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# The Correspondence Between Genetic, Morphological, and Climatic Variation Patterns in Scotch Pine

## I. Variations in Parental Characters[1])

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The native range of Scotch pine (*Pinus sylvestris* L.) includes most of Europe and northern and west-central Asia. The relatively recent glaciation in these areas and the activities of man have resulted in changing environments. Consequently displaced origins, genetic differentiation and new genetic combinations have developed among the continuous populations as well as in the isolated populations of southern Europe and west-central Asia. MIROV (1961) considered Scotch pine as a complex of pines. CARLISLE (1958) listed 144 named variants.

The annual planting of millions of Scotch pine seedlings in north-eastern and north-central United States has resulted in a practical demonstration of the great amount of variability. It has also shown the economic necessity to obtain the proper seed. A comprehensive study of the performance of trees from 176 different places is being conducted in north-central United States as part of the NC-51 project (WRIGHT, 1963; WRIGHT and BULL, 1963). Early results based on juvenile characteristics of the seedlings have shown genetic differences between seed origins.

My study was made to determine the variability present within native stands and between regions within the natural range of Scotch pine in Europe and Asia, and to compare this variability with genetic differences determined through WRIGHT'S and BULL'S study of seedling origins grown under a common environment.

The parental-stand specimens were obtained from the same stands or stand areas from which WRIGHT and BULL collected their Scotch pine seed for the NC-51 origin test. Therefore wherever reference is made in this study to a stand or to a region the designations given by WRIGHT and BULL are used.

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.

### Literature Review

VIDAKOVIĆ (1958, 1960) studied the significance of seed. cone and cone scale characters as taxonomic determinants in European black pine (*Pinus nigra* ARN.). He found that seed color, seed mottling and the form of the seed and cones were most useful in differentiating between populations.

STASZKIEWICZ (1960, 1961, 1962) used 10 characteristics of the cone of Scotch pine to divide his population samples from Poland, Czechoslovakia, Switzerland, France, Scotland, Sweden and Finland into 6 morphological types of cones, each type distinguished by some characteristic feature.

GERHOLD (1959) studied the chloroplast pigments and nutrient elements in the needles of 6 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) determined differences in the essential oils of Scotch pine from several European countries.

The results of KING (1965a, 1965b), PAULEY *et al.* (1965) and STEINBECK (1965) corroborated and strengthened the genetic differences reported by WRIGHT (1963) and WRICHT and BULL (1963) on the NC-51 Scotch pine project.

FIELDING (1953), CRITCHFIELD (1957), SCHOENIKE *et al.* (1959) and THOR (1961) used seed, cone and cone scale differences to determine variation patterns in Monterey pine (*P. radiata* D. DON), lodgepole pine (*P. contorta* DOUGL.) jack pine (*P. banksiana* LAMB.), and loblolly pine (*P. taeda* L.) respectively.

### Methods

The characters studied in the parental populations (*Table 1*) were principally those of the cone and seed since these have proven to be of value. Needle length and twist were also studied because they could be analyzed in the juvenile progenies grown under a common environment by WRIGHT. In all, 19 different characters were studied on each individual.

Thirty-nine stands from 13 countries were sampled. In each stand one cone and one needle fascicle was collected from each of a number of young trees growing in full sunlight. The location of the sample on each tree was standardized. The number of trees sampled per stand was usually 20 but in a few cases was as few as 10 and as many as 34. The period of collection for all countries except Spain was August, 1960, to March, 1961. Spanish collections were made during the period December, 1961, to February, 1962.

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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 1.* The components of variance were 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 2.*

In addition to *Tables 1 and 2* some of the measurement data is presented graphically in *Figures 1, 2 and 3* for a biometric comparison of the region samples. *Table 3* is a summary of significant parental character differences between regions.

