GEOGRAPHIC VARIATION IN EUROPEAN LARCH

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INTRODUCTION

All living organisms vary somewhat from individual to individual, and frequently populations of the same species vary from other populations. Exceptions to individual variation may be vegetatively propagated clones or some types of twins, but as Goldstein (1963) states, all creatures have a specific nature, and represent wholes having the character of individuality". We easily recognize individual variation in human beings and some other higher animals, both because of pronounced phenotypic differences, and because we are very familiar with observing these traits. However, an American, faced for the first time by large numbers o2 an unfamiliar aboriginal people, may have more difficulty in discriminating between individuals. To continue the analogy, the major ethnic groups of Homo sapiens can be distinguished easily, as can geographic races of certain trees that are characterized by phenotypic differences. Individual variation within a tree provenance is less easy to distinguish, just as it is among people. We need to know individuals better. We had a good example yesterday of Dave Cooks long familiarity with his trees so that he can call each by name.

Sometimes there seems to be as pronounced variations between individuals within a given provenance as between prove nances. There are thus variations common to large populations and individual variations within them. Some species exhibit greater variability than others--at least by observable characteristics. European larch (Larix decidua Mill.) may be said to be moderately variable.

VARIATION AMONG POPULATIONS

Two different forms of variability are commonly recognized, ecotypic and clinal. Nienstaedt (1960) has stated that ecotypic variation is where the distinguishing characters are adaptive. Variation between ecotypes is discontinuous, without gradations, while clinal variation, although usually adaptive in nature, results from environmental gradients. However, tree species may exhibit clinal variation in one character and ecotypic in another. Since variation patterns are not the same for all characters, clinal variation of one character may be superimposed on ecotypic variation in another character. A species population is "a complex of ecotypes or clines in relatively delicate adjustment to a variety of environments".

TYPES OF VARIATION IN EUROPEAN LARCH

When a species has a discontinuous range, as in this species, it is not surprising that ecotypic variation is commonly found. The range of larch was probably much more extensive, but it became isolated in pockets, much as in the case of Norway spruce (Picea abies) and many other species. During historic times man has introduced it into many other areas. However, the natural range is fairly well known, and within this several authors have separated ecotypes such as the commonly known Sudeten, Carpathian and Alpine groups. Altitudinal ecotypes have also been recognized (Rubner, 1954; Vincent, 1958). This has been especially true of Alpine larch (Leibundgut and Kunz, 1952). Clinal variation is less well-documented. Photoperiodic response due to latitude and changes in the length of the growing season occasioned by latitude or altitude may be classed as clinal variations. However, Fischer (1952) could not demonstrate any really clinal variation in Alpine larch based on altitude a lone.

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EXAMPLES OF VARIATION IN EUROPEAN LARCH

These will be drawn from a sampling of more recent literature. Schoenike (1961), in his review of the genus, estimated that there are 4000 titles to literature on larch, and that there may well be 6000. He was probably conservative. I have chosen to classify types of variation roughly as (A) Morphological Differences, (B) Variations in Response to the Environment, and (C) Variation in Susceptibility to Biotic Influences. Variations in geographic populations will be emphasized.

Morphological Differences

Phenotypic differences have led some botanists to divide L. decidua into varieties and forms, or even separate species. No attempt will be made to discuss these here; Ostenfeld and Larsen (1930), Simak (1958) and others have dealt with these in detail.

Seed size and weight.--Seed weights have been found to be greater in Alpine sources compared to those from Sedeten and the Tatra Mts., which are low in weight (Genys, 1960; Heiken and Soegaard, 1962). Thulin and Miller (1964) noted that seed size increased with altitude, and that seed from the western Alps was heavier than that from the eastern Alps, as well as from east European sources. Bouvarel and Lemoine (1958) asserted that seed size was a valuable diagnostic character for determining origin.

Cone size and shape.--Polish races have been reported to have smaller cones with more rounded scales and more undulating scale margins than other provenances (Gathy, 1959a; Schoenike, 1961). High altitude Alpine sources have been reported to have larger cones than low altitude sources. However, Edwards (1954) noted that cones varied greatly in size even on the same tree.

