have wide seeds.

Correlations Between Stands Within Regions

Of greater meaning than anlyses of unstratified data are analyses which show the relationship between stands from similar areas of origin. Table 20 and 21 present the significant correlations when the data are so analyzed. The actual and expected numbers of significant relationships for the 19 northern stands (regions A, C, and G) are as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (17 d.f.)	.693	.575	.456
Number of r's exceeding amount needed			
Actual	9	19	35
Expected (171 combinations)	0.2	1.7	8.5

For the 14 southern stands (regions J, K, M, N, and Turkey), the actual and expected numbers are as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (12 d.f.)	.780	.661	.532
Number of r's exceeding amount needed			
Actual	7	18	35
Expected (171 combinations)	0.2	1.7	8.5

Although both Table 20 and 21 contain 35 significant correlations at the five per cent level of significance or higher the correlations are distributed differently. Cone length, cone width, and length of apophysis are still highly correlated. The basal angle of the cone (Figure 10) which was not correlated with any other cone character in the northern region was negatively correlated with apophysis thickness in the southern region (r = -.77) indicating that the thicker apophyses on the cones in the southern area resulted in a greater opening of the cones and more rapid dissemination of the enclosed seed.

Seed width was very highly significantly correlated with seed length (r = .85) in the northern area, but the value of r in the southern area was only .57 indicating a change in seed shape. This was noted during measurement as a change from angular to a fully rounded seed. In the southern area seed length was correlated with the width of the open cone and with apophysis length, but in the northern region the only correlation with a basic cone-scale measurement was a negative one with apophysis thickness.

In the northern area there was no correlation between the form of the cone (cone length/open-cone width) and the form of the apophysis (length/width) while in the southern area they were negatively correlated with an r of -.76.

These basic form and measurement differences between the two areas represent changes resulting from differing environments and selection pressures. Greater protection of the seed in the cone and larger seed with greater food storage would be expected in areas where growing season environment was less favorable as in a Mediteranean type climate as compared to the moist cool summers of the northern areas.

Discussion

Comparisons among Tables 17 through 21 show that correlations are strictly applicable only to the data from which they were calculated. They must be interpreted accordingly. Relations which are evident when one compares trees from very different regions are not necessarily applicable to stands within a limited area or to the individual trees within a stand.

Certain relationships are strong no matter how a comparison is made. Cone length and width are highly correlated when one considers individual trees within stands. This is also true when comparing stands or regions. This means that variations in the shape or length-width ratio are relatively minor.

In most of the individual stands and in comparisons involving stands within limited areas there was a high degree of relationship between apophysis size (length, width, or thickness) and cone width or cone length. This means in effect that cone size is governed more by size than number of cone scales.

It has already been intimated that the mere presence of a correlation may have little biological meaning. That appears to be the case in the relationships involving basal angle of the open cone. If one considers all stands (Table 18) or region means (Table 19), there are statistically significant negative correlations with cone width and apophysis thickness. Those trends are not evident within stands (Table 17) or between stands from the north (Table 20) or from the south (Table 21). They are apparently due to the fact that northern and southern trees happen to differ enough in the different traits to make the correlation large automatically if unstratified data are analyzed together.

Belonging to the same category are most of the relationships involving seed length or width and cone size or cone-scale size. As regards the southern population only there is a discernible trend for stands with long seeds to have narrow cones of thin cone scales. Possible biological importance of this was mentioned previously. That trend is not evident within single stands or within the northern population, so should probably not be interpreted as a cause-and-effect relationship.

Table 17.--Correlations of parental characters within 39 stands, expressed as the per cent of stands in which r exceeds the amount needed for significance at the 5 per cent level. Negative correlations are preceded by a minus sign.

Character Number	Cone length P6	Closed-cone width P7	Open-cone width P8	Length largest apophysis P12	Width largest apophysis P13	Thickness largest apophysis P14	Thickness of opposite apophysis P17	Basal angle of open cone P19	Seed length P28	Seed width P29	Leaf length P35	Leaf twist P38	Cone length/Closed-cone width P9	Cone length/Open-cone width P10	Length largest apophysis/Width largest apophysis P15	Length largest apophysis/Thickness largest apophysis P16	Thickness largest apophysis/Thickness opposite apophysis P18	Cone length/Length largest apophysis P20	Seed length/Seed width P30
P7	90																		
P8	92	82																	
P12	49	20	41																
P13	54	64	36	39															
P14	54	67	31	26	3														
P17	23	39	20	20	7	74													
P19	20[a]	-13	-36	7	-10	5[a]	0												
P28	39	29	46	25	11	11	7	4											
P29	14	25	11	4	18	7[a]	0	4	32										
P35	27	55	36	9	9	46[a]	46[a]	0	9	18									
P38	18[a]	-9	-9	9	9	0	0	0	0	0	36								
P9	59	-13	18	18	5	5[a]	13[a]	15[a]	7[a]	7[a]	9	0							
P10	39	10	18[a]	10[a]	31	13[a]	13[a]	33	7[a]	4	9	0	51						
P15	7	7[a]	10[a]	74	-51	10	7	5	7	-7	0	18	18	15[a]					
P16	15[a]	-44	10[a]	23	3	-92	-56	5	-4	7[a]	18	18	20	3	18[a]				
P18	7[a]	18	13[a]	7	-7	64	26	10[a]	0	0	9	0	-5	13[a]	20	-54			
P20	75	50	43	-75	14	14	11	-18	7	4	0	18[a]	29[a]	36	-82	-64	18[a]		
P30	21	7	14	7	4	11	-4	4	61	-32	9	0	11	7[a]	18	0	4	7[a]	

[a]The correlations were of the sign shown in most stands. However, there were 1 or 2 stands in which the direction of the correlation was reversed.

Table 18.--Significant between stand correlations for 19 parental characters using stand means of 39 parental stands.

Character Number	P6 Cone length	P7 Closed-cone width	P8 Open-cone width	P12 Length largest apophysis	P13 Width largest apophysis	P14 Thickness largest apophysis	P17 Thickness of opposite apophysis	P19 Basal angle of open cone	P28 Seed length	P29 Seed width	P35 Leaf length	P38 Leaf twist	P9 Cone length / Closed-cone width	P10 Cone length / Open-cone width	P15 Apophysis length / Apophysis width	P16 Apophysis length / Apophysis thickness	P18 Apophysis thickness / Thickness of opposite apophysis	P20 Cone length / Apophysis length
P7	***																	
P8	***	***																
P12	**	**	***															
P13	***	***	***	**														
P14	***	***	***	NS	***													
P17	***	***	***	NS	***	***												
P19	NS	-*	-**	NS	NS	-**	-**											
P28	***	***	***	NS	***	**	***	-**										
P29	***	***	***	NS	**	**	**	-**	***									
P35	**	**	*	NS	NS	NS	NS	NS	NS	NS								
P38	NS	NS	NS	NS	NS	NS	NS	-**	NS	NS	NS							
P9	***	NS	**	NS	**	NS	NS	NS	*	NS	**	NS						
P10	*	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	NS	**					
P15	-**	-**	NS	NS	-***	NS	-***	NS	-***	-**	NS	NS	NS	-***				
P16	-**	-***	-**	NS	NS	-***	-***	***	*	NS	NS	NS	NS	NS	***			
P18	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-**	NS		
P20	***	***	***	NS	***	***	***	-***	***	***	*	NS	**	***	-***	-***	NS	
P30 Seed length / Seed width	NS	NS	NS	NS	**	NS	NS	NS	***	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS Non-significant correlation.
\- Negative correlation.
* r = .377 significant at the 5 per cent level of significance.
** r = .410 significant at the 1 per cent level of significance.
*** r = .508 significant at the 0.1 per cent level of significance.

Table 19.--Significant between region correlations for 19 parental characters using regional means for the 10 regions, A, C G, H, I, J, K, L, M, and N (see Table 4).

Character Number	P6 Cone length	P7 Closed-cone width	P8 Open-cone width	P12 Length largest apophysis	P13 Width largest apophysis	P14 Thickness largest apophysis	P17 Thickness of opposite apophysis	P19 Basal angle of open cone	P28 Seed length	P29 Seed width	P35 Leaf length	P38 Leaf twist	P9 Cone length / Closed-cone width	P10 Cone length / Open-cone width	P15 Apophysis length / Apophysis width	P16 Apophysis length / Apophysis thickness	P18 Apophysis thickness / Thickness of opposite apophysis	P20 Cone length / Apophysis length	P30 Seed length / Seed width
P7	***																		
P8	***	***																	
P12	*	*	*																
P13	**	**	**	*															
P14	**	**	**	NS	NS														
P17	**	**	**	NS	*	***													
P19	NS	NS	NS	NS	NS	-*	-*												
P28	**	**	**	NS	**	NS	**	NS											
P29	**	**	**	NS	*	NS	*	NS	***										
P35	*	*	NS	NS	NS	NS	NS	NS	NS	NS									
P38	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS								
P9	***	**	**	*	**	NS	NS	NS	*	NS	**	NS							
P10	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS						
P15	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-*	NS	-*					
P16	NS	NS	NS	NS	NS	-**	-**	**	NS	NS	NS	NS	NS	NS	NS				
P18	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS			
P20	**	**	**	NS	*	*	**	NS	**	*	*	NS	-*	NS	-*	-*	NS		
P30	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	

NS Non-significant correlations.
\- Negative correlation.
* r = .715 significant at the 2 per cent level of significance.
** r = .765 significant at the 1 per cent level of significance.
*** r = .972 significant at the 0.1 per cent level of significance.

Table 20.--Significant between-stand correlations for 19 parental characters using stand means for regions A, C, and G only.

Character Number	P6 Cone length	P7 Closed-cone width	P8 Open-cone width	P12 Length largest apophysis	P13 Width largest apophysis	P14 Thickness largest apophysis	P17 Thickness of opposite apophysis	P19 Basal angle of open cone	P28 Seed length	P29 Seed width	P35 Leaf length	P38 Leaf twist	P9 Cone length / Closed-cone width	P10 Cone length / Open-cone width	P15 Length largest apophysis / Width largest apophysis	P16 Length largest apophysis / Thickness largest apophysis	P18 Thickness largest apophysis / Thickness opposite apophysis	P20 Cone length / Length largest apophysis	P30 Seed length / Seed Width
P7	.91																		
P8	.83	.74																	
P12	.50	NS	.58																
P13	.75	.81	.72	.58															
P14	NS	.52	.64	.50	.52														
P17	NS	.54	.61	NS	.57	.84													
P19	NS	NS	NS	NS	NS	NS	NS												
P28	NS	NS	NS	-.49	NS	NS	NS	NS											
P29	NS	NS	NS	NS	NS	-.53	NS	NS	.85										
P35	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS									
P38	NS	NS	NS	NS	NS	NS	NS	-.59	57	NS	NS								
P9	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS							
P10	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS						
P15	NS	NS	NS	NS	-.48	NS	NS	NS	NS	-.57	-.53	NS	NS	NS					
P16	NS	NS	NS	NS	NS	-.89	-.84	NS	NS	NS	NS	NS	.54	NS	NS				
P18	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.60	NS			
P20	.51	.53	NS	NS	NS	NS	NS	NS	NS	.62	.62	NS	NS	.58	-.69	NS	NS		
P30	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.54	NS	NS	NS	NS	NS	NS	

NS Non-significant correlation.
r = .456, .575, and .693 for significance at the 5, 1, 0.1 per cent levels respectively.

Table 21.--Significant between-stand correlations for 19 parental characters using stand means for regions H, J, K, M, N, and Turkey.

Character Number	P6 Cone length	P7 Closed-cone width	P8 Open-cone width	P12 Length largest apophysis	P13 Width largest apophysis	P14 Thickness largest apophysis	P17 Thickness of opposite apophysis	P19 Basal angle of open cone	P28 Seed length	P29 Seed width	P35 Leaf length	P38 Leaf twist	P9 Cone length / Closed-cone width	P10 Cone length / Open-cone width	P15 Length largest apophysis / Width largest apophysis	P16 Length largest apophysis / Thickness opposite apophysis	P18 Thickness largest apophysis / Thickness opposite apophysis	P20 Cone length / Length largest apophysis	P30 Seed length / Seed width
P7	.83																		
P8	.90	.84																	
P12	NS	NS	.76																
P13	.60	NS	NS	NS															
P14	.70	.73	.61	NS	NS														
P17	NS	NS	NS	NS	NS	.73													
P19	NS	-.54	NS	NS	NS	-.77	-.72												
P28	NS	NS	.54	NS	NS	NS	NS	NS											
P29	NS	NS	.71	.55	NS	NS	NS	NS	.57										
P35	NS	NS	NS	NS	NS	NS	NS	NS	-.54	NS									
P38	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS								
P9	.54	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS							
P10	NS	NS	NS	-.70	NS	NS	NS	NS	NS	-.57	NS	NS	NS						
P15	NS	NS	NS	.81	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.76					
P16	NS	NS	NS	NS	NS	NS	-.79	.66	NS	NS	NS	NS	NS	-.56	.61				
P18	NS	NS	NS	.57	NS	NS	-.57	NS	NS	NS	NS	NS	NS	NS	.61	NS			
P20	NS	NS	NS	-.56	NS	NS	.57	NS	NS	NS	NS	NS	NS	.73	-.84	-.79	NS		
P30	NS	NS	NS	NS	NS	NS	NS	NS	.63	NS	NS	NS	NS	NS	NS	NS	NS	NS	

NS Non-significant correlation.

r = .532, .661, and .780 for significance at the 5, 1, and 0.1 per cent levels respectively.

CHAPTER VII

CORRELATIONS INVOLVING PARENTAL AND JUVENILE CHARACTERISTICS OF ENTIRE STANDS

Materials and Methods

The 19 parental characters measured on the cone, seed, and leaf specimens of 33 of the 39 parental stands of Scotch pine sampled were analyzed for simple correlations with 14 of the juvenile characters measured by Wright and Bull (1963) on the 122-origin replicated Scotch pine provenance test conducted at East Lansing, Michigan. Six of the parental stands sampled were not represented in the provenance test.

All data were entered on punch cards and processed through the Control Data Corporation 3600 computer at Michigan State University on a correlation-regression program.

The parental and juvenile data were grouped by areas of climatic similarity prior to analysis as follows:

Group 1 Regions A, C, G, and H (19 stands).

Group 2 Regions I and L (6 stands).

Group 3 Regions J, K, M, and N (8 stands).

Grouping in this manner reduced the degrees of freedom considerably, as compared with an analysis based on stands from the entire range. However, it had the advantage of eliminating the many meaningless correlations which almost always result when very diverse types of data are considered together.

The resulting correlations were assembled in Table 22, organized for ready comparison between the three area groupings. The most important fact presented was the failure of the correlations obtained to present a consistent pattern. The actual and expected numbers of significant correlations were as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed,			
group 1, 17 d.f.	.693	.575	.456
group 2, 4 d.f.	.974	.917	.811
group 3, 6 d.f.	.925	.834	.707
Number of r's exceeding amount needed			
Actual	25	102	190
Expected (912 combinations)	.9	9.1	45.5

It can be seen that 24 per cent of the correlations significant at the five per cent level of significance can be expected to be meaningless.

Discussion

Presumably the most meaningful correlations are those which were significant in all three areas (there are two examples of this, one involving a change in sign) or in two of the three areas. Thus there is strong evidence that stands having large seeds (characters P28, P29) produce progeny which are taller, greener in the winter, have longer needles, and produce buds later in the autumn. Also that stands with long needles (character P35) produce progeny which are taller at age 3 and which have longer needles. Or that stands in which the ratio cone length/apophysis length is high produce progeny which are greener in the autumn, have later bud formation, or produce longer needles. Note that it is the same progeny traits in each case, and that they are associated with rather diverse parental characters. This fact hints that there is not necessarily a direct cause-and-effect relationship between a given parental trait and its associated progeny trait. Rather, it is more likely that the evolutionary factors which resulted in smaller seeds or more slender cones in the far northern stands also resulted in earlier bud set, deeper yellow foliage, and shorter needles in the seedlings.

There are some instances in which the direction of a correlation is reversed between areas 1 (Scandinavia through Germany), 2 (Great Britain), and 3 (southern Europe). This certainly means that one cannot forecast for the entire species from a part, but it does not necessarily mean that the relationships are not valid for the respective areas. As already emphasized by Wright and Bull (1963), many progeny traits reach their highest development in the central portion of the species' range. For example, height growth and needle length of the progeny decrease as one proceeds outward from a center in northern France-Belgium-western Germany in almost any direction. That is not true for the parental traits, which vary in a more irregular manner. Hence the change in direction of relationship as one proceeds from northern to southern Europe.

Table 22.--Significant correlations between parental and juvenile characteristics within group 1, consisting of regions A, C, G, and H, group 2, consisting of regions I and L, and within group 3, consisting of regions J, K, M, and N, using stand means.