*Table 1.* — 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 |
| P 6 | Cone length | 27.80** | 1.53* |
| P 7 | Cone width, closed | 15.20** | 2.42** |
| P 8 | Cone width, open | 8.30** | 3.70** |
| P 9 | Cone length/width ratio, closed | 3.49** | 1.13 |
| P 10 | Cone length/width ratio, open | 3.87** | 2.51** |
| P 11 | Cone basal angle, open | 3.09* | 3.26** |
| P 12 | Largest apophysis length | 2.10 | 2.59** |
| P 13 | Largest apophysis width | 9.73** | 2.75** |
| P 14 | Largest apophysis thickness | 9.76** | 1.91** |
| P 15 | Apophysis length/width ratio | 6.76** | 1.85** |
| P 16 | Apophysis length/thickness ratio | 6.51** | 2.51** |
| P 17 | Apophysis thickness on concave side | 5.09** | 3.96** |
| P 18 | Index of cone asymmetry | 1.96 | 16.37** |
| P 20 | Ratio, cone length to length of largest apophysis | 21.86** | 13.95** |
| P 28 | Seed length | 21.67** | — |
| P 29 | Seed width | 42.09** | — |
| P 30 | Seed length/width ratio | 5.76** | — |
| P 35 | Leaf length | 15.00** | 2.59** |
| P 38 | Leaf twist | 1.41 | — |

* Significant at 5 per cent level. Greater than 2.27 or 1.50 for between-region and within-region comparisons respectively.
** Significant at 1 per cent level. Greater than 3.17 or 1.89 for between-region and within-region comparisons respectively.

*Table 2.* — 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 |
| P 6 | Cone length | 7.5 | .4 | 92.1 |
| P 7 | Cone width, closed | 8.8 | 1.2 | 90.0 |
| P 8 | Cone width, open | 10.7 | 2.9 | 86.4 |
| P 9 | Cone length/width ratio, closed | 54.0 | .7 | 45.3 |
| P 10 | Cone length/width ratio, open | 30.8 | 4.7 | 64.5 |
| P 11 | Cone basal angle | 30.6 | 6.9 | 62.5 |
| P 12 | Largest apophysis length | 22.2 | 3.5 | 74.3 |
| P 13 | Largest apophysis width | 12.0 | 2.1 | 85.9 |
| P 14 | Largest apophysis thickness | 16.5 | 1.4 | 82.1 |
| P 15 | Apophysis length/width ratio | 23.4 | 2.0 | 74.6 |
| P 16 | Apophysis length/thickness ratio | 18.9 | 2.9 | 78.2 |
| P 17 | Apophysis thickness on concave side | 16.3 | 4.8 | 78.9 |
| P 18 | Index of cone asymmetry | 13.8 | 21.3 | 64.9 |
| P 20 | Ratio, cone length to length of largest apophysis | 1.1 | 1.5 | 97.4 |
| P 35 | Leaf length | 8.4 | 1.3 | 90.3 |

## Results

*Characteristics of Value in Separating Populations*

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

P 6. Cone length.
P 7. Cone width, closed.
P 8. Cone width, open.
P 13. Largest apophysis width.
P 20. Ratio cone length to length of largest apophysis.
P 28. Seed length.
P 29. Seed width.
P 35. 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. 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 1*). Therefore seed width is one of the most definitive characters in developing regional patterns.

When seed width and length were plotted by regional group and latitude *(Figure 1)* 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 East Anglia, 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

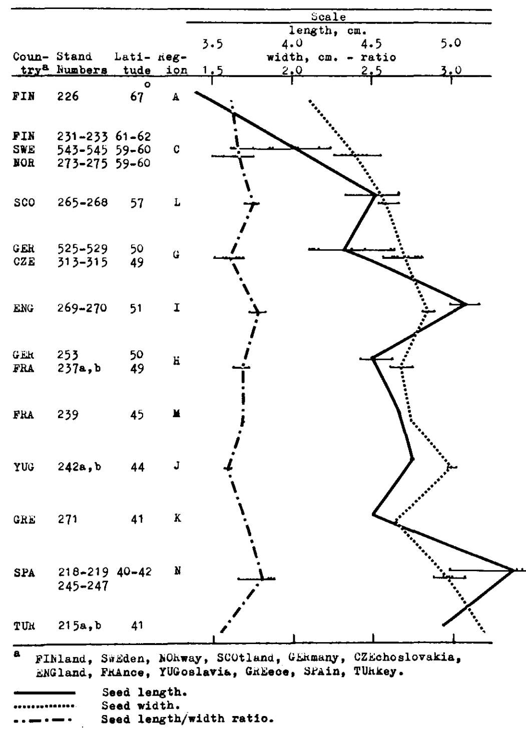


*Figure 1.* — Regional variation pattern in length, width, and length-width ratio of Scotch pine seed.

evidence indicates that the East Anglia 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, West German (No. 253), French, Yugoslavian, and Greek populations 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 1)*.