Needle structure.--Gathy (1959b) studied needles of several provenances and found that the character of the transfusion tissue varied. Conductive tissue was relatively more abundant in Alpine origins compared to Sedeten larch.

Bark thickness. Sudeten and Scotch origins had thinner bark than Tyrolean in Sweden according to Schotte (1917).

Heartwood formation.--Schotte (1917) and Leibundgut and Kunz (1952) found that heartwood developed earlier in Sudeten larch than in Alpine larch.

Specific gravity of wood.--Schotte (1917) stated that Sedeten larch formed denser wood than Tyrolean when planted in Sweden.

Crown form.--The Scotch race had smaller crowns and fewer branches than the Tyrolean when planted in Sweden, and yet Edwards (1954) noted that Sudeten had wider crowns than Alpine provenances.

Branching type.--Cieslar (1899) found differences in branch structure among different sources. Morandini (1958) also noted significant differences in the number of branches among IUFRO[2] sources planted in Italy. The IUFRO plots at Drummond Hill, Scotland, also showed differences: No. 31 from Neuminster had fine twigs at right angles to the stem, while provenances from the central Alps had ascending branches. Those from the northern Alps were more drooping. Silesian larch was characterized by large numbers of fine branches (Author's notes, 1956). Branch thickness appears to be greater in high elevation sources from the Alps (Schoenike, 1961). Sedeten larch is of the fine-branching, ascending type. Similar observations were made by Genys (1960).

[2] International Union of Forest Research Organizations; 1944 experiment.

Bole form.--This is also most variable and may be caused by the environment as well as genetically, Schotte (1917) observed that in Sweden, the Scotch sources were usually straight-boled and the Tyrolean tended to be crooked. Genys (1960) found small crooks most common in low elevation provenances from western Austria. Sudeten larch had significantly more crooks than high elevation origins. Carpathian sources were found to have more cylindrical boles after 50 years than Sudeten sources (St. Astny, 1960). Fischer (1954) concluded that bole form was inherited, while Gohrn (1956) showed that stem form was better on poor soils than on those rich in nitrogen. Similar observations have been made in Scotland on Japanese larch (L. leptolepis).

Sweep and lean.--Trees from Sudeten and Slovakia had significantly more leaning trees than other provenances in the IUFRO sources studied by Genys (1960).

Variation in Response to the Physical Environment

Photoperiod.--Zelawski and his co-workers (cited by Schoenike, 1961) studied photoperiodic sensitivity of larch and reduced the annual growth cycle to two months under laboratory conditions, but appear not to have tested geographic variability extensively. Robak (1957) found that provenances from regions of shorter summer day length than that of the growing site in Norway formed their terminal buds earlier. In the experiments of Leibundgut (1962) one-year seedlings from different provenances differed in height growth in response to two different photoperiods, and there was a significant difference in the extent of side-branching.

Time of beginning and ending growth.--Among Alpine provenances those from high altitudes flushed earlier and were more damaged by late spring frosts than those from low altitudes; they also shed their needles earlier in the fall in experiments cited by Schoenike (1961). Leibundgut (1959) also noted that Alpine sources differed widely in the time of annual height growth, high altitude sources completing their growth earlier. Burger (1935) had observed that high altitude provenances completed height growth after 50 to 60 days, while lowland larch grew for 80 to 90 days. The date when half the growth was completed differed by a month in some cases according to Leibundgut and Kunz (1952). The author (Baldwin, 1955; 1958), while demonstrating great variation in the pattern of height growth among IUFRO sources, could not find such marked differences in the length of the growing season of larch planted in New Hampshire. The dates when half the growth was completed showed no definite altitudinal cline observed by the Swiss workers. Use of different series of provenances may account for this.

Height growth.--Variation in the total height attained at a given age has been often observed since the time of Cieslar. While ratings of different provenances may vary with age, usually the fastest growing sources can be recognized early. Edwards (1954) observed significant differences at one year in nursery seedlings, and the author (Baldwin, 1949) at 4 years. In these cases Sudeten larch had the greatest height and Alpine races were poor. Genys (1960) found the east European larches from Poland, Slovakia and Sudetenland, as a group, superior to those from Alpine areas. Schober (1958) found the same to be true, but some sources from the western Alps also grew well. St. Astny (1960) reported that Sudeten sources grew faster in youth, but at 50 years were equalled by those from the Carpathians; the latter were expected to surpass them during the next decade. Thus Schier's (1963) conclusion that the growth capacity of a source is expressed during the first 5 years may need qualification. It seems well established, however, that in all countries where they have been planted, the east European sources have outgrown others in height.