PARENTAL CHARACTER		REGIONS	Height, age 3 J34	Seed weight / Height, age 1 J7/5	Foliage color 9/59 J9	Foliage color 10/59 J12	Foliage color 8/60 J13	Foliage color 12/60 J16	Foliage color 12/61 J31	Earliness of color J20	Bud color J18	Date of bud formation J19	Initiation of Growth J17	Secondary leaf presence J27	Leaf length J29	Pullability J24
			JUVENILE CHARACTER													
P6	Cone length	A,C,G,H	NS	NS	NS	NS	NS	.53	NS	NS	NS	.47	NS	NS	.47	NS
		I & L	NS	NS	NS	.84	NS	NS	NS	NS	NS	.96	NS	NS	.96	NS
		J,K,M,N	NS	NS	NS	NS	.72	NS	NS	NS	NS	NS	.81	.79	NS	NS
P7	Closed-cone width	A,C,G,H	NS	NS	NS	NS	NS	.54	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	.87	NS	NS	.87	NS	NS	NS	NS	NS	.94	NS	NS	.94	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.71	-.73	NS
P8	Open-cone width	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	.84	NS	NS	.84	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.81	NS	NS	NS
P12	Length largest apophysis	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.94
P14	Thickness largest apophysis	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	.91	NS	NS	NS	NS
		J,K,M,N	-.77	NS	.91	NS	.83	.87	NS	NS	NS	NS	NS	.73	-.84	NS
P17	Thickness of opposite apophysis	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	.90	NS	.89	.90	.72	NS	NS	NS	.74	NS	NS	NS
P19	Basal angle of cone	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	-.81	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	.71	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.77	NS
P28	Seed length	A,C,G,H	.70	NS	-.69	.72	.71	.56	.61	.69	.62	.75	.68	.73	.74	NS
		I,L	.91	NS	NS	.88	NS	NS	NS	NS	NS	.86	NS	NS	.92	NS
		J,K,M,N	NS	-.72	.75	NS	NS	.76	NS	NS	NS	.79	.77	NS	NS	.77
P29	Seed width	A,C,G,H	.86	.50	-.74	.85	.89	.63	.75	.63	.61	.84	.86	.90	.84	-.58
		I,L	.92	NS	NS	.92	NS	NS	NS	NS	NS	.94	NS	NS	.91	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.77	NS	NS	NS
P35	Leaf length	A,C,G,H	.59	NS	NS	NS	.51	.63	.60	.51	NS	.62	.48	.52	.69	-.50
		I,L	.81	NS	NS	.86	NS	NS	-.82	NS	NS	.99	NS	NS	.94	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	-.86	NS	NS	NS	NS	NS	NS
P38	Leaf twist	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
P9	Cone length / Closed-cone width	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	.86	NS	NS	NS	NS	NS	NS	NS	NS	.83	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
P10	Cone length / Open-cone width	A,C,G,H	.64	NS	NS	.74	.60	.62	.54	.59	NS	.64	.63	.63	.54	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.80
P15	Apophysis ln. / Apo. width	A,C,G,H	-.57	NS	NS	-.60	-.58	-.55	-.53	NS	NS	-.56	-.62	-.57	-.51	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.71	NS	NS
P16	Apophysis ln. / Apo. thickness	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	.94	NS	-.86	NS	-.89	NS	NS	NS	NS	NS	-.74	-.76	.75	NS
P18	Apo. thickness / Apo. opposite thickness	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	-.71	-.85	NS	NS	NS	NS	NS
P20	Cone length / Apophysis length	A,C,G,H	.68	NS	-.46	.76	.61	.74	.65	.66	NS	.76	.62	.65	.69	NS
		I,L	.91	NS	NS	NS	NS	NS	NS	NS	NS	.89	NS	NS	.93	NS
		J,K,M,N	-.84	NS	NS	NS	.83	NS	NS	NS	NS	NS	.73	.89	NS	NS
P30	Seed length / Seed width	A,C,G,H	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		I,L	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
		J,K,M,N	NS	NS	NS	NS	NS	NS	NS	.74	NS	NS	NS	NS	NS	.71

Generally speaking, the parental characters of seed size, leaf length, and the ratio cone length/apophysis length were of the most value in forecasting progeny performance, but even with these care must be taken to apply the relationships only within an area within which they are presumed to be applicable. The other measured parental characteristics are of value in delimiting populations which are genetically different but not in telling how the seedlings grow.

CHAPTER VIII

CORRELATIONS INVOLVING CLIMATE

Materials and Methods

Meteorological data was obtained for the 121 origins represented in Wright and Bull's (1963) provenance test and for the parental specimen stands where they differed from or added to the original provenance collection. The data was assembled from information received from the various cooperators who originally supplied seed or parental specimens, the weather services of the country of origin, the Great Britain Meteorological Office (1958), and from the Foreign Area Section of the United States Weather Bureau, United States Department of Commerce.

The remoteness of the stands and the wide area of distribution of Scotch pine made it impractical to assemble daily weather data. All information was assembled on a monthly and annual basis.

The basis of the precipitation and temperature data was usually a 20-year record, although in some instances this period was as long as 50 years. While it would have been desirable to use comparable years of record, wars, catastrophes, and lack of long established weather stations in some areas resulted in the use of the best data available.

The precipitation data was recorded in millimeters as average monthly precipitation (weather characters 20-31), average monthly precipitation on a yearly basis (weather character 32), and total annual precipitation (weather character 33).

Temperature data was recorded in degrees centigrade as the number of plus six degree months in a year (character 34), average monthly temperature (weather characters 35-46) and average monthly temperature on an annual basis (weather character 47).

In addition to the climatic characterisitics listed above, 18 combinations of monthly precipitation and temperature figures were used to further measure plant-climate relationships as follows:

Identifying Number	Description of Meteorological Data
48	Average temperature for period April-June
49	Average temperature for period May-July
50	Average temperature for period July-August
51	Average temperature for period July-September
52	Total precipitation, September-June
53	September-June precipitation as per cent of total annual
54	Total precipitation, October-April
55	October-April precipitation as per cent of total annual
56	Total precipitation, April-June
57	April-June precipitation as per cent of total annual
58	Total precipitation, May-June
59	May-June precipitation as per cent total annual
60	Total precipitation, July-August

61	July-August precipitation as per cent of total annual
62	Total precipitation, May-August
63	May-August precipitation as per cent of total annual
64	Ratio of average April-June temperature to precipitation for April-June
65	Ratio of average July-August temperature to precipitation for July-August

The sampling of Scotch pine provenances cut across so many areas of diverse weather patterns that correlating the data as a whole resulted only in an abundance of meaningless but statistically significant correlations interspersed among those correlations of real biological significance. As an example, when the 16 juvenile characters used in this study (Table 23) were used to get simple correlations with 14 temperature characteristics there were 172 correlations out of a possible 224 combinations significant at the one-tenth of one per cent level of significance. Many of these correlations were artificial and biologically meaningless as determined by scatter diagrams and the only real test was by the power of the correlation (r) and by stratifying the observations.

Another basis for stratification other than diverse weather patterns was through the knowledge that many of the parental and juvenile characteristics reached an optimum at mid-range, or at about 50 degrees north latitude. While not universally true, particularly considering some of the east-west gradients, it was considered correct enough to use in stratifying the data.

Table 23.--Description of juvenile characteristics used in correlations with meteorological and geographical data of origin and the grades used in scoring the Scotch pine progeny.

Character and Number		Date	Unit of Measure	Range	Lowest value assigned to	Highest value assigned to
J5	Seed weight	11/56	mg.	2.9-12.2	Light seed	Heavy seed
J6	Seed length	11/58	mm.	3.4-5.9	Short seed	Long seed
J7/5	Ratio 1-yr.ht./seed wt.	5/60	Number	8-26	Low ratio	High ratio
J9	Foliage color	6/59	Grade	4-8	Yellow-green	Green
J12	Foliage color	10/59	Grade	8-20	Maroon	Green
J13	Foliage color	8/60	Grade	8-16	Green	Dark green
J16	Foliage color	12/60	Grade	4-32	Yellow-green	Dark green
J17	Initiation of growth	1960	Day of year	113-116	Early initiation	Late initiation
J18	Bud color	5/60	Grade	4-24	Bright green	Brown
J19	Time of bud set	9/59	Day of year	200-269	Early set	Late set
J20	Earliness of leaf color		Number	1-5	Early color	Late color
J24	Pullability	7/59	Number	8-18	Easy to lift from soil	Hard to lift from soil
J27	Presence of secondary lvs.	9/59	Grade	0-4	None present	Present on 50% of seedlings
J29	Leaf length	8/60	cm.	25-43	Short needle	Long needle
J31	Foliage color	12/61	Grade	4-40	Yellow	Blue-green
J32	Height, 3-yr.	1961	mm.	118-708	Short seedling	Tall seedling

The juvenile data was studied in relation to meteorological conditions by separating the regions into A through F, G, H, and J through N (less Region L, Scotland).

The parental data, which contained fewer observations, was studied by grouping regions A through G, and H through N (including Turkey, which in the parental study was separated from Wright's region K).

All data were entered on punch cards and processed through Michigan State University's Control Data Corporation 3600 data processing system on a correlation-regression program.

Literature Review

Lehotsky (1961) reported that altitude had an effect on seed and cone quality in Scotch pine. He collected seed from 4-5 trees at 600, 700, 870, and 1100 meters altitude. These seed were sown in nurseries at 640, 750, 870 and 1050 meters altitude. Measurement of seedling height at two years showed that at each nursery, stem height decreased with increasing altitude of provenance.

Callaham (1959) reported a highly significant influence of elevation on the height and diameter growth of 20-year-old ponderosa pine and Jeffrey's pine (*Pinus jeffreyi* Grev. and Balf.) in a provenance test of seven altitudinal collection of Jeffrey pine (3,500-8,500 feet).

McLemore *et al.* (1961) found that the dry-matter content of the previous year's needles collected from two plantations of loblolly pine in Mississippi and Louisiana showed no correlation with mean annual rainfall, January or July temperature, length of growing season, or the ratio of July temperature to mean annual rainfall. The provenances tested represented 25 counties from the geographical and climatic extremes of the range of loblolly pine. The authors state the different results of Langlet (1959) could be attributed to the greater importance of low temperature for Scotch pine.

Langlet (1961), in reporting on Central European spruce provenances tested in Sweden, stated that growth was affected by latitude as much as altitude, i.e., that mean temperature and length of growing season were the important factors in spruce. However, as compared with Scotch pine, both racial character and climatic response depended far more on local climate than on latitude as such, and no effect of day length could be observed.

Critchfield (1957) found that each of the principal morphological characteristics of lodgepole pine (leaves, cones, anatomy of leaves) was unique in its variation pattern. Leaf width was tied more closely to elevation than geographic location. He found that latitude, which has an important influence on local climate in California, showed no clear-cut association with any single morphological characteristic throughout the whole of the species range (California to Alaska and eastward to Colorado).

Goddard and Strickland (1962) reported that longitude, latitude, and early and late rainfall, as independent variables, accounted for 88 per cent of regional variation observed in highly significantly different groups of wood specific gravity in slash pine (_Pinus elliottii_ Engelm.).

Squillace and Silen (1962) reported on a 30-year-old (10-origin, 5 plantation) and a 45-year-old (20 origins in one plantation) provenance test of ponderosa pine. They found that growth rate was related to average annual temperature and the April-May temperature of seed source localities. Growth was not correlated with the number of frost-free days, however. The two strongest climatic variables found in simple correlations were September-through-June precipitation as a per cent of annual and April-May temperature. Growth of the trees of different sources was unrelated to springtime precipitation (April through June).

Kraus (1962) reported that red pine shoot growth was found significantly correlated to the moisture deficiencies of the previous year's food storage period (July 15-August 30) and the current year's shoot elongation period (May 15-July 15) for three sites in central lower Michigan. The study included 18 red pine trees in three stands and included meterological data of 10-20 years duration.

Langlet (1959), in reviewing his studies of Scotch pine variability, stated that the dry matter content of needles shows a remarkably close relationship with the conditions in the native habitats of different provenances in respect to latitude and duration of the period of vegetation (expressed as the number of days with an average temperature of +6°C. or more). He found an even closer relationship between the dry matter content and the length of the first day of the year with a normal average temperature of +6°C.

Meyer and Borman (1963) found both a geographic and altitudinal cline in the ratio of cone/bract length in a phenotypic variation study of balsam fir (Abies balsamea (L.) Mill.). They also reported that leaf length was correlated with altitude.

Schoenike (1963) in reporting natural variation in jack pine (Pinus banksiana Lamb.) stated that, of six environmental factors, precipitation and latitude had the most effect on morphology and tree growth.

Weather Patterns Within Scotch Pine Distribution Area

In regions A through F, Scandinavia, Baltic area, Poland, and Northwest U.S.S.R., the per cent of the total annual rainfall which occurs during the period April to August decreases with increasing latitude, increases with increasing east longitude, and increases with increases in elevation (Table 24). Temperatures during the period May through September decrease with increasing latitude and temperatures during the period September through April decrease with increasing east longitude and with elevation increase (Table 25).

The higher latitudes have an increased amount of precipitation during the April through June period in relation to temperature while increasing east longitude shows a reduction in precipitation during the same period in relation to temperature.

In region G, Northeast Germany and Czechoslovakia, the rainfall during the period April through August shows an even sharper decrease with increasing latitude, particularly during the month of June, and there is an increasing amount of the total annual precipitation during the period May to August with increasing east longitude

Table 24.--Correlation of latitude, longitude, and elevation with precipitation data in regions A-F, G, H, and J, K, M, and N.

	Regions											
	A-F			G			H			J,K,M,& N		
Meteoro-logical Data	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2	Elev. 3
Actual precipitation in												
January	NS	-.57	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
February	NS	-.52	.35	NS	NS	NS	NS	NS	NS	NS	NS	NS
March	NS	-.59	.35	NS	NS	NS	NS	NS	NS	NS	NS	NS
April	.32	-.71	-.35	-.63	NS	.51	-.53	NS	NS	NS	NS	NS
May	NS	-.63	-.43	-.66	NS	.56	-.66	NS	.66	NS	NS	NS
June	NS	NS	NS	-.84	NS	.62	-.65	NS	.73	NS	NS	NS
July	NS	-.48	NS	-.62	NS	.49	NS	NS	NS	NS	NS	NS
August	NS	-.49	NS	-.58	NS	.45	NS	NS	NS	.50	NS	NS
September	NS	-.45	NS	NS	NS	NS	-.57	NS	.57	NS	NS	NS
October	.34	-.56	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
November	NS	-.58	-.34	NS	NS	NS	NS	NS	NS	NS	NS	NS
December	NS	-.57	-.33	NS	NS	NS	.48	-.49	-.37	NS	NS	NS
Monthly av.	NS	-.58	NS	-.42	NS	NS	NS	NS	NS	NS	NS	NS
Sept-June	NS	-.58	-.33	NS	NS	NS	NS	NS	NS	NS	NS	NS
Oct.-April	NS	-.59	-.34	NS	NS	NS	NS	NS	NS	NS	NS	NS
April-June	NS	-.62	-.34	-.78	NS	.60	-.64	NS	.69	NS	NS	NS
May-June	NS	-.51	NS	-.79	NS	.62	-.68	NS	.70	NS	NS	NS
July-Aug.	NS	-.51	NS	-.62	NS	.49	NS	NS	NS	.42	NS	NS
May-Aug.	NS	-.52	NS	-.76	NS	.59	-.50	NS	.58	NS	NS	NS
Precipitation as per cent of annual total												
Sept.-June	.49	-.78	-.60	NS	NS	NS	NS	NS	NS	-.80	NS	.48
Oct.-April	.53	-.86	-.49	.45	-.38	NS	NS	NS	NS	-.60	NS	.50
April-June	-.51	.58	NS	-.59	NS	.46	-.88	.65	.84	NS	.51	.50
May-June	-.54	.73	NS	-.54	NS	.43	-.82	.66	.70	NS	.48	NS
July-Aug.	-.49	.76	.60	NS	NS	NS	NS	NS	NS	.80	NS	-.48
May-Aug.	-.54	.80	NS	-.49	.43	.37	-.49	.68	NS	.55	NS	-.46
$r_{.05}$		.316			.368			.456			.368	
$r_{.01}$		.407			.472			.575			.472	
$r_{.001}$		.505			.580			.693			.579	

NS = Non-significant correlations

Table 25.--Correlation of latitude, longitude, and elevation with temperature data for regions A-F, G, H, and J, K, M, and N.

Meteoro-logical Data	Regions										
	A-F			G			H			J,K,M & N	
	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2	Elev. 3	Lat. 1	Long. 2
Average temperature in											
January	NS	-.84	-.60	NS	-.72	-.55	.76	-.82	-.69	-.38	NS
February	NS	-.78	NS	NS	-.74	-.53	.63	-.76	-.71	NS	NS
March	NS	-.86	-.60	NS	-.45	NS	NS	NS	-.54	-.41	NS
April	NS	-.69	-.58	NS	NS	NS	NS	NS	NS	-.45	.51
May	-.46	NS	-.49	NS	NS	NS	NS	NS	-.47	NS	.63
June	-.64	NS	NS	NS	NS	-.39	-.47	.54	NS	-.42	.59
July	-.49	NS	NS	NS	NS	NS	-.56	.68	NS	-.59	.60
August	-.50	NS	-.33	NS	NS	-.39	-.59	.67	NS	-.67	.61
September	-.35	-.49	-.55	NS	NS	NS	-.46	NS	NS	-.56	.48
October	NS	-.80	-.62	NS	NS	-.55	NS	NS	NS	-.56	.48
November	NS	-.85	-.67	NS	-.50	-.70	NS	NS	NS	-.57	.39
December	NS	-.86	-.60	NS	-.48	-.41	.66	-.68	-.49	-.61	NS
Monthly av.	NS	-.62	-.60	NS	NS	-.45	NS	NS	NS	-.53	NS
April-June	-.41	-.48	-.50	NS	NS	NS	NS	NS	NS	-.41	.59
May-July	-.57	NS	NS	NS	NS	NS	-.38	.59	NS	-.46	.62
July-Aug.	-.51	NS	NS	NS	NS	-.37	-.59	.68	NS	-.63	.61
July-Sept.	-.46	NS	-.38	NS	NS	NS	-.64	.63	NS	-.61	.57
6° months	-.51	-.33	-.43	.42	NS	NS	NS	NS	NS	NS	NS
Ratios											
$\frac{\text{Apr.-June prec.}}{\text{Apr.-June temp.}}$	.64	-.38	NS	-.56	NS	.64	-.51	NS	.67	NS	NS
$\frac{\text{July-Aug. prec.}}{\text{July-Aug. temp.}}$	NS	-.52	NS	-.48	NS	.55	NS	NS	NS	.47	NS

There were no correlations in regions J,K,M, and N with elevation.

NS = Non-significant correlation

and with elevation. Winter temperatures decrease with increasing east longitude and with elevation. Temperature during the period April through August increases more than precipitation as latitude increases, but decreases in relation to precipitation as elevation increases.

In region H, western Germany, eastern France, and Belgium, precipitation decreases with increased latitude during the period April through August, and increases during the same period with increased east longitude and with elevation. Temperatures increase with latitude during the period December through February and decrease during the period June to September, however, winter temperatures decrease and summer temperatures increase as east longitude increases and winter temperatures decrease as elevation increases. The amount of precipitation during the period April to June increases with relation to temperature as latitude increases but is reversed with elevation increases.

In regions J, K, M, and N, Yugoslavia, Greece, south central France, and Spain, the per cent of total annual precipitation decreases during the period September through April with latitude increases but increases with elevation. The per cent of total annual rainfall occurring during the period April to June increases with increasing east longitude.