Cone length, open cone width and length/width ratios are presented graphically in *Figure 2.* Trees from north of the Arctic Circle had the smallest cones; however, only one

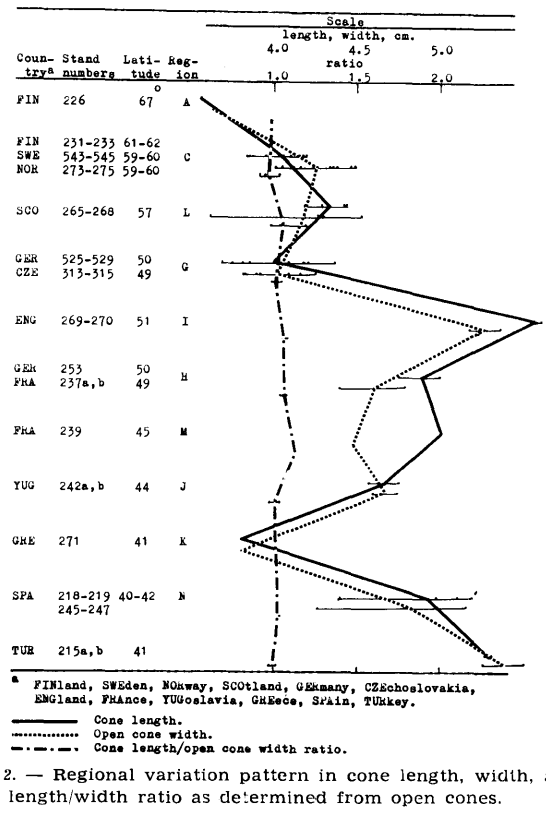


*Figure 2.* — Regional variation pattern in cone length, width, and length/width ratio as determined from open cones.

such stand was sampled. Hence it is not possible to say whether the northern-most population differs significantly from the more southerly ones, but that is a possibility.

The Greek and Yugoslavian parents, were also small-coned 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 East Anglia, England (Nos. 269 and 270), had the largest cones of all. Those were from planted stands. As previously mentioned under seed dimensions these 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 seed 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. 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. 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 or origin of a sample *(Tables 1 and 2)*.

The longer apophysis could be an indication of fewer seeds per cone if associated with greater 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 1)***. Of all the characters studied, the percentage of the total variance attributable to between-region differences was highest for that ratio ***(Table 2)***. 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 3***, the ratio is seen to in-

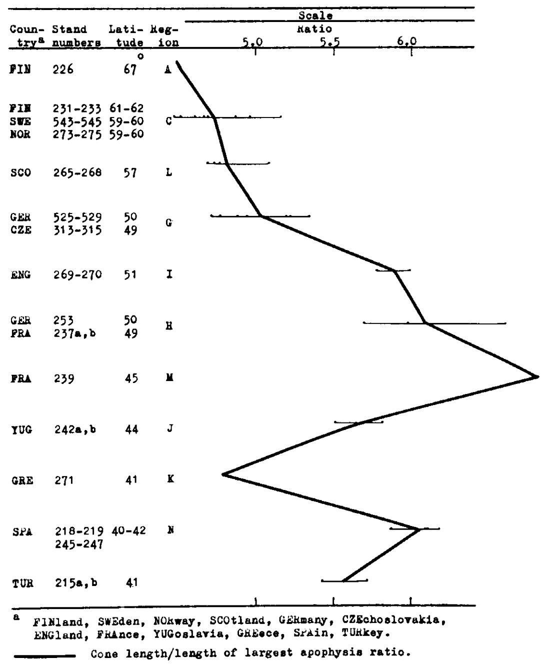


*Figure 3.* — Regional variation pattern in the cone length/length of largest apophysis ratio.

crease from north to south to a maximum in southern central France. 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). Yugoslavia (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 has geographic significance. So also does 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 is its small size for the south-central French stand number 239, which has nearly the widest apophysis of any sample.

Thickness of the apophysis is of evolutionary significance in the genus *Pinus* 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 significance than did cone or seed size *(Tables 1 and 2)*. There was a noticeable tendency for this trait to parallel cone width; that is, for wide cones to have thick apophyses.

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. This gave a ratio which was a measure of asymmetry. Thickness of the opposite apophyses, however, closely follows the pattern of thickness of the largest apophysis and the ratio of the two measures showed that there were no significant differences in asymmetry.