Autumn coloration and needle fall.--High elevation sources commonly turn yellow earlier in the fall than those from lower elevations. This can be observed in young seedlings in the nursery.

Frost resistance.--Day (1957, 1958) found differences in resistance to frost during the early stages of flushing.

Snow damage.--Defoliation caused by late snow was highest in the case of Sedeten and Slovakian provenances and less in high altitude sources from Italy and Switzerland according to the observations oGenys (1960). Trees from ares aof heavy snow-fall are usually less subject to snowbreak and bending by snow than those from relatively snowless regions.

Drought resistance.--There was wide variation in "transplanting tolerance"--survival after late spring planting--in sources planted in Saskatchewan (Cram, 1952). Wachter (1961) found that Sudeten larch was more sensitive to drought than Alpine origins, and that among the latter, high altitude sources suffered least. This was partly attributable to the fact that the Alpine sources had completed their growth earlier, before the onset of the drought.

Shade tolerance.--Schotte (1917) reported that Sudeten larch grew better in dense shade and in mixture with shade tolerant trees than Tyrolean larch.

Variation in Susceptibility to Biotic Enemies

Insects.--Low elevation Austrian origins were less afflicted by the woolly larch aphid (Chermes strobilobius Kalt.) than other IUFRO sources (Genys, 1960).

Diseases.--Many authors have observed a differential injury from larch canker, Dasyscypha willkommii (Hartig) Rohm. Sudeten sources have often been reported as highly resistant (Rubner, 1954; Edwards, 1954; McComb, 1955; Gohrn, 1956; Schober, 1958; Genys, 1960; Wachter, 1961). Silesian and Polish sources are also cited as highly resistant (Schoenike, 1961), as also Scotch larch in Sweden (Kiellander, 1956). Similar observations were made by Fischer (1952) and Mayer and Plochmann (1954). High level Alpine sources were more susceptible to canker than low elevation larch according to Schoenike (1961). It is providential that the fastest growing races are the most resistant.

Animals.--Cook (1954, 1965) observed differences in the severity of attack by red squirrels among different sources. Again, Sudeten provenances appeared less attacked than Alpine ones. Porcupines are some of the worst enemies of European larch in America, but no well-controlled experiments have been made to determine their preferences, if any, for different provenances. The intensity of feeding is apparently inversely proportional to the distance from denning areas. They certainly show a great preference for European larch over other species of larch.

Individual Variation

Selection of plus and minus trees in uniform stands, with confirmation of variation by progeny testing is a common method of assessing individual variation. Kleinschmidt (1955) studied 14 plus trees and found that they could be divided into two main classes: (1) slender, small-crowned trees with many side branches, small, light-green needles, and fast-growing, and (2) broad-crowned trees with few but large side branches and large grey-green needles, and less rapid-growing. Fischer (1950) and Leibundgut and Kunz (1952) considered stem form to be more commonly an individual variation than one common to all trees in a provenance. Cook (1960) estimated that the frequency of exceptionally good plus trees may be only one to five trees per thousand.

SUMMARY

This very incomplete sampling of the literature is sufficient to indicate that geographic variation in European larch is very widespread, and that certain aspects have been repeatedly confirmed, not only by observation of native stands, but by planting in several countries far outside the range of larch. Taxonomists have used phenotypic characters to name new varieties and forms, and ecologists have sought the causes of ecotypic variation in the environment. It seems that there is still much work for the geneticist to prove to what extent different characters are heritable. Furthermore, as geographic distinctions are confirmed, more attention should be focused on individual variation. We no longer need to be content to classify ecotypes and geographic races, but should search for outstanding individuals within the best populations Such variations are now less well-documented, but when fully exploited may prove equally rewarding as provenance research.

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