In summary, regions A-F have less rainfall in the east but a higher percentage of the annual amount occurs during the summer with lower summer temperatures in the north and lower winter temperatures to the east and at the higher elevations. Region G has decreased amounts of summer rainfall in the north and increasing rainfall at higher elevations with lower winter temperatures as elevation increases and to the east. Region H has the same precipitation pattern, growing season temperatures are less to the north and higher to the east. Regions J, K, M, and N have a greater percentage of the total annual rainfall occurring during the summer to the north and east at the lower elevations.

These changing patterns of summer and winter precipitation and temperature with latitude, longitude, and elevation changes make it impractical to study parental and juvenile correlations with meteorological data for the distribution area as a whole.

Correlations Involving Parental Characteristics and Climate

Nineteen cone, seed, and leaf characteristics of parental specimens were analyzed for possible simple correlations with meteorological data. Separate analyses were made for northern Europe (regions A, C, G, northern and central Scandinavia, northeast Germany, Czechoslovakia, Table 26), and central and southern Europe (regions H, J, K, M, N, western Germany, Belgium, France, Spain, Turkey, Table 27).

The northern area, comprising regions A through G had the following actual and expected numbers of correlations significant at the various levels:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (17 d.f.)	.693	.575	.456
Number of r's exceeding amount needed			
Actual	23	66	156
Expected (874 combinations)	.87	8.7	43.5

Apophysis thickness increased as the percentage of total annual precipitation occurring during the period July-August increased. Apophysis thickness decreased with lower temperatures and the thickness in relation to length decreased with higher temperatures during the period September-December. Thinner apophyses are associated then with cold, dry winters and cold summers.

Seed length and width increased as a higher percentage of the annual precipitation occurred during the April-June period and as temperature increased throughout the year.

An increased amount of leaf twist is associated with increased temperatures during May and June.

The various measurements of cone length and width, of apophysis width, and of leaf twist are omitted from Table 26. They were found not to be correlated with any climatic characteristics. On the other hand, three of the seven ratios involving some of those same traits were correlated, especially with temperature data.

Table 26.--Correlations between parental characteristics and meteorological data for north European Scotch pine (regions A, C, and G).

Meteoro-logical Data	Parental Characteristics									
								Ratios		
	Apophysis length	Apophysis thickness	Opp. Apophysis thickness	Seed length	Seed width	Leaf length	Leaf twist	Apo. length / Apo. width	Apo. length / thickness	Cone length / Apo. length
	P12	P14	P17	P28	P29	P35	P38	P15	P16	P20
Actual precipitation in										
January	NS	NS	NS	NS	NS	NS	NS	NS	.62	NS
February	NS	-.58	NS	NS	NS	NS	NS	NS	.62	NS
April	NS	NS	NS	NS	.56	NS	NS	NS	NS	NS
May	NS	NS	NS	.61	.68	NS	NS	NS	NS	NS
June	NS	NS	NS	.50	.61	NS	NS	NS	NS	NS
August	.52	.63	.53	NS	NS	NS	NS	NS	NS	NS
October	.63	.63	NS	NS	-.62	NS	NS	.60	NS	.47
April-June	NS	NS	NS	.55	.67	NS	NS	NS	NS	NS
May-June	NS	NS	NS	.59	.68	NS	NS	NS	NS	NS
July-Aug.	NS	-.48	.46	NS	NS	NS	NS	NS	NS	NS
Entire year	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Precipitation as per cent of annual total										
Sept.-June	NS	-.61	-.60	NS	NS	NS	NS	NS	.69	NS
April-June	-.50	NS	NS	.52	.68	NS	NS	-.60	NS	NS
May-June	-.50	NS	NS	.51	.62	NS	NS	-.59	NS	.55
July-Aug.	NS	.61	.61	NS	NS	NS	NS	NS	-.69	NS
Average Temperature in										
January	NS	-.53	NS	.68	.82	.56	NS	NS	NS	NS
February	NS	-.48	NS	.67	.81	.65	NS	-.57	NS	NS
March	NS	-.54	NS	.86	.90	.48	NS	-.49	NS	.53
April	-.48	-.54	NS	.87	.89	.51	NS	-.54	NS	.61
May	-.51	-.56	NS	.88	.85	.50	.49	-.48	NS	.64
June	-.51	-.52	NS	.79	.70	.52	.49	-.46	NS	NS
July	NS	NS	-.47	NS	NS	NS	NS	NS	NS	NS
August	NS	-.61	-.53	.50	.55	NS	NS	NS	.54	NS
September	NS	-.63	-.46	.66	.77	.55	NS	NS	.54	NS
October	NS	-.58	NS	.70	.81	.52	NS	NS	.51	NS
November	NS	-.60	NS	.58	.74	.55	NS	NS	.55	NS
December	NS	-.63	.50	.58	.73	.50	NS	NS	.60	NS
April-June	-.51	-.56	NS	.87	.85	.52	NS	-.51	NS	.62
May-July	NS	-.55	-.47	.78	.70	.51	NS	NS	NS	.53
July-August	NS	-.60	-.51	NS	.59	NS	NS	NS	NS	NS
Entire year	NS	-.59	NS	.77	.85	.55	NS	NS	.49	.49
No. 6° months	NS	-.66	NS	.77	.88	NS	NS	NS	.56	.55

r = .456, .575, .693 for significance at the 5, 1, and 0.1 per cent levels respectively.

NS = Non-significant correlation

Table 27.--Correlations involving relationships between parental cone, seed, and leaf characteristics and meteorological and geographical data of origin for regions H, I, J, K, L, M, and N.

Meteorological Data	Parental Characteristics								Ratios		
	Cone length	Closed-cone width	Open-cone width	Apophysis thickness	Opp. Apophysis thickness	Basal angle of open cone	Seed length	Seed width	Apo. length / Apo. thickness	Cone length / Apo. length	Seed length / Seed width
	P6	P7	P8	P14	P17	P19	P28	P29	P16	P20	P30
Actual precipitation in											
January	-.52	-.61	-.45	-.69	-.55	.62	NS	-.62	.69	-.70	NS
February	-.59	-.66	-.50	-.68	-.54	.58	NS	-.59	.63	-.69	NS
March	-.58	-.63	-.50	-.56	NS	NS	NS	-.47	NS	-.49	NS
April	-.52	-.57	-.45	-.46	NS	NS	NS	NS	NS	NS	NS
May	-.52	-.48	NS	NS	NS	NS	NS	NS	NS	NS	NS
June	-.62	-.53	-.54	-.51	NS	NS	-.55	NS	NS	NS	NS
July	-.62	-.61	-.62	-.68	-.58	.55	-.70	-.69	NS	-.53	NS
August	-.50	-.50	NS	-.60	-.65	.55	-.74	-.53	.60	-.62	NS
September	-.67	-.71	-.62	-.70	-.50	.55	-.45	-.67	.50	-.57	NS
October	-.61	-.69	-.57	-.74	-.57	.63	-.48	-.70	.62	-.64	NS
November	-.59	-.63	-.50	-.63	-.49	.47	NS	-.51	NS	-.58	NS
December	-.56	-.62	-.48	-.67	-.56	.54	NS	-.59	.60	-.65	NS
Total Annual	-.63	-.67	-.57	-.68	-.54	.53	-.45	-.60	.53	-.60	NS
Sept.-June	-.62	-.67	-.55	-.67	-.51	.51	NS	-.58	.51	-.59	NS
October-Apr.	-.59	-.66	-.51	-.67	-.52	NS	NS	-.58	.56	-.63	NS
May-June	-.59	-.52	-.50	-.48	NS	NS	NS	NS	NS	NS	NS
July-Aug.	-.58	-.58	-.55	-.67	-.63	.56	-.74	-.63	.56	-.59	NS
May-Aug.	-.61	-.58	-.55	-.59	-.53	NS	-.62	-.51	NS	-.49	NS
Precipitation as per cent of annual total											
Sept.-June	NS	NS	NS	NS	NS	NS	.60	NS	NS	NS	.73
October-Apr.	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.69
April-June	NS	.45	NS	NS	NS	-.64	NS	.75	-.64	NS	-.47
May-June	NS	.46	NS	-.62	NS	-.60	NS	.72	-.60	NS	-.60
July-Aug.	NS	NS	NS	NS	NS	NS	-.60	NS	NS	NS	-.73
May-Aug.	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.81
Average temperature in											
June	NS	.48	NS	.61	NS	-.62	NS	.66	-.67	.55	NS
July	NS	NS	NS	.60	NS	-.68	NS	.69	-.71	.57	NS
August	NS	.45	NS	.67	.53	-.70	.46	.72	-.72	.53	NS
September	NS	.53	NS	.69	.55	-.69	NS	.66	-.70	.60	NS
October	NS	NS	NS	.45	NS	-.45	NS	.52	NS	NS	NS

Table 27.--Continued

Meteorological Data	Parental Characteristics								Ratios		
	Cone length	Closed-cone width	Open-cone width	Apophysis thickness	Opp.apophysis thickness	Basal angle of open cone	Seed length	Seed width	Apo. length / Apo. thickness	Cone length / Apo. length	Seed length / Seed width
	P6	P7	P8	P14	P17	P19	P28	P29	P16	P20	P30
Average temperature in											
April-June	NS	NS	NS	.52	NS	-.58	NS	.57	-.54	NS	NS
May-July	NS	NS	NS	.57	NS	-.60	NS	.65	-.62	.52	NS
July-Sept.	NS	.48	NS	.66	.53	-.70	NS	.71	-.72	.57	NS
Entire year	NS	NS	NS	.52	NS	-.51	NS	NS	-.51	NS	NS
Ratios											
June-Apr. prec. / June-Apr. temp.	-.56	-.59	-.47	-.50	NS	NS	NS	NS	NS	NS	NS
July-Aug. precip. / July-Aug. temp.	.57	.61	.53	.71	.64	-.61	.69	.69	-.64	.65	NS

r = .444, .561, .679 for significance at the 5, 1, 0.1 per cent levels of significance respectively.

NS = Non-significant correlation.

All the monthly average temperatures were correlated with several of the parental traits. Probably the late spring-early summer temperatures tell the best story but it is not greatly different from the story told by average annual temperature of the number of months in which the average temperature is greater than 6° C.

The parental-climatic correlations for the southern area are presented in Table 27. The actual and expected numbers of correlations significant at the various levels were as shown in the following tabulation. Several parental characters such as apophysis length and width, leaf length, and leaf twist are omitted because they were found not to be significantly related to any of the climatic data.

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (18 d.f.)	.679	.561	.444
Number of r's exceeding amount needed			
Actual	34	142	241
Expected (874 combinations)	.9	8.7	43.5

The parental characters dependent on climate differed between the northern and southern areas. For example, cone length was negatively correlated with almost any measure of precipitation in the south but not in the north. And there was no consistent relation between leaf length and temperature in the south although there was in the north.

Also, the relations between precipitation and parental traits were much more constant in the south than in the north. Note the similarity between all lines in the top half of Table 27, and the relative unimportance of seasonal distribution of rainfall on most parental traits except the length-width ratio of the seeds. The total annual precipitation explains almost as much of the variability in any trait (except seed shape) as does the precipitation for any month or combination of months.

In the south, cone size increased as precipitation decreased. This is particularly true as regards precipitation in the last six months of the year. The relationship was evident whether cone length or cone width was considered. Thickness of the apophysis followed the same trend, as did the ratio cone length-apophysis length.

Basal angle of the opened cone increased as precipitation increased. That is, cones from wet areas opened less fully than did cones from dry areas.

The only parental trait to show a consistent relation with season distribution of rainfall was seed shape. The ratio length-width increased as the percentage of the rainfall occurring during the winter months increased. That is, the seeds were narrower in areas with wet winters.

Summer temperature was more important than winter temperature. In fact the temperatures from November through May were scarcely correlated with any parental trait. Seed width, apophysis thickness, and the number of scales per cone all increased in areas with warm summers whereas the basal angle of the opened cones decreased in those areas.

It was felt that a ratio of summer precipitation to summer temperature might explain more of the variability in the southern parents than would any single measurement of climate. Accordingly that ratio was calculated and correlated with the parental traits. The correlations were significant with nearly all traits shown in Table 27, but the story was little if any better than if total annual precipitation was used.

A word about the size of the correlations. Many of them are strong enough to be statistically significant and to give clues as to the processes underlying the variation in parental traits. Few are large enough to explain the majority of the variation in a parental trait. Only in the north are the relationships strong enough that r exceeds 0.8, or r^2 exceeds 0.64. Even most of the significant ones are below 0.7, r^2 being below 0.49. Thus, from the standpoint of forecasting where one might locate the stand with the largest cones, or the longest leaves, one can use the climatic data only as a general guide, and must do considerable searching in areas with the requisite climate. Presumably much of the unexplained variation is due to soil and genetic factors.

Correlations Involving Juvenile Characteristics and Climate

Sixteen juvenile characteristics measured on nursery stock grown in East Lansing, Michigan, in a replicated provenance test were analyzed for possible correlations with meteorological and geographical data from the place of origin of the seed. As previously mentioned the geographic ecotypes of Wright (1963) were grouped into four areas that are more or less homogeneous in climate to assist in developing true correlations. These four areas are:

Regions A-F	Poland, Baltic, Scandinavia north to Arctic Circle
Region G	Northeast Germany and Czechoslovakia
Region H	Western Germany, eastern France, and Belgium
Regions J, K, M and N	Spain, southern France, Yugoslavia, Greece, Turkey

In regions A through F, Poland north to the Arctic Circle, the actual and expected numbers of correlations were as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (36 d.f.)	.316	.407	.505
Number of r's exceeding amount needed			
Actual	88	154	235
Expected (784 combinations)	.78	7.8	39

The correlations between juvenile characteristics and meteorological and geographical data are shown in Table 28.

In the northern areas, increased third year seedling height was associated with increased temperatures during the period April-September, with an increased number of $+6^{\circ}$ C. months in the year, and with a lesser amount of precipitation during the months of April-June in relation to increases in temperature. This would mean that the tallest seedlings came from the south and from the lower elevations.

Table 28.--Correlations involving relationships between juvenile characteristics and meteorological and geographical data of origin for regions A through F, northern Europe.

Meteorological and Geographical Data	Juvenile Characteristics									
	Seed weight J5	Height, 3-yr. J34	Foliage color 12/61 J31	Earliness of color J20	Bud color J18	Date of bud formation J19	Start of bud growth J17	Second. leaf presence J27	Leaf length J29	Pullability J24
Actual precipitation in										
January	NS	NS	.34	NS	NS	NS	NS	NS	-.47	NS
February	NS	NS	.33	NS	NS	NS	NS	NS	-.44	NS
March	NS	NS	.41	NS	NS	NS	NS	NS	NS	NS
April	NS	NS	.48	NS	NS	NS	NS	NS	-.52	NS
May	NS	NS	.35	NS	.53	NS	NS	.45	NS	NS
June	NS	NS	.34	NS	.34	NS	NS	NS	NS	NS
August	NS	NS	NS	NS	.38	NS	NS	NS	-.35	NS
September	NS	NS	NS	NS	.34	NS	NS	NS	-.38	NS
October	NS	NS	NS	NS	NS	NS	NS	NS	-.51	NS
November	NS	NS	NS	NS	NS	NS	NS	NS	-.49	NS
December	NS	NS	.36	NS	NS	NS	NS	NS	-.46	NS
Monthly av.	NS	NS	.34	NS	.34	NS	NS	NS	-.47	NS
Sept.-June	NS	NS	.34	NS	.32	NS	NS	NS	-.48	NS
Oct.-April	NS	NS	.36	NS	NS	NS	NS	NS	-.48	NS
April-June	NS	NS	.37	NS	.40	NS	NS	.36	-.37	NS
May-June	NS	NS	NS	NS	.46	NS	NS	.38	NS	NS
July-Aug.	NS	NS	NS	NS	.35	NS	NS	NS	-.39	NS
May-Aug.	NS	NS	NS	NS	.40	NS	NS	NS	-.34	NS
Per cent of total annual precipitation										
Sept.-June	NS	NS	.38	.41	NS	NS	NS	NS	-.49	NS
Oct.-April	NS	NS	.49	.37	NS	NS	NS	NS	-.61	NS
April-June	NS	.41	NS	NS	NS	NS	.51	NS	.63	NS
May-June	.36	.39	-.43	NS	NS	.41	NS	NS	.68	NS
July-Aug.	NS	NS	-.38	-.42	NS	NS	NS	NS	.49	NS
May Aug.	NS	NS	-.42	-.36	NS	NS	NS	NS	.59	NS

r = .316 significant at the 5 per cent level of significance.
r = .407 significant at the 1 per cent level of significance.
r = .505 significant at the 0.1 per cent level of significance.
NS = Non-significant correlation.

Table 28.--Continued

Meteoro-logical and Geograph-ical Data	Juvenile Characteristics									
	Seed weight	Height, 3-yr.	Foliage color 12/61	Earliness of color	Bud color	Date of bud formation	Start of bud growth	Second. leaf presence	Leaf length	Pullability
	J5	J34	J31	J20	J18	J19	J17	J27	J29	J24
Average temperature in										
January	NS	NS	.51	.58	.32	.46	NS	.46	-.40	-.53
February	NS	NS	.49	.36	NS	NS	NS	NS	-.43	-.33
March	NS	NS	.59	.59	.37	.55	NS	.58	NS	-.53
April	NS	.47	.52	.56	.44	.66	.36	.72	NS	-.54
May	NS	.60	.43	.51	.55	.66	.48	.88	NS	-.45
June	.53	.54	NS	NS	.39	.43	NS	.60	NS	NS
July	.43	.36	NS	NS	NS	NS	NS	.48	NS	NS
August	.44	.51	.34	.42	.36	.50	.37	.67	NS	NS
September	NS	.55	.54	.61	.43	.68	.42	.79	NS	-.45
October	NS	NS	.61	.61	.36	.61	NS	.65	NS	-.53
November	NS	NS	.54	.59	NS	.50	NS	.55	-.37	-.51
December	NS	NS	.50	.56	NS	.45	NS	.48	-.38	-.51
Monthly av.	NS	.41	.44	.53	.44	.62	NS	.63	NS	-.54
April-June	NS	.57	.46	.52	.51	.67	.43	.79	NS	-.47
May-June	.48	.56	NS	NS	.46	.53	.41	.72	NS	NS
July-Aug.	.44	.45	NS	NS	NS	.39	NS	.59	NS	NS
July-Sept.	NS	.52	NS	.47	.39	.54	.38	.71	NS	NS
6 months	.41	.63	.51	.35	.47	.69	.52	.77	NS	NS
Ratios										
Apr.-June prec. / Apr.-June temp.	-.39	-.49	NS	NS	NS	-.39	-.33	-.32	.58	NS
July-Aug. prec. / July-Aug. temp.	NS	NS	NS	NS	NS	NS	NS	NS	-.47	NS
Latitude	-.58	-.74	NS	NS	-.39	-.63	-.57	-.54	-.72	NS
Longitude	.38	NS	-.56	-.43	NS	NS	NS	NS	.59	.40
Elevation	NS	-.43	NS	-.49	-.32	-.43	-.43	-.58	NS	.45

Foliage color (character J31) was recorded with the low number representing yellow and the high numbers representing blue-green. The yellow predominated where the temperatures during the period August through May were higher and the percentage of total annual rainfall occurring during the winter period, October through April, was highest. Extreme yellowing of foliage then occurred in areas with milder winters and dryer summers. Earliness of yellow coloring followed the same pattern.