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. Significant differences were obtained *(Table 1)*. Shorter and thicker scales were found in the French, Turkish, and Spanish than in the other populations.

The basal angle of the open cones 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.

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 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 should also have a high growth rate in comparison to other geographical races of Scotch pine.

The measurement of leaf twist 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 separation of the Czechoslovakian from the German and the Turkish from the Greek populations. For the analysis of variance the data from 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 trees within stands — 351, total — 389.

When grouped in this manner, between-region variances accounted for 62 to 97 percent of the total variances in the various characteristics. Stands-within-region variances generally accounted for less than 5 percent of the total variances, the exception being the index of cone symmetry (character P 18 in *Tables 1 and 2).*

The large between-region differences indicate that the regional grouping was natural. Furthermore, they indicate that it is possible to determine 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 region of origin.

The between region differences have been summarized by character in *Table 3.*

Finland north of the Arctic Circle (region A) is represented by a single stand which is significantly different at the one percent 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 percent 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 percent 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 percent level in cone length and the cone length/length of largest apophysis ratio.

Scotland is significantly different from the East German Czechoslovakia population (region G) at the one percent 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 percent 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 East Anglia, 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 percent 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 percent level of significance, and in seed length and width at the five percent 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 3*, 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, Czechoslovakia, Hungary, Poland, Switzerland, and the Central Massif of France. On the basis of ten cone measurements he could recognize six different geographic varieties. The ranges of these varieties were as follows:

Northern Finland.
Sweden.
Scotland.
Poland.
Northeastern Czechoslovakia.
Czechoslovakia, Switzerland, and Central Massif of France.

A comparison between his data and mine show general agreement with regard to the five varieties. On the other hand, my data indicate that his sixth variety is heterogenerous and should be split.

**Summary**

Six hundred and eighty-nine cone, seed and leaf specimens of Scotch pine were collected from 39 stands in Europe and Asia by cooperators in several countries. Nineteen variable characters were selected for study and measurement. Individual tree measurements were grouped by stand and region, and then were subjected to analyses of variance.

The variation patterns of 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 length.
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.

Computation of the components of variance for the above characters showed that more than 85 per cent of the variance was attributable to between-region differences, and less than three per cent to stands-within-region. The variation pattern based on the definitive differences of these eight characters indicated that the Scotch pine populations sampled could be separated into 11 regions. These grouped populations were identifiable entities based upon the signi-

*Table 3.* — Summary of significant parental differences between regions

| Region | 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.

ficant 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.

Comparisons were made of the regional grouping based on the parental measurements and a regional grouping based on juvenile characters in an associated 122-origin provenance study in a uniform environment in East Lansing, Michigan, reported by WRIGHT and BULL (1963). The groupings were nearly identical. In other words, it is possible to delimit a race or variety of Scotch pine 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.

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# Patterns of Height Growth Initiation and Cessation in Douglas-fir


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### Introduction

Although studies of patterns of growth initiation or bud burst in Douglas-fir *(Pseudotsuga menziesii* [MIRB.] FRANCO) have been reported earlier (for a review see SWEET, 1965) the genetic variation in this characteristic continues to attract attention because the relative time of bud burst often determines the success or failure of Douglas-fir introduced into areas with late frosts or widely fluctuating weather conditions during spring such as in northwestern Europe. This short paper also reports on the relationship between the relative time of bud burst and cessation of terminal growth and, in addition, adds some details of local variation.

### Methods and Results

The observations reported here were made in a breeding arboretum near Corvallis, Oregon, containing plants from throughout the natural range of the species. The experimental design is that of complete randomization at a spacing of 12 by 12 feet. Observations were made during the second to eighth year after planting before any crown competition occurred. Time of bud burst was defined as the time when any bud, regardless of position in crown had opened to expose the new needles. Observations were made at three to five days intervals.

### Growth Initiation

Plants originating along an east-west transect across western Oregon were first selected for study. The earliest of these selected trees in bud burst each year were those originating from the vicinity of Corvallis *(Fig. 1)* while those from the Oregon Coast Range only 20—40 miles west of Corvallis and 100—200 ft. higher in elevation were the latest. The earliness of the Corvallis plants and those from Sweet Home is in accordance with the conclusions drawn by MUNGER *et al.* (1936) that Douglas-fir from broad, open valleys are early. The lateness of the Coast Range plants is more difficult to explain since no weather data are available from that area. However, the area around Corvallis