Bud color, where green was scored low and tan high, showed that tan was associated with higher temperatures throughout the year but particularly in April to May and with increased amounts of rainfall during the period April to June.

The formation of buds was scored as the date of the year that they formed. Late formation was correlated with warmer temperatures throughout the year, particularly during the April-June period, more 6° C. months, and a greater amount of the annual precipitation occurring during the May-June period.

The early presence of secondary leaves was strongly correlated ($r = .77$) with an increased number of 6° C. months, warmer temperatures throughout the year and a greater amount of precipitation during the April-June period.

Leaf length was correlated with a greater percentage of annual precipitation occurring during the growing season, April-August, with colder winters, and with higher amounts of precipitation during the period April-June in relation to temperature for the same period.

In other words, growth characteristics were all positively correlated with more favorable environmental factors of warmer temperatures and greater amounts of precipitation during the growing season. Or, they were negatively correlated with latitude, and elevation. Only leaf length was positively correlated with increasing east longitude.

Region G, Northeast Germany and Czechoslovakia, had the lowest number of correlations. The actual and expected numbers of correlations are as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (27 d.f.)	.368	.472	.580
Number of r's exceeding amount needed			
Actual	2	15	45
Expected (784 combinations)	.78	7.8	39

Approximately 87 per cent of the correlations at the five per cent level of significance can be expected to be biologically meaningless.

The correlations for this area are summarized in Table 29.

Yellowing of the foliage was associated with higher temperatures, particularly during the winter and was negatively correlated with increased east longitude and increased elevation. This would be expected since the winters are colder to the east and at the higher elevations in this area.

Table 29.--Correlations involving relationships between juvenile characteristics and meteorological and geographical data of origin for region G, eastern Germany and Czechoslovakia.

Meteorological and Geographical Data	Juvenile Characteristics						
	Seed Weight J5	Foliage color 6/59 J9	Foliage color 12/60 J16	Foliage color 12/61 J31	Bud color J18	Second. leaf presence J27	Pullability J24
Actual precipitation in							
April	-.53	NS	NS	NS	NS	NS	NS
May	-.45	NS	NS	NS	NS	NS	NS
June	NS	NS	NS	NS	-.37	-.47	-.45
August	NS	NS	NS	NS	NS	NS	-.40
April-June	-.48	NS	NS	NS	NS	-.39	-.41
May-June	-.44	NS	NS	NS	-.38	-.43	NS
July-Aug.	NS	NS	NS	NS	NS	NS	-.39
May-Aug.	-.45	NS	NS	NS	NS	-.43	-.45
Precipitation as per cent of total annual							
April-June	NS	.38	NS	NS	-.42	NS	NS
Latitude	NS	NS	NS	NS	NS	NS	NS
Longitude	NS	NS	-.50	-.59	NS	NS	NS
Elevation	NS	NS	-.54	NS	NS	NS	NS
Average temperature in							
January	NS	NS	.57	NS	NS	NS	NS
February	NS	NS	.47	.55	NS	NS	NS
March	NS	.43	NS	.55	NS	NS	NS
April	NS	.42	NS	.45	NS	NS	NS
July	NS	NS	.38	NS	NS	NS	NS
August	NS	NS	.39	NS	NS	NS	NS
September	NS	.41	NS	NS	NS	NS	NS
October	NS	NS	.57	.41	NS	NS	NS
December	NS	NS	.49	NS	NS	NS	NS
July-Sept.	NS	.38	.38	NS	NS	NS	NS
Average annual	NS	.39	.48	.46	NS	NS	NS
6° months	NS	NS	NS	NS	NS	NS	.89
Ratios							
$\frac{\text{Apr.-June prec.}}{\text{Apr.-June temp.}}$	-.52	NS	NS	NS	NS	NS	NS
$\frac{\text{July-Aug. prec.}}{\text{July-Aug. temp.}}$	-.43	NS	.38	NS	NS	NS	NS

r = .368, .472, .580 for significance at the 5, 1, and 0.1 per cent levels of significance.

NS = Non-significant correlation.

Bud color is greener as the per cent of annual precipitation occurring during the growing season increases.

Increasing amounts of rainfall in June appears to favor retention of primary leaves and delay formation of secondary leaves.

The development of a strong root system is highly correlated (r = .89) with an increase in the number of 6° C. months in the year.

In region H, western Germany, eastern France and Belgium, the actual and expected number of correlations are as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (17 d.f.)	.456	.575	.693
Number of r's exceeding amount needed			
Actual	9	26	57
Expected (784 combinations)	.78	7.8	39

Approximately 69 per cent of the correlations significant at the five per cent level of significance and 30 per cent at the one per cent level are biologically meaningless.

The correlations between juvenile characters and meteorological and geographical data of origin for region H are shown in Table 30.

Third year seedling height is negatively correlated with increased amounts of the total annual rainfall occurring during the growing season, April through June, and, in this region, is positively correlated with increasing latitude where the growing season temperatures are lower.

Table 30.--Correlations involving relationships between juvenile characteristics and meteorological and geographical data of origin for region H, western Germany, eastern France, and Belgium.

Meteorological and Geographical Data	Juvenile Characteristics									
	Seed length J6	Height, 3-yr. J34	Foliage color 5/59 J9	Foliage color 10/59 J12	Foliage color 8/60 J13	Earliness of color J20	Bud color J18	Date of bud formation J19	Second. leaf presence J27	Leaf length J29
Actual precipitation in										
January	NS	NS	NS	NS	NS	.47	-.87	NS	NS	NS
February	NS	NS	NS	NS	NS	NS	-.91	NS	NS	NS
April	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.73
May	NS	NS	NS	NS	NS	NS	NS	.46	NS	-.66
June	NS	NS	.64	NS	NS	NS	NS	NS	NS	-.64
July	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.57
August	NS	NS	.63	NS	NS	NS	NS	NS	NS	-.55
September	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.74
October	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.57
November	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.52
December	NS	.50	NS	NS	NS	NS	NS	NS	-.48	NS
Total annual	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.56
Sept.-June	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.55
Oct.-Apr.	NS	NS	NS	NS	NS	NS	-.75	NS	NS	NS
April-June	NS	NS	.48	NS	NS	NS	NS	NS	NS	-.71
May-June	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.68
July-Aug.	NS	NS	.54	NS	NS	NS	NS	NS	NS	-.57
May-Aug.	NS	NS	.53	NS	NS	NS	NS	NS	NS	-.67
Per cent of total annual precipitation										
Sept.-June	NS	NS	NS	.48	-.51	NS	NS	NS	NS	NS
Oct.-April	NS	NS	NS	NS	NS	NS	-.75	NS	NS	NS
April-June	NS	-.61	.49	NS	NS	NS	NS	.66	.64	-.47
May-June	NS	-.60	NS	NS	NS	NS	NS	.60	.52	NS
July-Aug.	NS	NS	NS	-.48	.51	NS	NS	NS	NS	NS

r = .456 significant at the 5 per cent level of significance.
r = .575 significant at the 1 per cent level of significance.
r = .693 significant at the 0.1 per cent level of significance.

NS= Non-significant correlation.

Table 30.--Continued

Meteorological and Geographical Data	Juvenile Characteristics									
	Seed length J6	Height, 3-yr. J34	Foliage color 9/59 J9	Foliage color 10/59 J12	Foliage color 8/60 J13	Earliness of color J20	Bud color J18	Date of bud formation J19	Second. leaf presence J27	Leaf length J29
Average temperature in										
January	-.68	NS	NS	NS	NS	NS	NS	NS	NS	NS
February	-.65	NS	-.54	NS	NS	NS	NS	NS	NS	NS
March	NS	NS	-.67	NS	NS	NS	NS	NS	NS	NS
April	NS	NS	-.49	NS	NS	NS	NS	NS	NS	NS
May	NS	NS	-.68	NS	NS	NS	NS	NS	NS	NS
August	NS	-.50	NS	NS	NS	NS	NS	NS	NS	NS
September	NS	NS	.50	NS	.62	NS	NS	NS	NS	NS
October	NS	NS	-.48	NS	NS	NS	NS	NS	NS	NS
December	-.47	NS	NS	NS	NS	NS	NS	NS	NS	NS
	NS	NS	-.60	NS	NS	NS	NS	NS	NS	NS
April-June	NS	NS	-.52	NS	NS	NS	NS	NS	NS	NS
July-August	NS	-.47	NS	NS	NS	NS	NS	NS	NS	NS
July-September	NS	-.53	NS	NS	NS	NS	NS	NS	NS	NS
Ratios										
Apr.-June prec. / Apr.-June temp.	NS	NS	.58	NS	NS	NS	NS	NS	NS	-.66
July-Aug. prec. / July-Aug. temp.	NS	NS	.52	NS	NS	NS	NS	NS	NS	NS
Latitude	NS	.59	NS	NS	NS	NS	NS	-.58	NS	NS
Longitude	.61	NS	NS	NS	NS	NS	NS	NS	NS	NS
Elevation	NS	NS	.68	NS	NS	NS	NS	NS	.67	NS

Late summer foliage yellowing is positively correlated with late winter lower temperatures and increased growing season precipitation.

Green bud color is highly correlated ($r = .87$, $r = .91$) with increased precipitation during January and February and to a lesser extent ($r = .75$) with increased precipitation during the October-April period.

Leaf length is positively correlated with decreased amounts of precipitation during the period April-November and with decreased amounts of precipitation during the period April-June in relation to temperature. Since growing season precipitation decreases with latitude in this region the longer needles would occur at the higher latitudes, where the summers are also cooler.

In regions J, K, M, and N, Yugoslavia, northeast Greece, southern France, Spain, and Turkey, there is essentially a Mediterranean climate. The actual and expected correlations in this region are as follows:

	Significance Level		
	0.1 Per cent	1 Per cent	5 Per cent
Value of r needed (27 d.f.)	.368	.472	.579
Number of r's exceeding amount needed			
Actual	8	61	136
Expected (784 combinations)	.78	7.8	39

The correlations between juvenile characters and meteorological and geographic data of origin for regions J, K, M, and N are shown in Table 31.

Table 31.--Correlations involving relationships between juvenile characteristics and meteorological and geographical data of origin for regions J, K, M, and N, the Mediterranean area.

Meteorological and Geographical Data	Juvenile Characteristics										
	Seed weight	Seed length	Seed weight / Height, 3-yr.	Foliage color 12/61	Foliage color 10/59	Foliage color 8/60	Foliage color 12/60	Earliness of Color	Date of bud formation	Start of bud growth	Second. leaf presence
	J5	J6	J7/5	J31	J12	J13	J16	J20	J19	J17	J27
Actual precipitation in											
January	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.42	-.43
February	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.43	-.47
March	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.49
April	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.40	-.45
May	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.51	NS
June	NS	-.52	.37	NS	NS	NS	NS	NS	NS	-.55	NS
July	NS	-.56	.43	NS	NS	NS	-.43	NS	-.37	-.56	NS
August	NS	-.65	.51	NS	.37	NS	-.44	NS	-.43	-.52	NS
September	NS	-.44	NS	NS	NS	NS	NS	NS	NS	-.47	NS
October	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.43	-.46
November	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.47	-.46
December	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.43	-.53
Total annual	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.49	-.42
Sept.-June	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.47	-.44
Oct.-April	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.43	-.46
April-June	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.50	-.39
May-June	NS	-.44	NS	NS	NS	NS	NS	NS	NS	-.54	NS
July-Aug.	NS	-.60	.47	NS	NS	NS	-.44	NS	-.40	-.54	NS
May-Aug.	NS	-.53	NS	NS	NS	NS	-.39	NS	NS	-.55	NS
Per cent of total annual precipitation											
Sept.-June	.37	.74	-.56	NS	NS	NS	NS	.43	.45	NS	NS
Oct.-April	NS	.48	NS	NS	NS	NS	NS	NS	NS	NS	-.41
April-June	NS	NS	NS	NS	NS	NS	NS	.38	NS	NS	.37
May-June	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	.41
July-Aug.	-.37	-.74	.56	NS	NS	NS	NS	-.43	-.45	NS	NS
May-Aug.	NS	-.49	NS	NS	NS	NS	NS	NS	NS	NS	NS

r = .368 significant at the 5 per cent level of significance.
r = .472 significant at the 1 per cent level of significance.
r = .579 significant at the 0.1 per cent level of significance.

NS = Non-significant correlation

Table 31.--Continued

Meteorological and Geographical Data	Juvenile Characteristics										
	Seed weight	Seed length	Seed weight / Height, 3-yr.	Foliage color 12/61	Foliage color 10/59	Foliage color 8/60	Foliage color 12/60	Earliness of color	Date of bud formation	Start of bud growth	Second. leaf presence
	J5	J6	J7/5	J31	J12	J13	J16	J20	J19	J17	J27
Average temperature in											
January	NS	NS	NS	.43	.40	NS	.54	NS	.39	NS	NS
February	NS	NS	NS	.39	.43	NS	.54	.45	.51	NS	NS
March	NS	.39	-.41	NS	NS	NS	NS	NS	NS	NS	NS
April	NS	.43	-.52	NS	NS	-.39	NS	NS	NS	NS	NS
May	NS	NS	-.48	NS	NS	-.51	NS	NS	NS	NS	NS
June	NS	.41	-.48	NS	NS	-.44	NS	NS	NS	NS	NS
July	NS	.50	-.58	NS	.39	-.47	NS	NS	NS	NS	NS
August	.39	.58	-.63	NS	.44	-.49	NS	.40	NS	NS	NS
September	NS	.51	-.58	NS	.48	NS	NS	NS	NS	NS	NS
October	NS	.51	-.57	NS	.45	NS	NS	NS	NS	NS	NS
November	NS	.45	-.57	NS	.42	NS	NS	.38	NS	NS	NS
December	NS	.46	-.44	NS	.37	NS	NS	.58	NS	NS	NS
Monthly av.	NS	.48	-.55	NS	.42	NS	NS	.38	NS	NS	NS
April-June	NS	.40	-.50	NS	NS	-.46	NS	NS	NS	NS	NS
May-July	NS	.43	-.52	NS	NS	-.48	NS	NS	NS	NS	NS
July-Aug.	NS	.54	-.61	NS	.42	-.48	NS	.37	NS	NS	NS
July-Sept.	NS	.53	-.60	NS	.44	-.44	NS	.38	NS	NS	NS
6° months	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Ratios											
Apr.-June prec. / Apr.-June temp.	NS	NS	NS	NS	NS	NS	NS	NS	NS	-.47	NS
July-Aug. prec. / July-Aug. temp.	NS	-.62	.51	NS	NS	NS	-.45	NS	NS	-.52	NS
Latitude	-.52	-.67	.67	NS	-.53	NS	NS	-.62	-.46	NS	NS
Longitude	NS	NS	NS	-.50	NS	-.86	-.37	-.50	NS	NS	NS
Elevation	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

In this area, the ratio of first year height to seed weight, a measure of vigor, was positively correlated with increased growing season precipitation during June-August and with lower temperatures during the period March through December, but particularly during the months of July and August.

Foliage color does not present any clear correlations. This was expected since foliage color was generally green to blue-green throughout the area.

Earliness of winter color changes was correlated with a smaller per cent of the total annual rainfall occurring during the period July-August and with warmer winters.

Early formation of buds was associated with increased precipitation during July and August.

Early growth start was correlated with increased precipitation throughout the year, particularly during the months of June to August, and with increasing precipitation during the period April-June with respect to temperature increases.

The presence of secondary leaves was negatively correlated with increased precipitation during the period October-April.

Discussion

The origins sampled within the Scotch pine distribution area covered such a wide variation in weather patterns that it was essential to treat the material as groups from more or less similar meteorological conditions for study. The breakdown was not entirely satisfactory but further stratification would have resulted in groups with too few degrees of freedom for statistical study. The high percentage of meaningless correlations resulted in reliance on the size of the correlation coefficient rather than on mere statistical significance.

A study of the various weather patterns showed that precipitation in region A-F decreased from west to east with increasing summer rainfall to the east and at higher elevations. In regions G and H precipitation decreased from south to north in the growing season but increased during the same period with increases in elevation. In regions J, K, M, and N precipitation was greater in the summer than in the winter at higher latitudes but more in the summer than in the winter at higher elevations.

Temperatures in region A-F decreased in the summer with latitude, and in the winter with increasing east longitude and elevation. In region G there was no pattern of correlation with latitude but winter temperatures decreased from west to east and with increasing elevation. In region H summer temperatures decreased with increasing latitude and winter temperatures increased, the reversal was true from west to east and with increasing elevation.

Correlations of climatic data with the parental characteristics of cone, seed, and leaf measurements showed an overall pattern of greater temperature effects in the north area and greater precipitation effects in the southern area. Apophyses were shorter and thicker as temperature increased in the southern area, but were shorter and thicker as temperatures decreased in the north area. They were also shorter and thicker as winter precipitation decreased in the northern area. Because this is a protective mechanism for the seed it would be expected to increase with less favorable environmental conditions within the area of growth.

Seed length and width increased as average annual temperatures increased in the north. In the south they increased as growing-season temperature increased. However, larger seed were associated with more growing season rainfall in the north area and with less precipitation in the south area. The causal mechanisms were apparently different in the two areas since selection pressures would not be the same. In the north better environmental conditions during the growing season produced larger seeds, but in the south larger seeds were needed for survival during the dryer and hotter spring and early summer.

The ratio of July-August precipitation/temperature was unimportant in the northern area since precipitation was not a critical factor. In the southern area, however, this ratio was important. Decreasing precipitation/temperature ratio was positively correlated with increases in cone length, cone width, apophysis thickness, seed length and width, and cone scales. The hotter and dryer the July-August period the larger and thicker were the cones and seeds.

Juvenile characteristics of seedlings grown in a provenance test in Michigan showed a few interesting correlations with meteorological and geographical data of origin.

Third year height was positively correlated with increased precipitation and temperature in the growing season in the north area, regions A-F. There were no correlations in region G. However, in region H third year height was negatively correlated with increased precipitation (higher percentage of total annual precipitation) during the period April-June and with increased temperatures during the period July-September. There were no correlations for this characteristic in regions J' K, M, and N. This reversal indicates that other factors may be responsible for the height growth, either at the point of origin (soils, planted stands, differing critical thresholds) or at the nursery site in the form of environmental interactions.

Yellowing of foliage following the growth period was positively correlated with higher winter temperatures in the north region, higher summer and winter temperatures in region G, lower temperatures during the period February-May in region H and colder summer temperatures and higher winter temperatures in regions J,K,M, and N. This yellowing was positively correlated with more winter precipitation in the north region and less summer rainfall in the southern regions.

Late bud formation was correlated with higher temperatures throughout the year in the north, not correlated with temperature in region G or H, and was correlated with the lower latitudes in the southern region. Late bud formation was correlated positively with increased precipitation during the period May-June in the north region, with increased precipitation during the period April-June in region H. But it was negatively correlated with July-August precipitation in the south regions. In the north higher temperatures would indicate a longer growing season and later bud set. In the south, where the length of the growing season is not limiting, the late summer dry period is the determining factor.

The early presence of secondary leaves is associated with higher yearly temperatures in the north, and greater percentages of the total annual precipitation occurring during the period April-June in region H and in regions J, K, M, and N. The more favorable environment in the temperature-critical north and precipitation-critical south apparently results in early presence of secondary leaves.

Multiple Correlation Analyses

An attempt was made to determine the effects of multiple climatic and geographic variables on the juvenile traits in order to better explain the variation in these characters. The initial multiple regression equations were set up on the best logical estimates of the variables responsible for correlations. Subsequent intelligence shows that new variables could have been used to better advantage.

Multiple correlations and regressions were run on third-year seedling height and on winter foliage color in December, 1961, as dependent variables with the following independent variables:

Total annual precipitation
North latitude
East longitude
Average monthly temperature
Number of 6 degree months in the year

The data for the four groups of stands were run separately on a correlation-regression program. The resulting output data for the Mediterranean group is shown in Table 32. The output data include several factors which were useful in describing the effect of any one of the independent variables on the dependent variable. The beta weights, which are independent of units, give an accurate estimation of the value of the independent variable in determining the regression coefficient. The F-value is used to test that any regression coefficient or beta weight is significantly different from zero. The R^2 deletes show the coefficient of determination which would have been obtained had the independent variable not been included in the equation.

Beta weights for the foliage color in December, 1961, indicates that the effect of each independent variable on the regression coefficient was in the following descending order of importance:

Increasing east longitude

Increasing north latitude

Total annual precipitation

Average monthly temperature

Number of months per year averaging more than 6 degrees centigrade

The R^2, coefficient of multiple determination, is equal to .378 for winter foliage color. Referring to the R^2 deletes it can be seen that the deletion of the variable "number of months per year averaging 6 degrees centigrade" has an insignificant effect (R^2 delete = .371). Increasing east longitude, on the other hand, reduces R^2 to .146, indicating that this variable is the principle factor. In confirmation, a glance at Table 31 shows that east longitude is negatively correlated at the 5 per cent level of significance with winter foliage color, character P31, and that there are no other correlations. The use of

Table 32.--Multiple correlations and regressions for the Mediterranean stands for the juvenile characters, winter foliage color, December, 1961, and third-year height.

Regression coefficient	Independent Variable	Beta weight	R^2 delete
Winter Foliage Color, December, 1961, as Dependent Variable (R^2 = .378)			
69.499			
-.002	grade per mm total annual precipitation	-.286	.335
-.636	grade per degree of north latitude	-.340	.306
-.217	grade per degree of east longitude	-.591	.146
-.285	grade per degree of average monthly temperature	-.132	.371
-.087	grade per month of av. 6 degree C. temperature	-.036	.377
Third-year Height as a Dependent Variable (R^2 = .290)			
154.778			
+ .034	mm. per mm total annual precipitation	.529	.145
+ 4.970	mm. per degree of north latitude	.352	.213
+ .579	mm. per degree of east longitude	.209	.261
+ 2.925	mm. per degree of average monthly temperature	.179	.277
+ 4.769	mm. per month of av. 6 degree C. temperature	.260	.240

multiple correlations in this case would have assisted in developing a true picture of the multiple effects of the various variables measured, but would not have changed the results of the simple correlations analysis.

The results of the multiple regressions for winter foliage color showed that east longitude was the most important factor in the northern regions, that in Northeastern Germany, Czechoslovakian area east longitude had the greatest effect. However, even that effect was small. In western Germany, eastern France and Belgium north latitude was the most effective variable. In the Mediterranean area east longitude had the greatest effect on the multiple regression.

Multiple regressions for third-year height showed that in the north there was little choice between the independent variables but that north latitude was the most important. In northeastern Germany and Czechoslovakia the number of 6° months and total annual precipitation were almost equally effective. In western Germany, eastern France and Belgium north latitude was most effective in the regression, and in the Mediterranean area total annual precipitation accounted for the majority of the regression coefficient.

In many instances the multiple correlations and regressions were not significant and the mass of data involved in this study discouraged their use since the simple correlations for the many variables involved were sufficient for the purpose.

CHAPTER IX

TAXONOMY

Shaw (1914) placed Scotch pine (Pinus sylvestris L.) in series Lariciones of the section Pinaster under the subgenus Diploxylon on the basis of large ray cell pits, cones dehiscent at maturity, and seed wing blades thin at base (Lariciones), an effective articulated seed wing and persistent fascicle sheath (Pinaster), and bases of the fascicle bracts decurrent and two vascular bundles in the leaves (Diploxylon).

The cones, seeds, and leaves of Scotch pine, the subjects of this study, have been described by Shaw (1914) as:

> Leaves binate, from 3 to 7 cm. long; hypoderm inconspicuous; resin-ducts external; cones from 3 to 6 cm. long, reflexed, symmetrical or sometimes oblique, ovate-conic, deciduous; apophyses dull pale tawny-yellow of a gray or greenish shade, flat, elevated, or protuberant, and often much more prominent on the posterior of the cone, the umbo with a minute prickle or its remnant.

Rehder (1940) states that the leaves are stiff, usually twisted, and bluish-green; that the cone-scale apophyses are flat, sometimes pyramidal, with a small umbo.

The wide distribution of Scotch pine and the many isolated populations along the southern and eastern limits of its range have resulted in considerable genetic diversity. Numerous Latin names have been proposed for various populations. Several authors have described infraspecific taxa without attempting to relate them to the remainder of the species. Others have attempted to catalogue and describe the variation of the entire species. The more prominent of these monographic treatments are summarized below.

The word "variety" is used here to describe a geographically limited population which is described on the basis of its phenotypic characteristics in the wild. The words "race" or "ecotype" are restricted to populations whose genetic distinctness was studied by means of appropriate uniform-environment progeny tests.

The descriptions are those of the authors whose publication is cited.

Schott (1907) recognized the following geographic varieties. Although he did not cite authors, they have been added where it is certain that he was using a name in the same sense as an earlier author.

var. lapponica (Fries) Hartm. Lapland, middle and northern Scandinavia, northern Finland. Crown spruce-like, slender, pointed, trunk predominately straight, branches inclined, ascending, or drooping; foliage dense, needles green, short, persisting for 4-7 years; cones more yellowish; apophyses convex and hooked; seed small, brown, seed wings reddish-brown.

var. scotica Beissn. Scotland. Needles shorter and more blue-green than in the case of the principal variety (borussica), 3-6 cm. long; cones shorter, about 3.5 cm. long, symmetrical, apophyses on the bottom of the cones smooth (flat), on the upper part more or less pyramidal.

var. _borussica_. Northeast German lowlands. Form between that of _rigensis_ (_septentrionalis_); cones violet-green to golden brown; seed not markedly brown but on the contrary black, brown-mottled, seed wing gray-violet; needles larger than _lapponica_; the best of the pine in Germany, a very long period of life and greater height with less volume than in _batava_ or _superrhenana_.

var. _batava_. Lower Rhine. Form between _borussica_ and _superrhenana_; early flowering, longer needles, bears cones early, shorter life but fast growing.

var. _septentrionalis_. South and west Scandinavia, northwest Russia. (syn. _P_. _s_. _rigensis_ Desf.). Young trees very fast growing; bark very red; stem tall and straight; branches small, numerous twigs very dense; needles very glossy, long and flat.

var. _supperrhenana_. Upper Rhine. (syn. _P_. _s_. rubra Endl., P. s. haguenensis Loud.) Form between _batava_, _borussica_, and _vindelica_, about similar in height to _borussica_ but with greater wood volume, poor trunk form and greater amount of branching, branches large and scattered in contrast with _lapponica_; foliage bluish-green, particularly in early stage, seeds large.

var. _vindelica_. Northern pre-Alps, North Switzerland, Austria. Frequently straight growing and straighter than _superrhenana_, although not as straight growing as the northern pines, needles short.

var. _pannonica_. Western Hungary. Similar to _superrhanana_ in habit, cone scales flat, crowned and reflexed, seed predominately black, smaller with superior germinating power over _superrhenana_; fast growing, profuse flowering and regular ripening of cones.

var. _aquitana_. Massif Centrale, France, and central Asia. Form resembling _vindelica_, early flowering time (April to early May), seed black, small, wings frequently pale violet, foliage deep-green, short and bright.

Elwes and Henry (1908) stated that the following varieties, occurring in the wild state, have been distinguished.

var. _genuina_ Heer. This is the common pine, growing on good soil in Germany, southern Scandinavia, Poland, and northwestern Russia. Two subvarieties have been distinguished on the continent and in cultivation (_rigensis_ and _haguenensis_).

subvar. _rigensis_ (syn. _Pinus rigensis_ Desf.). Baltic Provinces of Russia, and, according to Willkomm occurs in north Germany, Poland, and Russia. Stem very straight and cylindrical, rising to a great height with few lateral branches; bark very red, stripping off above in very thin papery scales.

subvar. haguenensis Loud. Forest of Haguenau in Alsace. Vigorous in growth but defective on account of its tendency to form numerous irregular branches, so that the stem is not so clean and does not reach the same height as rigensis; bark is not red, and is not so fine scaled as in rigensis.

var. scotica. Highlands of Scotland. Differs in redder bark of the stem; in the shorter, more glaucous leaves (1.5 inches long), often persistent for four years; and in the shorter cones (1.5 inches long), which are symmetrical, with apophyses usually flat near the base, tending to be pyramidal in the upper part of the cone.

var. engadinensis Heer. Engadine Alps. Bark reddish; needles short, 1 to 1.5 inches long, thick and stiff, persistent to five years; buds resinous; cones ovoid-conic, 2 inches long, oblique at the base; apophyses convex on the outer side of the cone, umbo large and blunt. A small tree, rarely reaching 30 feet high.

var. uralensis Fischer. Ural and Altai Mountains. Distinguished by having short and stiff needles.

var. lapponica. (syn. Pinus lapponica Mayr). Northern Norway, Sweden, and Finland. This variety is considered by Willkomm and Christ (Flora de la Suisse, 197, and Suppl. 31 (1907)) to be identical with variety engadinensis, with which it agrees in the short, straight, stiff leaves, persistent for five years, in the resinous buds, and in the small cones with hook-like apophyses. Mayr, however, considers it to be a distinct species, and gives the characters which distinguish it from the common form of P. sylvestris without pointing out in what respect it differs clearly from variety engadinensis.

var. nevadensis Christ. Sierra Nevada Mountains in south Spain. Needles broad, short, and stiff, very white on their flat surface; female flowers erect, purple-red; cone short stalked, nearly sessile, reddish-gray, lustreless, oblique; cone scales with very high curved pyramidal umbos on outer side of cone.

var. reflexa Heer. High moors in Bern Canton, Switzerland, poor sandy soils of Prussia. Needles soft, about 6 cm. long; cones long and slender with long hooks (6 mm.) on the apophyses; cone scales dark red-brown and glossy; commonly a small tree with an irregular crown reaching 19 m.

Beissner (1909) listed Schott's varieties and also the following.

var. genuina Heer. Haguenau area of France. This is the common form of the pine. Form usually pointed with tall stem; cones symmetrical and well developed; cone scales either flat or convex; bark ash-gray to gray-brown; buds gray or reddish-gray, female flowers pale or greenish-red.

var. reflexa Heer. (Range and description as in Elwes and Henry).

var. nevadensis Christ. (Range and Description as in Elwes and Henry).

var. engadensis Heer. Engadine Alps, Tyrol. A branchy tree, slender pyramidal, prostrate form reaching a height of 10 m. with an umbrella shaped crown when with other trees; bark thin, reddish; needle short, thick and stiff, 3 cm. gray-green, sharp pointed and persistent 7 or 8 years, cones ovoid-conic, small, oblique at base, light yellow, symmetrical; cone scales glossy yellow; apophyses convex on the outer of the cone, umbo large and blunt.

Beissner-Fitschen (1930) recognized Schott's varieties. They added some comments to some of the varieties and in addition listed varieties armena, turfosa, and katakeimenos.

var. rigensis hort. (syn. Pinus rigensis Desf. Cat. Hort. Par. Arbr. II (1829) 61 and P. s. septentrionalis Schott, Forstwiss. Cbl. (1907) 278) South and west Scandinavia and Lithuania. Tree very fast growing when young. Bark very red; stem very straight and tall; branches small and numerous, twigs very thick; needles very long glossy and wide.

var. scotica Schott Forstwiss Cbl. (syn. P. scotica Willd. Herb.) (1907) 278. Scotland. Needles shorter and more bluish-green than P. sylvestris, 36 mm. long; cones shorter, 3.5 cm. long, symmetrical; cone scales with the exposed portion flat near the base, tending to be pyramidal in the upper part of the cone.

var. lapponica Fries K. Svenska V. et. Acad. (1888) (syn. Pinus friesiana Wichura Flora XLII (1859) 409; P. lapponica Mayr Fremdl. Wald- u. Parkb. (1906) 348. Lapland, middle and north Scandinavia, north Finland. (Description as in Schott.)

var. engadinensis Heer Verh. Schweiz. Nat. Ges. Luzern (1862). In Engadine Alps, upper Inn valley by Martinsbruck and Finstermünz. (Description as in Beissner (1909)).

var. armena. (syn. Pinus armena K. Koch Linn. XXII p. 297). Crimea, Caucasus, Asia Minor and Persia. Leaves are glossy green, acute, and densely cover the branches; staminate catkins nearly round or broad oval; conelets wide oval often with small points and the edge lightly serrate; young cones on thick very short penduncles, when matured they stand erect or horizontal; slightly glossy and yellowish-brown; upper cone scales usually with raised apophyses on upper half of cone slightly raised or flat on under side.

var. turfosa Woerlein Ber. Bayr. Bot. Ges. III (1893). (syn. Pinus turfosa Willkomm). Bogs of northwest Germany, Baltic Sea shores on heather moors usually among Sphagnum, also on Scandinavian peninsula, Denmark, and northern Russia. Plant only .5 to 2 m. high, usually high shrub with a straight, erect central shoot, forming a small, flat crown later in life. The short needles (25 mm.) are curved and often fall in the second year. It produces numerous small cones with well developed seed.

var. katakeimenos Graebner Naturw. Wochenschr. XIV (1899) 546. Sand dunes on the Baltic coast, in Sweden, and northern Russia. A dwarf form with prostrate stems and branches up to 50 cm. long, but not raised more than 2.1 m. above the ground. The young shoots are very long and slender, and bear normal leaves and cones.

The varieties listed in Beissner (1909) as published by Schott (1907) and not listed above (septentrionalis, borussica, batava, superrhenana, vindelica, pannonica, and aquitana) were as described under Schott (1909).

Rehder (1949) apparently used a very conservative approach and listed only four varieties. Varietal descriptions are from Rehder (1940).

var. rigensis Loud. Bark very red, stem straight and tall. Silviculturally the most important variety. (Range and further description as in Beissner-Fitschen (1930)).

var. scotica Beissner. Bark redder; leaves shorter, about 3.5 cm. long; cones shorter, about 3.5 cm. long. (Range and further description as in Beissner-Fitschen (1930)).

var. lapponica (Fries) Hartman. Of narrower pyramidal habit; leaves broader and shorter, remaining alive 4-7 years; cones more yellowish. (Range and further description as in Schott (1907)).

var. engadinensis Heer. A slow growing pyramidal form with grayish-green, thick and rigid leaves 2.5 to 3.5 cm. long persisting for 7 or 8 years; cones oblique with partly convex apophyses. (Range and further description as in Beissner (1909)).

Svoboda (1953) divided the varieties of Scotch pine into three principal groups on the basis of climatic type and topography. His first group, from central and northern Europe, was listed as, "Borovice severska (*P. s. septentrionalis*), klimatypy (areal vyznacen srafovane)," and included 16 varieties. The second group, from Asia Minor, southern and southwestern Europe, was listed as "Borovice horska (*P. s. montana*), klimatypy (areal nesrafovan)," and included 15 varieties. The third group from south central Russia, Siberia, and north central Asia, was listed as "Borovice stepni (*P. s. stepposa*)," and included 4 varieties. The following are the 35 varieties recognized by Svoboda.

var. *lapponica* Fries. (Range as in Schott.) (syn. *Pinus lapponica* Mayr.)

var. *scotica* Schott. (Range as in Schott).

var. *norvegica*. Subarctic and maritime Norway.

var. *suecica*. Southern Norway, central and south Sweden (syn. var *septentrionalis* Schott).

var. *fennica*. Finland.

var. *borealis*. Northern Russia (extreme north is var. *lapponica*).

var. *uralensis* (Fischer). (Range as in Elwes and Henry).

var. borussica Schott. (Range as in Schott).

var. polonica. Mountainous area of south Poland.

var. baltica. (syn. P.s. rigensis Desf.). (Range as in Elwes and Henry.)

var rossica. Central Russia.

var. ucrainica. Northwestern Ukraine.

var. sarmatica (Zapal.). Southeast central Russia.

var. baschirica. Northeast central Russia.

var. obensis. Urals.

var. jakutensis Sukac. Eastern Siberia.

var. nevadensis (Christ). Sierra Nevada Mountains of south Spain.

var. iberica. North central Spain.

var. pyreneica. Central and western Pyrenees.

var. aquitana Schott. (syn. P. s. avernensis Bayer). Massif Centrale of France.

var. alpina. Upper Inn valley, southern Switzerland and northwest Italy. (syn. P. s. rhaetica Brügger, P. s. engadinensis Heer.)

var. <u>vindelica</u> Schott. (Range as in Schott.)

var. <u>superrhenana</u> Schott. (syn. <u>P</u>. <u>haguenensis</u> Loud.). (Range as in Schott.)

var. <u>pannonica</u> Schott. (Range as in Schott.)

var. <u>hercynica</u> Münch. (syn. <u>P</u>. <u>s</u>. <u>bohemica</u> (Sim.-Kav.)).

var. <u>carpatica</u> Klika. Eastern Czechoslovakia.

var. <u>romanica</u>. Mountains of northwestern Romania.

var. <u>rhodopaea</u>. Mountains of northeastern Greece and southern Bulgaria.

var. <u>illyrica</u>. Central Yugoslavia.

var. <u>pontica</u> C. Koch. (syn. <u>P</u>. <u>s</u>. <u>armena</u> Koch, P. s. <u>pontica</u> Bayer.) Western Turkey.

var. <u>caucasica</u> (Busch-Fisch.) (syn. <u>P</u>. <u>hamata</u> D. Sosn., <u>P</u>. <u>s</u>. var. <u>hamata</u> Stev., <u>P</u>. <u>kochiana</u> Klotzch.). Northern Turkey, Armenian S.S.R., Georgian S.S.R.

var. <u>scythica</u>. South central Russia in Steppe region.

var. <u>kasachstanica</u>. East central Russia and Kazakh S.S.R.

var. <u>altaica</u> Ledeb. Altai Mountains of Siberia.

var. <u>mongolica</u> Litv. (Fomin). Mongolia.

Carlisle (1958) published a guide to the taxonomy of Scotch pine in which he names 13 geographic variants and an additional 13 possible variants. He considered varieties as collections of many forms (habit, cone, leaf, and flowering parts) where certain forms predominated to distinguish that variety when studied as a whole. His descriptions of the varieties he knew best were therefore comparative rather than definitive. Table 33 summarizes Carlisle's views on the 4 varieties he knew best. The remaining 22 named varieties are listed but described only where additional characteristics have been added since the description was made by the original author. Carlisle's descriptions closely follow those found in Schott, Beissner, and Beissner and Fitschen. These 22 varieties are (with authorities as cited by Carlisle):

var. borussica Schott. (Range and description as in Schott.)

var. batava Schott. (Range and description as in Schott.)

var. superrhenana Schott. (Range and description as in Schott.)

var. vindelica Schott. (Range and description as in Schott.)

var. hercynica Münch. Southern and mid-German mountains; to 1,000 m. in the Schwarzwald and to more than 630-720 m. in mid-Germany. The stem is very straight and the crown narrow and pointed, with slender and flexible branches. In lower situations the stem remains straight, but the narrow, pointed crown is less marked. It forms valuable

Table 33.--Principal comparative characteristics of four Scotch pine varieties as given by Carlisle (1958).

	Characteristics					
Variety	Crown Width	Leaf and Size	Leaf Persistence	Cone Color	Length	Remarks
Scotica	Broad	Glaucous, 44 mm.	2-5 years	Gray-brown, gray-green-brown	45 cm. mean	Buds red-brown.
lapponica	Narrow	Less glaucous	4-7 years	Straw-yellow, brownish-yellow	36 cm. mean	Leaves often yellowish or violet in winter
septentrionalis	Broad	Not glaucous 35-43 mm.	3-6 years	Gray-brown-green	4.0 cm. mean	
rigensis	Narrow	Not glaucous	--	Gray, sometimes tinged with violet	--	Buds yellowish to red. Bark pronounced reddish yellow down to 1 to 2 m. above soil

stands. A somewhat similar type occurs in northeast Germany, but var. *hercynica* is quite different from var. *superrhenana* (Münch, 1924).

var. *haguenensis* Loudon. (Range and description as in Elwes and Henry.)

var. *engadinensis* Heer. (Range and description as in Beissner (1909)).

var *aquitana* Schott. (Range and description as in Schott.)

var. *subillyricum* Corona. Trentino Province of Italy.

var. *pannonica* Schott. (Range and description as in Schott.)

var. *nevadensis* Christ. (Range and description as in Beissner (1909)).

var. *armena* Beissner. (Range and description as in Beissner and Fitschen (1930)).

var. *altaica* Ledebour. Altai Mountains of Russia. A tree 15 m. high with a compact pyramidal crown and short leaves.

Carlisle stated that the following varieties had been mentioned in literature but that little is known of them except that they occur in certain geographic areas:

var. caucasica Busch. (syn. P. caucasica Busch). Caucasus Mountains.

var. altissima Loudon. (Probably synonymous with var. caucasica). Caucasus Mountains.

var. uralensis Fischer. Ural Mountains of Russia. Has short stiff needles.

var. sibirica Ledebour. Altai Mountains of Siberia up to 900 m. and in Sungaria and Kirghiz in Russia. It has short leaves and cones with numerous scales, some being flattened and others bearing a prominent, pyramidal apophysis. (Carlisle considered it syn. with altaica.)

var. jacutensis Sukacz.

var. annulata Jurinson.

var. funebris Kom. Mentioned by Kruberg (1937) as growing in eastern Siberia.

var. mongolica. Mentioned by Kruberg (1937) as growing in Siberia.

var. cretacea Kalenicz. Occurs in Russia on calcareous sites.

Gaussen (1960) tended to discount the value of chemistry, wood anatomy and hybridization and to emphasize needle anatomy and the size of pollen grains as a means of arriving at his species of the genus Pinus. However, his determination of valid varieties was somewhat arbitrary. His monograph of the genus Pinus lists the following 25 varieties of Scotch as authentic under 7 classifications or groupings (author citations are Gaussen's):

I. Nordic variety.

var. lapponica Fries.

II. Baltic varieties.

var. septentrionalis Schott
var. rigensis Desf.

III. Scotland variety.

var. scotica Schott.

IV. Varieties of the Western Mountains of Europe.

var. hercynica Münch.
var. aquitana Schott
var. vindelica Schott
var. pyreneica Svob.
var. iberica Svob.
var. catalaunica Gaus.
var. brigantiaca Gaus.

V. Varieties of the lower altitudes of the middle and southern areas.

var. haguenensis Loud.
var. batava Schott
var. borussica Schott (considered var. sylvestris by Gaussen)
var. engadinensis Heer
var. nevadensis Christ
var. pannonica Schott
var. carpatica Klika
var. vocontiana Guinier and Gaus.

VI. Non-geographic trees deformed by hostile environment.

var. turfosa (Willk.) Woer.
var. katakaimenos Graeb.

VII. Eastern forms.

var. armena K. Koch (syn. P. kochiana Klotzsch)
var. uralensis Fischer
var. siberica Ledeb.
var. yamazutai Uyek.

Gaussen dismisses as not sufficiently known or characterized the following varieties although he states that they are probably varieties with special characters:

var. sarmatica Zapal (along with the climatic types rossica Svob., and Baschirica Svob.)
var. rhodopaea Svob.
var. illyrica Svob.

Table 34 summarizes the varieties of Scotch and the geographic regicns where they predominate.

Weidemann (1930) summarized tne 1907 IUFRO Scotch pine European provenance tests. The results, based on 16 outplantings in Sweden, Germany, Belgium, Hungary, and the Netherlands, of 12 origins from the Ural Mountains of U.S.S.R., Northern Sweden, Scotland, Latvia, Prussia, northeast and western Germany, Belgium, Central Mountains of France, eastern and southern Czechoslovakia, and central Bulgaria, showed that geographical differences existed between the origins. The separate published reports summarized by Weidemann showed that the various provenances could be characterized as follows:

North Sweden. Very slow growth and straight stems.

Latvia. Moderately fast growth, straight stems, pointed crowns.

Prussia. Similar to Latvian but with slightly more crooks.

German. Fast growth, crooked stems, pointed crowns, variable form.

Table 34.--Summary of the named varieties of Scotch pine and the geographic regions in which they predominate.

Geographic Area	Schott 1907	Elwes and Henry 1908	Beissner 1909	Beissner and Fitschen 1930	Rehder 1949	Svoboda 1953	Carlisle 1958	Staszkiewicz 1960, 61, 62	Gaussen 1960
	Author and Date								
1. N. Scandinavia, N. Russia	LAPP	LAPP	LAPP	LAPP	LAPP	LAPP	LAPP	LAPP	LAPP
2. N. Russia	SEPT	RIGE	SEPT	--	--	BORE	--	--	SEPT
3. Cent. Norway, Sweden, Finland	--	--	--	RIGE	--	--	SEPT	--	SEPT
4. S. Norway, Cent. Sweden	SEPT	--	SEPT	RIGE	--	SUEC	SEPT	SUEC	SEPT
5. S. Finland	SEPT	--	SEPT	RIGE	--	FENN	SEPT	--	SEPT
6. S. Sweden	SEPT	--	SEPT	RIGE	--	SUEC	SEPT	SUEC	SEPT
7. Norway	SEPT	--	SEPT	--	--	NORV	SEPT	--	SEPT
8. Scandinavia, W. Russia, N. Germany	--	--	--	SEPT	--	--	--	--	SEPT
9. S. and W. Scandinavia, NW. Russia	SEPT	RIGE	SEPT	--	--	--	SEPT	--	SEPT
10. Latvia, Esthonia	SEPT	RIGE	SEPT	RIGE	RIGE	BALT	RIGE	--	RIGE
11. Poland	--	--	--	--	--	--	--	POLO	POLO
12. Bogs of NW. Germany and Poland	--	--	--	TURF	--	--	--	--	TURF
13. Dunes of S. Baltic Coast	--	--	--	KATA	--	--	--	--	KATA
14. Scotland	SCOT	SCOT	SCOT	SCOT	SCOT	SCOT	SCOT	--	SCOT
15. NE. Germany lowlands	BORU	--	BORU	BORU	--	BORU	BORU	--	--
16. S. Poland, Mtns.	--	--	BORU	BORU	--	POLO	--	SUBC	POLO
17. E. Cent. Germany	--	--	--	--	--	HERC	--	--	ROSS
18. Lower Rhine, NE France, Belgium	BATA	--	BATA	BATA	--	SUPE	BATA	--	BATA
19. Vosges Mtns., France	BATA	--	BATA	BATA	--	VIND	BATA	--	HERC
20. Alsace and Rastadt areas of France and Germany	BATA	HAGU	BATA	BATA	--	SUPE	HAGU	--	HAGU
21. Upper Rhine	SUPE	--	SUPE	SUPE	--	SUPE	SUPE	--	VIND
22. N. Alps and foothills	VIND	--	VIND	VIND	--	VIND	VIND	--	VIND
23. S. and Cent. Germany, Mtns.	--	--	--	--	--	HERC	HERC	--	HERC
24. Engadine Alps, Austria	VIND	ENGA	ENGA	ENGA	ENGA	ALPI	ENGA	--	ENGA
25. Switzerland, Bern Canton	VIND	REFL	REFL	VIND	--	VIND	--	--	--
26. SE. France, W. Switzerland, Jura Mtns.	--	--	--	--	--	VIND	--	MERI	VOCO
27. SW. Alps	--	--	--	--	--	--	--	--	BRIG
28. S. Swiss Alps and N. Italy	--	--	--	--	--	ALPI	SUBI	--	--
29. Central Massif, France	AQUI	--	AQUI	AQUI	--	AQUI	AQUI	MERI	AQUI
30. S. Central Massif, France	AQUI	--	AQUI	AQUI	--	AQUI	AQUI	CAUS	AQUI
31. Cent. and W. Pyrenees	--	--	--	--	--	PYRE	--	--	PYRE
32. NE. Spain	--	--	--	--	--	--	--	--	CATA
33. N. Cent. Spain	--	--	--	--	--	IBER	--	--	IBER
34. S. Cent. Spain	--	NEVA	NEVA	--	--	NEVA	NEVA	--	NEVA
35. E. Czechoslovakia	--	--	--	--	--	CARP	--	MERI	CARP
36. W. Hungary	PANN	--	PANN	PANN	--	PANN	PANN	MERI	PANN
37. Cent. Yugoslavia	--	--	--	--	--	ILLY	--	--	--
38. S. Bulgaria, NE. Greece	--	--	--	--	--	RHOD	--	--	--
39. Rumania	--	--	--	--	--	ROMA	--	--	--
40. W. Turkey	--	--	--	ARME	--	PONT	ARME	--	ARME
41. E. Turkey, Armenian and Georgian SSR., Iran, Crimea	--	--	--	ARME	--	CAUC	ARME	--	ARME
42. Caucusus Mtns. of Georgian SSR and Turkey	--	--	--	ARME	--	CAUC	CAUC	--	ARME
43. N. Cent. Russia	--	--	--	--	--	ROSS	--	--	--
44. SE. Cent. Russia	--	--	--	--	--	SARM	--	--	--
45. Ukrainian SSR	--	--	--	--	--	UCRA	--	--	--
46. SE. Russia and Kazakh SSR	--	--	--	--	--	KASA	--	--	--
47. NE. Cent. Russia W. of Urals	--	--	--	--	--	BASC	--	--	--
48. Siberia (Lat. 60o - 69o), Ob to Yenesei R.	--	--	--	--	--	OBEN	--	--	--
49. Ural Mtns.	--	URAL	--	--	--	OBEN	URAL	--	URAL
50. Steppe area of Russia	--	--	--	--	--	SCYT	--	--	--
51. Altai Mtns. Siberia, S. to Kirghiz and Sungaria	--	URAL	--	--	--	ALTA	ALTA	--	SIBI
52. N. Cent. Siberia, Yenesei to Olenek and Lena rivers		--	--	--	--	JAKU	JAKU	--	--
53. E. Siberia to Manchuria	--	--	--	--	--	--	FUNE	--	YAMA
54. Mongolia	--	--	--	--	--	MONG	MONG	--	--

Key to varietal names:

ALPIna, ALTAica, AQUItana, ARMEna, BALTica, BASChirica, BATAva, BOREalis, BORUssica, BRIGantiaca, CARPatica, CAUCasica, CAUSsicola, ENGAdinensis, FENNica, FUNebris, HAGUenensis, HERCynica, IBERica, ILLYrica, JAKUtensis, KASAchstanica, KATAkemeinos, LAPPonica, MERIdionalis, MONGolica, NEVAdensis, NORVegica, OBENsis, PANNonica, POLOnica, PONTica, PYREneica, RHODopaea, RIGEnsis, ROMAnica, ROSSica, SARMatica, SCOTica, SCYThica, SIBIrica, SEPTentrionalis, SUBCarpatica, SUBIllyricum, SUECica, SUPErrhenana, TURFosa, UCRAinica, URALensis, VINDelica, VOCOntiana, YAMAzutai.

Scotland. Slow growth, variable form, many forked and a few crooked stems.

U.S.S.R. (Ural Mountains). Very slow growth, variable in form.

France. (Central Mountains). Slow growth, variable in form.

Belgium. Crooked stems, large branches, very fast growth.

Mortality due to war, fire, and other causes reduced the amount of information that could be gained, particularly for the origins not included in the above summary.

There is essential agreement in height growth between the relative rates of growth reported in provenance experiments by Weidemann (1930), Langlet (1936, 1937), Vincent and Polnar (1953), Wright and Baldwin (1957). The greatest growth rate was shown by the Belgian origin, followed by the origins from Germany, Netherlands, Latvia, Rumania, southern Scandinavia, Scotland, central Scandinavia, northern Scandinavia, in that order.

In 1957 Wright and Baldwin reported on the New Hampshire planting of the 1938 IUFRO provenance test. They measured mortality, average height, diameter, branch diameter, basal sweep, lean, crooks, large crooks, porcupine damage, and fruiting. Significant differences between origins were found principally in height, and the per cent of trees with basal sweep, lean and crooks. The regions defined by these differences were:

Northern Norway, Sweden, and Finland
Central Norway and Sweden, and central and southern Finland
South central Norway and Sweden
Scotland

Latvia, Esthonia
Poland, Germany, Czechoslovakia, and Hungary
Belgium
Romania
Italy
Netherlands

Gerhold (1959) reported on analyses of color, pigments, and nutrient elements in needles of six of the geographic races represented in the 1938 IUFRO plantings in New Hampshire. The six races tested were from the Netherlands, north central Germany, Poland, Czechoslovakia, Sweden (64° latitude), and Norway (62° latitude). He found statistically significant differences in the concentrations of elements in needles between races. Trees from northern origins contained more chlorophyll in the summer and less in the winter than other origins. Gerhold stated that latitudinal effects (i.e. day length) etc. only could not explain the variation pattern.

Staszkiewicz (1960, 1961, 1962) studied the populations of Scotch pine in Poland, Czechoslovakia, Switzerland. France, Scotland, Sweden, and Finland and, on the basis of ten measurements taken from the cones, separated the populations as follows:

Northern Sweden and Finland	var. lapponica
Central and southern Sweden and Prussia	var. suecica
Poland	var. polonica
Northeast Czechoslovakia and southern mountainous Poland	var. subcarpatica
Czechoslovakia, Switzerland, Italy, Hungary, central mountains of France	var. meridionalis

Southern portion of the central mountains of France — var. caussicola

Wright and Bull (1963) reported the following geographic ecotypes of Scotch pine based on one year data for 64 provenances and three year data for 122 provenances grown in Michigan:

A Northern Norway, Sweden, and Finland
B North central Sweden
C Central and southern Norway, central Sweden, and southern Finland
D Southern Sweden and Latvia
E Siberia and Ural Mountains
F Poland
G South and East Germany, Czechoslovakia, and Austria
H Western Germany, eastern France, Belgium, Italy, and Hungary
I England
J East central France, central Austria, and Yugoslavia
K Greece, Georgian S.S.R., and Turkey
L Scotland
M Central Mountains of France
N Spain

Significant differences were found between provenances in seed measurements, height, foliage color, time of color change, bud color, form, and start and cessation of growth, lammas shoots, secondary leaf formation, leaf length, and ease of pulling (measure of type of root formation and of root development.)

The 1938 IUFRO test results and Michigan provenance test results are based on genetic differences in origins grown under a common environment.

This study, based on the biometric differences in cone, seed, and leaf characteristics of specimens from living wild populations from 33 of the 122 origins included in the three year provenance test reported on by Wright and Bull (1963), has confirmed the geographic ecotypes of the 1963 report except for areas B and D, which were not sampled. In addition, parental morphological differences indicate a separation of the Turkish and Greek populations and show that the Czechoslovakian population is different from the East German in cone characters and in leaf twist.

It is also reasonable to assume that further differentiations could be made in Wright and Bull's regions E, G, H, and J, since they consist of areas which have been described by previous authors as separate entities, i.e., the populations in the Ural Mountains and in the Altai Mountains of the U.S.S.R., the populations in eastern France and Hungary, and the western Alps and Yugoslavia.

Except in the instances of the isolated populations along the southern and eastern limits of the distribution of Scotch pine one would expect a gradual transition from one variety to another based upon the gradualness of the environmental differences and the size and density of the populations. Selection is a slow continuing process and there have been relatively recent geological and meteorological changes wrought by the complex glaciation pattern of a large part of the area occupied by Scotch pine. While the genetic and morphological changes in Scotch pine may not be abrupt it is a fact that there are proven differences in populations. These populations can be defined biometrically and genetically. Table 35 is a list of geographical varieties based on genetic and biometric studies and descriptions based on field study and research by Ledebour (1833), Steven (1838), Schott

Table 35.--Varieties of Scotch pine (Pinus sylvestris L.) and the regions in which they predominate.

Variety	Geographical Area
lapponica	Northern part of Norway, Sweden, and Finland, and northwest Russia.
septentrionalis	Central and southern Norway, central Sweden, southern Finland.
rigensis	Southern Sweden and Baltic Provinces of Russia.
scotica	Highlands of Scotland.
polonica	Poland.
borussica	Northeast German lowlands.
hercynica	South and east Germany and central Austria.
haguenensis	Western Germany, eastern France, and Belgium.
vindelica	Southeast central France, Switzerland, and western Austria.
engadinensis	Engadine Alps, upper Inn Valley, and eastern Switzerland.
aquitana	Central mountains of France (Massif Centrale).
iberica	North central Spain.
nevadensis	Sierra Nevada Mountains of southern Spain.
carpatica	Northeastern and eastern Czechoslovakia.
pannonica	Western highlands of Hungary.
illyrica	Central mountains of Yugoslavia.
rhodopaea	Southern Bulgaria, northeast mountains of Greece.
armena	Northeast Turkey, Armenia, Georgian SSR, and Iran.
uralensis	Ural Mountains in USSR and area immediately to west.
altaica	Altai Mountains in USSR south to Kirghiz and Sungaria.
mongolica	Eastern Siberia and Manchuria.

(1905), Münch (1924), Komarov (1934), Kruberg (1937), Sukatchev (1938), and others previously mentioned or cited as authors of the varietal names.

The highly variable nature of Scotch pine makes it difficult to define varieties except on a population study basis. Most authors have pointed out that stands are mainly identifiable on the basis of the predominance of certain types over others rather than as distinctly different trees morphologically, particularly when speaking of contiguous areas. Some areas have easily identifiable forms such as those occupied by varieties _lapponica_, _rigensis_, _engadinensis_, _nevadensis_, or the noble race of the Vosges Mountains of France. Other varieties, however, are not so easily identified.

The area of collection for the specimens of Linnaeus is in doubt. Annotations on sheet 1135.2 in the Linnaean Herbarium in apparently Linnaeus' hand, include the name "Kalm" with no other information as to the region of collection. Kalm, a student of Linnaeus, collected in Europe and in the United States. On another sheet (1135.1) is the annotation "ex Leche" indicating a Scandinavian specimen. Elwes and Henry (1908) described Heer's variety _genuina_ as containing two races, _rigensis_ and _haguenensis_, and give the range of _genuina_ as growing on good soil in Germany, southern Scandinavia, Poland, and northwest Russia. Many authors define varieties as being morphologically different from a standard or common Scotch pine without reference as to the locale of the typical variety _sylvestris_. Until a lectotype of _Pinus sylvestris_ is designated, it will not be possible to refer to a "typical" variety of the species. It may also be necessary to typify a number of the other varieties as well as variety sylvestris.

The synonomy which follows is based on the studies of geographical varieties by previously cited authors, published provenance tests, and biometric studies of parental populations. The varieties accepted here are not considered complete since future investigations into serology, anatomy, etc., and the more mature characteristics of origins now being observed in provenance tests should provide additional information on genetic and phenotypic differences.

P. sylvestris var. lapponica (Fries) Hartman, Handb. Skand. ed. ed. 5, 214 (1849)

P. sylvestris var. lapponica Fries, Summa Veget. Scand. 1:58 (1846), nom.

P. frieseana Wichura in Flora, 42:409 (1859) - Ascherson and Graebner, Syn. Mitteleur. Fl. ed. 2, 1:345 (1912)

P. lapponica (Hartm.) Mayr, Fremdl. Wald- u. Parkbäume 348 (1906)

P. sylvestris var. borealis Svodoba, Lesni Dreviny A Jejich Porosty, Cast I, Praha. 203. (1953)

P. sylvestris var. frieseana Caspary (Wichura), Die Nuphar der Vogesen und des Schwarzwaldes. Halle, (1870).

P. frieseana Wichura. Flora XLII, 409 (1859).

Higher proportion of narrow crowns than var. scotica and var. septentrionalis with branches persisting low down on the stem; leaves not glaucous, often yellowish or violet in winter, short, averaging 41 mm., persisting 4-7 years; Cones short, mean length 3.6 cm; seed mean length 3.4 mm., mean width 2.1 mm., mean weight 4.4 mg. Mean pollen air-sac length 37 microns.

Distribution: Northern Norway, Sweden, and Finland, northwestern Russia to about 70 degrees North Latitude. Merging southwards into var. septentrionalis.

P. sylvestris var. rigensis Loudon, Arb. Brit. 4:2157 (1838).

P. rigensis Loddiges. Cat. ex. Loudon, Hort. Beit. 4:387 (1830) nom - Desfontaines ex Moroques in Mem Soc. Agri. Orleans, Ser. 2, 25:43 pl. 5, fig. 10 (1885) pro. syn.

P. rigensis Desfontaines, Cat. Hort. Par. Arbr. II (1829) 61.

P. sylvestris var. baltica Svoboda, Lesni Dreviny a Jejich Porosty Praha (1953).

P. sylvestris var. rigensis Hort. ex Beissner-Fitschen Nadelholz-Kundr (1930) 416.

P. sylvestris var. rigensis (Desfontaine) Ascherson and Graebner Synopsis dev Mitteleur. Fl. I. 13d Leipzig (1912).

P. sylvestris var. rigensis Loudon (Fischer) [?]

P. sylvestris var. septentrionalis Schott, Forstwiss. Cbl. 278 (1907) pro parta.

Crowns pyramidal, lance shaped, stems straight with ascending branches; bark pronounced reddish-yellow down to about 1-2 meters above soil; leaf mean length is 58 mm. without a pronounced glaucous sheen; seed mean length is 4.0 cm., buds are green-tan.

Distribution - Southern Sweden and Baltic Provinces of U.S.S.R.

P. sylvestris var. scotica Beissner, in Jager and Beissner, Ziergeh. ed. 2, 488 (1884).

P. sylvestris var. scotica (Wildenow) Schott, in Klika, Siman, Novak, & Kavka, Jehlicnate, Nakladatelstvi Ceskoslovenske Akademie ved. Praha (1953)

P. sylvestris var scotica Schott, Beissner, Handbuch der Nadelholzkunde. (1909) 431. - Schott, Forstwiss. Cbl. (1907) 278 - Carlisle, A Guide to the Named Variants of Scots Pine (Pinus sylvestris L.). Forestry, XXXI: 204, (1958) - Svoboda, Lesni Dreviny a Jejich Porosty. Cast 1, Praha 201 (1953).

P. sylvestris var. montana Sang, in Loudon, Encyclopaedia Plants. London (1855).

P. scotica Willdenow ex Endlicher Syn. Conf. 172 & Conf. (4 (1840)).

P. sylvestris horizontalis Antoine (sec. Schott (1909))[?]

P. horizontalis Don (of Forfar sec Schott (1909)) [?]

Older trees are flat crowned with narrow crowns rare. Leaves glaucous, 4.5 cm. long, twisted, green throughout the year; Persist 2-5 years; cones short, mean length is 4.5 cm. mean width closed 2.2 cm.; seed mean weight 7.2 mg., mean length is 4.5 mm., mean width 2.6 mm; buds green to green-tan; pollen air-sac length 38 microns.

Distribution - Highlands of Scotland.

P. sylvestris var. *polonica* Svoboda, Lesni Dreviny a Jejich Porosty. Cast 1, Praha. 206 (1953).

Cone mean length 3.6 cm., mean width 1.9 cm. (Staszkiewicz (1960)).

Distribution - Poland north of mountains along southern border.

P. sylvestris var. *borussica* Schott. Forstwiss. Cbl. 278 (1907).

P. sylvestris var. *baltica* Svoboda Lesni Typy. Praha. (1950).

Crown variable, slender crowns in north and east with moderate branch development to heavier branches and wider crowns southward, vigorous growth; long life; leaf length cm.; seed mean length 4.0 mm., mean weight 6.2 mg.

Distribution - Northeast German lowlands.

P. sylvestris var. *hercynica* Münch, Allg. Forst- u. Jagdztg. c. 540, (1924).

Stem is straight and the crown narrow and pointed with slender, flexible branches except at lower elevations where the crown may be broader; leaf mean length 5.4 cm.; cone mean length 4.1 cm., mean width closed 2.1 cm.; seed mean length 4.3 mm. mean width 2.7 mm.

Distribution - Southern and Mid-German mountains to 1,000 m. and in Black Forest to 630-720 m. merging into var. borussica in north-east.

P. sylvestris var. haguenensis Loudon, Arb. Brit. (1838).

P. scariosa Loddiges ex Loudon, Encyc. Trees, 953.

P. scariosa Loddiges Cat. of Plants in the Collection of Conrad Loddiges and Sons, London, ED XVI (1836).

P. sylvestris var. superrhenana Schott. Forstwiss. Cbl. 278 (1907).

P. haguenensis Loudon ex Beissner. Handb. Nadglholzk. 228 (1891).

P. sylvestris var. rubra Endlicher Synopsis Coniferarum (1847)

P. sylvestris batava Schott, Forstwiss. Cbl. 228 (1907).

P. sylvestris var. genuina subvar. haguenensis Elwes and Henry, the Trees of Great Britain and Ireland. Edinburgh (1908).

P. haguenensis Hort ex Lavallee. Arb. Segrez. 245 (1877).

Stem form inferior to var. borussica but producing large volume of wood, tendency toward large horizontal branches; leaf mean length 6.9 cm.; cone mean length 4.9 cm., mean width closed

2.4 cm.; seed mean length 4.5 mm., mean width 2.7 mm., mean weight 6.7 mg.

Distribution - Rhine River Valley, eastern France, and Belgium.

_P_. _sylvestris_ var. _vindelica_ Schott, Forstwiss. Cbl. (1907) 278.

_P_. _sylvestris_ var. _vulgaris_ Bauhin [?]

_P_. _genevensis_ Hort ex Carriere. Conif. ed. I. 372.

_P_. _genevensis_ Hort. ex Endlicher Synopsis Coniferarum. (1847) (4)

_P_. _sylvestris_ var. _vulgaris_ _genevensis_ Bauhin [?]

Distribution - Southeast central France, Switzerland, and western Austria.

_P_. _sylvestris_ var. _septentrionalis_ Schott. Forstwiss. Cbl. 278 (1907)

_P_. _sylvestris_ var. _suecica_ Svoboda, Lesni dreviny a jejich porosty. I. Praha. 202 (1953).

_P_. _sylvestris_ var. _fennica_ Svoboda, _ibid_.

_P_. _sylvestris_ var. _norvegica_ Svoboda, _ibid_.

Crowns variable but usually broad with branches persisting a short way down the stem, and a few narrow crowns with low persisting branches in eastern part of area. Leaves not glaucous, mean length 5 cm., persistent 3-6 years; cone short, mean length 4 cm.; seed mean length 3.9 mm., mean width 2.4 mm; mean pollen air-sac length is 37 microns.

Distribution - middle and western Scandinavia and northwestern Russia, merging into var. rigensis in south Sweden and Baltic Provinces of Russia.

P. sylvestris var. engadinensis (Heer) Hegi, Ill. Fl. Mitteleur. 1:100 (1907).

P. sylvestris subsp. engadinensis Ascherson and Graebner Syn. Mitteleur. Fl. ed. 2, 1 (1912).

Small tree, reaching height of 15 m. with branches persisting low down on stem. Leaves short, less than 3.5 mm. thick, stiff, persistent 4-5 years; cones small with convex apophyses bearing large blunt umbos.

Distribution - Engadine Alps, Tyrol, Upper Inn Valley, Switzerland.

P. sylvestris var. aquitana Schott. Forstwiss Cbl. (1907) 278.

P. sylvestris var. avernensis Bayer [?]

P. sylvestris var. caussicola Staszkiewicz, Floristica and Geobotanica Ann. IX, Pars 2: 174-187, (1963).

P. sylvestris var. pyreneica Svoboda, Lesni Dreviny a Jejich Porosty. Cast 1 213 (1953).

Leaves 4.6 cm. long twisted; cones moderately long, mean length 5.0 cm., mean width closed 2.5 cm.; seed mean length 4.7 mm., mean width 2.7 mm.

Distribution - Central Mountains of France (Massif Centrale).

P. *sylvestris* var. *iberica* Svoboda, Lesni Dreviny A Jejich Porosty Praha Cast 1. 212 (1953).

P. *sylvestris* var. *catalaunica* Gaussen, Les Gymnospermes, Actuelles and Fossiles. Chap. XI, Travaux du Laboratoire Forestier de Toulouse. Tome II, sect. 1, vol. 1, part 2 (1960) 161.

Leaves blue-green, mean length 4.8 cm. average twist about 210 degrees; cone mean length 5.0 cm., mean width closed 2.5 cm.; seed mean length 5.4 mm., mean width 3.0 mm.

Distribution - central and northern Spain.

P. *sylvestris* var. *nevadensis* Christ, Verh. d- Naturf. Ges. Basel, III Teil (1963) Heft. 4.

P. *sylvestris* var. *hispanica* Svoboda, Lesni Typy, Praha (1950).

Poor timber form with short, broad, stiff needles.

Distribution - Sierra Nevada Mountains of southern Spain up to 2,400 m. Southernmost natural population of Scotch pine (37 degrees north latitude).

P. *sylvestris* var. *carpatica* Klika, Poznamky k rasam (ekotypum) Borovice v Ceskoslovensku. Vest Ceskoslov. Akad. Zamedelske 10: 2-3.

P. *sylvestris* var. *carpatica* Domin. (1937).

P. *sylvestris* var. *subcarpatica* Staszkiewicz, Floristica et Geobotanica Ann. VII, pars 1, (1961) 158.

Leaf mean length 5.0 cm., twist approximately 280 degrees, cones, mean length 3.9 cm., mean width closed 2.0 cm., seed mean length 4.5 mm., mean width 2.7 mm.

Distribution - Carpathian Mountains of Czechoslovakia and Poland and eastern Czechoslovakia.

P. sylvestris var. *pannonica* Schott. Forstwiss. Cbl. (1907) 278.

P. sylvestris var. *meridionalis* Staszkiewicz, Acta Botanica, Acad. Scientiarum Hungaricae, Tomus VII, Fasciculi 3-4 (1961) 451-456. Pro parta.

P. sylvestris var. *bohemica* Siman (1923)

Cone mean length 3.9 cm., mean width 1.9 cm. (Staszkiewicz, (1961)).

Distribution - Western hill country of Hungary.

Remarks - Staszkiewicz (1961) considers this population as part of his variety *meridionalis* on the basis of cone samples but states that it is possible that it may be a separate variety when other characters are analyzed.

P. sylvestris var. *illyrica* Svoboda, Lesni Dreviny a Jejich Porosty, Cast 1, Praha. 212 (1953).

P. sylvestris var. *balcanica* Svoboda, Lesni Typy. Praha, (1950) Pro parta.

Leaf mean length 5.8 cm., twist 280 degrees; cone mean length 4.7 cm., mean width closed 2.4 cm.; seed mean length 4.7 mm.; mean width 3.0 mm.

Distribution - Central Mountains of Yugoslavia.

P. sylvestris var. *rhodopaea* Svoboda, Lesni Dreviny a Jejich Porosty. Cast 1. 219 (1953).

P. sylvestris var. *balcanica* Svoboda, Lesni Typy, Praha, (1950), pro parta.

Leaf mean length 4.1 cm., twist 180 degrees; cone mean length 3.8 cm., mean width closed 2.0 cm.; seed mean length 4.5 mm., mean width 2.6 mm.

Distribution - Mountains of northeast Greece and southern Bulgaria.

P. sylvestris var. *armena* K. Koch in Tchihatcheff Asie Min. 2 p. 496-499.

P. sylvestris var. *pontica* K. Koch

P. armena K. Koch, Linnaea 22: 296 (1849).

P. sylvestris var. *pontica* Bayer [?]

P. sylvestris var. *caucasica* (Busch-Fisch.)

P. hamata (Steven) Sosn. Fl. Tifl. 11 (1925).

P. sylvestris var. *hamata* (Steven) Komarov. Fl. U.S.S.R. 1, 170 (1934)

P. kochiana Klotzsch ex C. Koch, Linnaea 22: (1849) 296.

P. sylvestris var. *caucasica* Fischer

P. sylvestris var. *altissima* Loudon

P. *altissima* Ledebour ex Gordon. Pinatum 186.

P. *hamata* (Steven) Fomin. Mem. Acad. Sc. Ukraine, Cl. Sc. Phys. and Math. XI. 23 (1928).

P. *sosnowskyi* Nakai. Tyosen. Kaiho, No. 167 (Indig. Spec. Conif. and Taxads, Korba and Manchuria IV) 33 (1934)

Leaf mean length 5.4 cm., twist 180 degrees; cone mean length 5.3 cm., mean width closed 2.7 cm.; seed mean length 4.9 mm., mean width 3.2 mm.

Distribution - Crimea, Turkey, Caucasus, Armenian SSR, Georgian SSR and Iran.

P. *sylvestris* var. *uralensis* Fischer [?]

P. *sylvestris* var. *obensis* Svoboda, Lesni Dreviny a Jejich Porosty. Cast 1. 209 (1953).

P. *sylvestris* var. *sibirica* Ledebour (1883) pro parta.

P. *padufia* Ledebour ex Gordon. Pinatum 186.

P. *sylvestris* var. *altaica* Ledebour [?]

Distribution - Ural Mountains of U.S.S.R.

P. *sylvestris* var. *altaica* Ledebour, Fl. Altaica IV (1833).

P. *sylvestris* var. *sibirica* Ledebour, pro parta.

P. *sylvestris* var. *altaica* Komarov, Fl. U.S.S.R., Leningrad (1934)

P. *padufia* Ledebour ex Gordon. Pinatum 186. Pro parta.

Distribution - Altai Mountains of U.S.S.R. south to Kirghiz and Sungaria.

P. sylvestris var. *mongolica* Litvinof, Hossiji Trudy Botan. muz. Akad. nauk 1 (1902).

P. funebris Komarov in Acta Hort. Petrop XX (1901), Mitt. d. d. dendr. Gesllsch. (1903) 61.

P. yamazutai Uyeki Jour. Chosan Nat. Hist. Soc. No. 9, 20 (1929).

P. takahasii Nakai (1939) [?]

P. sylvestris subsp. *mongolica* Fomin (1936) [?]

P. sylvestris var. *jakutensis* Sukac [?]

Distribution - Northeastern Mongolia, southeast central Siberia, Manchuria.

Validity of the Named Varieties

The International Code of Botanical Nomenclature (1961) requires that on or after January 1, 1953, the name of a taxon, to be validly published, must have been published through distribution of printed material containing a description or reference to a description previously published and a Latin diagnosis in a form which complies with that required by the International Code. In addition, valid publication on or after January 1, 1958, requires the designation of the nomenclatural type.

The above requirements have not been met by Svoboda (1953) or by Gaussen (1960) and the names included in this discussion cited with the above authors cannot be considered to have been validly published.

Discussion

The synonymy of Scotch pine is probably one of the most complicated of all the pine species. Linnaeus included Scotch pine in his Species Plantarum (1753) with the notation that the species had two needles per fascicle and glabrous primary leaves. Prior to and since Linnaeus's description there have been numerous taxonomists, biologically oriented travelers, and horticulturists who have described a multitude of varieties and forms. Carlisle (1958) listed 144 varieties and forms in his resumé of the Scotch pine. Recent provenance tests and biometric studies of Scotch pine indicate that there are differences between populations, particularly along the eastern and southern edge of the distribution area among the isolated stands, and within the more or less continuous population extending from northern Europe to southern Europe. This does not imply discontinuity within these areas but rather a difference between the characters when measured at certain points. These samples are biometrically different and have been referred to as geographic varieties. Their existence has been proven genetically. Provenance tests conducted under uniform conditions of environment have proven the existence of races of Scotch pine.

The results of this study and the biometric and provenance studies reviewed provide sufficient data for confirming some of the varieties previously named or suggested, but are not considered sufficient evidence to preclude additional varieties or races, or further separations within the named varieties. Additional confirming taxonomic information is needed in the fields of physiology, serology, phylogeny, genetics, morphology, and anatomy to properly separate definitively the varieties of Scotch pine. In addition, varieties of Scotch pine are continually being raised to the status of species by some as noted in Price (1963).

Now that more is known concerning the natural populations careful studies should be made which include the examination or designation of type specimens so that the nomenclature may be accurately applied.

CHAPTER X

DISCUSSION

Problems in Methodology

The attainment of the objectives of this study required the acquisition of parental data and meteorological and geographical data of origin for as many of the original stands included in the 122-origin provenance test of Wright and Bull (1963) as possible. In addition intelligent and economical use had to be made of the acquired information in order to avoid an overpowering mass of data. The characters measured on the parental cone, seed, and leaf specimens were arrived at after a thorough study of the literature and of the specimens themselves. Scotch pine is probably the most variable of the pine species and previous work on other pines was not always applicable to this species. Character measurement was a tedious and time consuming operation. Only eight of the nineteen measurements proved necessary to establish differences. However, important correlations were developed because of the presence of the additional measurements. The dependence or independence of traits that are economically important, such as growth, needle length, and seasonal change of foliage color would not have been ascertained without the multiplicity of characters measured.

The use of six foliage color measurements taken at different periods of juvenile growth appears indefensible until one realizes that analysis of the data showed that change of color at various ages and times are controlled apparently by different mechanisms.

The use of nineteen parental characters or combinations of characters also provided an insight into evolutionary trends in different areas that would not have been evident had fewer characters been used. In the same way form ratios were not very useful in differentiating populations, but they were very useful in understanding the variability relationships.

The variability study of Scotch pine would have been expedited if climatic data had been available at the start. Unfortunately the climatic information was more difficult to obtain than the specimens so that several misadventures were taken before cause and effect relationships could be understood. The extremely wide distribution of Scotch pine over Europe and Asia, with the resultant highly variable environmental factors and occasional isolated populations, made the climatic study a necessity. The segmentation and movement of the original Scotch pine distribution by the glacial periods of the recent past were important factors to consider.

The climatic data were organized into months, an arbitrary measure of time, and into natural periods of the four seasons. Essentially the same information and more accurate results were obtained by the use of natural seasons of winter, shoot development and elongation period, growth period, and food storage period as climatic factors responsible for parent and juvenile characteristics based on physiological and biological phenomena. There was serious concern over the lack of evaporation-transpiration information. However, the use of the ratio of precipitation over temperature during periods of growth apparently sufficed.

Here again, as in the use of multiple measurements and characteristics of the parent and juvenile specimens, the presence of apparently non-essential data provided an insight into the effect of the changes and of the timing of precipitation and temperature on parent and juvenile characters. In essence a form of multiple regression or correlation was achieved without formal programming.

The statistical approach used would not have been possible had it not been for the availability of electronic computers. The complicated analysis of variance of 689 individual specimens and their 19 characters by tree, stand, region and area of distribution and the calculations of their components of variance would have been impractical without the assistance of the computer. The use of punch cards for all data permitted rapid rearrangement of the information to explore suggested new avenues of approach.

A study of sample size revealed that essentially the same information could have been obtained by the use of 10 cones and 20 leaves from each population. Mass collections of this magnitude in populations with the high variability of Scotch pine would result in a maximum error of the mean of 10 per cent.

Value of Parental and Climatic Data

Recognition of the genetically different populations.--The variation patterns in the cone, seed, and leaves of Scotch pine parent populations were most definitive in the following characters. They are listed in descending order of their differentiating value:

1. Seed width.
2. Cone length.
3. Ratio, $\frac{\text{Cone length}}{\text{Length of largest apophysis}}$
4. Seed length.
5. Closed-cone width.
6. Leaf length.
7. Width of the largest apophysis.
8. Open-cone width.

Analysis of the above characters showed that more than 85 per cent of their variability was attributable to between-region differences. The variation pattern based on the definitive differences of these eight characters indicated that the Scotch pine populations sampled could be separated into 10 regions. These grouped populations were identifiable entities based upon the significant differences existing between the regional means. The regions identified were:

Region A. Northern Scandinavia in the vicinity of the Arctic Circle.

Region C. Central and southern Scandinavia.

Region G. Northeastern Germany and Czechoslovakia.

Region H. Western Germany, eastern France and Belgium.

Region I. England.

Region J. Yugoslavia.

Region K. Northeastern Greece (Macedonia).

Region L. Scotland.

Region M. South central mountains of France.

Region N. Northern and central Spain.

Region T. North central Turkey.

The regions listed were found to coincide basically with those defined by Wright and Bull (1963) on the basis of three years of juvenile performance of Scotch pine in a 122-origin replicated provenance test at East Lansing, Michigan, with the exception of the Turkish population and the possible exception of the Czechoslovakian.

The juvenile characters measured in the provenance test provided sufficient information for the establishment of races of Scotch pine based on discernible genetic differences under the conditions of a uniform environment test. The analyses of the parental data confirmed and strengthened this separation into geographic varieties. The analyses of the parental populations revealed that there was a remarkable similarity between the results of the two studies and that the regional pattern obtained by juvenile performance, when applied to the parent data, provided very high between region components of variance.

Forecasting individual-tree performance.--Eight stands in Belgium, Norway, and East Germany were analysed on a single-parent-progeny individual tree basis to determine the relationships existing between single-parent-progeny performance in Michigan and characteristics of the parent tree in Europe. An exceptionally low number of parent-progeny correlations were found to exist, perhaps partially due to lack of comparable characters for comparison, genotype-environment interactions, and silvicultural treatments of the parent stands. There were no correlations between growth rates, where they could most reasonably be expected to exist. These results indicate that the use of parental characteristics for prediction of juvenile performance in Michigan would be of little value. This would not be necessarily true of more mature information collected on the provenance test, particularly after outplanting in a sufficient number of different environments to permit studies of genotype-environment interactions.

Analysis of silviculturally important traits such as clear stem length and diameter, crown shape and size, and foliage condition within parent stands supports previously reported relationships of crown diameter and stem diameter, and crown flattening with stem diameter and crown diameter. These relationships are those expected of trees approaching and reaching maturity. One stand, at Rövershagen, had twice the number of correlations present in each of the other four German stands. Selection in this stand for greater crown diameter would be accompanied by selection for greater stem diameter, fewer crooks, greater live-crown length, and less clear stem length. In the other four German stands selection for one trait would have relatively little effect on other traits. Selection based on single traits would be expected to produce favorable results, but indirect selection would be slow as shown by the fact that the coefficients of determination based on the correlations of traits indicate that progress would be greater than 50 per cent in only 8 out of 145 correlations.

Correlations between parent and progeny on an individual tree basis were exceedingly rare, 35 correlations significant at the 5 per cent level of significance among 1,260 combinations. Therefore, under the conditions of this test, two year juvenile performance characteristics under uniform environment conditions in Michigan as compared to parent performance in Europe, little progress would be achieved by attempting to base juvenile performance on the parental traits measured. As previously mentioned though, later measurements on the provenance test may provide a better base for correlation and further research into genotype-environment interactions may provide a better understanding of the reasons for the lack of correlation. At the present little can be gained by parental selection. Progeny testing then becomes a necessity in a selection program for tree improvement.

The relative lack of progeny-progeny correlations between characters infers that such traits as color, height, and time of bud set seem to have basically different physiological mechanisms. This result strengthens the previously noted situation in the parent-parent correlations in that one should treat each trait independently, and not expect selection in one trait to give a response in another.

Forecasting stand-progeny and ecotype performance.--The within-stand correlation part of the study was accomplished by comparing the number of stands exhibiting the same correlations. In general cone characters were correlated among themselves, but there was little interrelationship involved in the majority of the stands. Changing climatic patterns tended to nullify expected correlations. The importance of selection for single traits was emphasized by the low coefficient of determination of one trait by another.

When parental traits were analysed on a stand and regional basis many discrepancies were noted between the correlations obtained between regions and between stands. The increased number of correlations obtained on a stand basis pointed out that many of these apparent correlations were meaningless and due more to between region differences than to any gradual trends in cause and effect relationships. The deficiencies experienced in correlation by all stands was reduced by grouping the regions into areas of similarity of climate, a northern group, a Great Britain group, and a southern group. Comparison of the northern and southern group correlations showed that while there were the same number of significant correlations in each area the traits involved were different and at times the direction of the correlation was reversed.

Cone characters in general were correlated in both areas but the basal angle of the cone was positively but not significantly correlated ($r = .10$) with apophysis thickness in the north and significantly correlated negatively (r = -.77) in the south. Differences in the degree of correlation indicated basic form differences, probably resulting from differing environments and selection pressures.

The correlations resulting from unstratified data clearly indicates that there may be many apparent associations that may be meaningless, and that true correlations are increased over the meaningless by proper stratification of data.

The experience gained in analysing the parental data was employed in analysing the stand parental-juvenile data. The data were analysed by grouping the stand data into three regions of approximate similarity. Group 1, northern area, consisted of regions A, C, G, and H, group 2, Great Britain, of regions I and L, and group 3, Mediterranean area, of regions J, K, M, and N. While this grouping reduced the number of degrees of freedom it increased the validity of the correlations obtained. There were very few correlations, just as in the single-parent-progeny analysis, and only two instances of correlations between the same two characters in all three regions. In one of these instances seed length was significantly positively correlated with lateness of bud formation. In the other, height at age three was positively correlated with the ratio of cone length/apophysis length in the north and in Great Britain, but negatively correlated in the southern group. Significant correlations in two of the three groups give general trends and associations.

The correlations of precipitation and temperature data with geographic locations proved that the weather patterns of summer and winter varied between areas. In the northern area, for instance, the per cent of annual precipitation occurring during the growing season decreased with increasing latitude, but increased with increases in east longitude and elevation. In the southern or Mediterranean area the per cent of the total annual precipitation occurring during the period May to August increased with increasing latitude and decreased with elevation. These differences between area weather patterns were important in understanding correlations of climate and geography with parental and juvenile characters.

The parental characteristics showed an overall pattern of greater temperature effects in the north and greater precipitation effects in the southern area. Apophyses were shorter and thicker as temperature decreased in the north and shorter and thicker as temperature increased in the south. This seed protective mechanism was responding to a different set of critical factors.

Large seed were associated with more growing season precipitation in the northern area and with less precipitation in the southern or Mediterranean area. In the north better environmental conditions during the growing season produced larger seed, but in the south larger seeds were needed for survival during hot and dry spring and early summer seasons.

The juvenile characteristics of seedlings grown in Michigan had a few interesting correlations with meteorological and geographical data of origin.

Third year height was positively correlated with increased precipitation and temperature during the growing season in the north, not correlated in eastern Germany and Czechoslovakia, negatively correlated in western Germany, eastern France and Belgium, and not correlated in the Mediterranean area. Yellowing or decrease of greenness of foliage in the winter was positively correlated with higher winter temperatures and more winter precipitation in the north, higher summer and winter temperatures in eastern Germany and Czechoslovakia, lower temperatures during the period February to May in western Germany, eastern France and Belgium, and with cold summers and high winter temperatures and less summer rainfall in the Mediterranean area.

The foregoing data reveal the dangers of applying information based on a limited area to a species as a whole or to the area of distribution. The diverse climatic situations involved within such a wide distribution pattern requires restraint in the use of local or regional relationships.

Climatic data may provide a basis for inference in predicting ecotypic performance but not assurance that the expected will be realized. Only population studies based on climatic information can be used to accurately determine the reaction of the plant to its environment. This is not to say that broad implications can not be made on the basis of geography or climate as the limits of critical factors are approached, such as smaller trees as moisture or elevation becomes a critical factor to the development of a tree.

In much the same manner knowledge of parental performance can be used to develop only general relationships that can be expected to apply to ecotypes. The paucity of correlations obtained in the highly variable Scotch pine parent populations shows that the application of parental characteristics of a stand to other stands within an ecotype must be done with caution.

The use of climatic or parental data to forecast progeny performance is also limited as evidenced by the lack of correlations, the lack of pattern in the correlations obtained, and the reversal of the directions of correlations in some instances.

The general implications of the lack of pattern in correlations in a distribution wide or even a regional analysis of a character or between different characters is that progeny testing is the only assured method of acquiring performance information, and that parental or climatic data of origin is useful in developing expectations, but not actual performance. The progeny test of Wright and Bull (1963) would seem to indicate at this stage that parent populations exhibiting good qualities in desired characters should be tested regardless of their origin.

Trends in Evolution

The general evolutionary trends in the Genus *Pinus* were listed by Shaw (1914) as moving from symmetric, dehiscent, and deciduous cones to oblique, serotinous and persistent cones, from uninodal to multinodal shoots, and from soft and thin to liquified and thick cones with larger seed with articulated wings or no wings.

Evolution within the Scotch pine, however, has been in response to local conditions and not always in the same direction, or toward the same objectives, unless these objectives be basically stated as survival.

This study of Scotch pine emphasizes the point that evolution within a species as a whole is governed by its local environments, particularly in a widely distributed species covering a wide array of diversified climatic zones with their subsequent changes in selection pressures. Seed in the northern part of the distribution are smaller due to shorter growing seasons and lower temperatures, but more numerous to provide adequate propagation in a growing season where precipitation is not a critical item, but litter penetration and seed destruction by rodents may be. Seed in the Mediterranean area are large and well-stocked with the nutrients necessary to allow them to reach moisture in a less favorable growing season environment.

The larger cones have developed under the more favorable development conditions in the optimum development area of Scotch pine and also as protective devices for seed in areas where greater protection was needed.

The general evolutionary trends in the genus Pinus discussed by Shaw (1914) probably hold true when considering the overall long term development of the genus. However, evolution within a species is more directly associated with the environmental conditions, the plasticity of the species, and the response to selection pressures as discussed by Wright and Bull (1963). The distribution of Scotch pine was radically changed during the recent complex glaciation of Europe and Asia and subsequent changes in environment. Some populations were concentrated into islands of refuge. In some instances these populations have again expanded while others have remained as isolated populations, usually at the higher elevations. Selection pressures due to changes in environment have slowly modified these populations. Great Britain was at one time completely within the distribution area of Scotch pine, but at present there are only remnant populations in northern Scotland. This situation and the climatic differentials involved in the various areas of population have resulted in a complex pattern of selection pressures. The area of distribution is not stable and the results of glaciation have not been fully realized. Changes due to varying selective pressures are slow. This study provides sufficient information to indicate the direction of development in response to local pressures on the cone, seed and leaves of Scotch pine.

The direction of these evolutionary trends is toward survival within an environment and the fact that Scotch pine is so widely distributed attests to its ability to adapt to changes in environment. The pioneer qualities of this species is indicated by its ability to survive, even in such hostile environments as the sand dunes and the bogs along the North and Baltic Seas, and propagate.

The species variability resulting from the many environmental conditions under which the populations of Scotch pine have developed insures adequate material for selection and breeding programs designed for the improvement of Scotch pine.

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