

THE ECOTYPE CONCEPT AND FOREST TREE GENETICS

by Hans Nienstaedt/

Introduction

Provenance, provenience, or seed source is not a well defined term. It usually signifies a seed collection made at a known location within a more or less limited population. The fame of certain proveniences such as the Riga source of Scotch pine in western Europe, German spruce (i.e. Norway spruce of German origin) in Sweden, or Sudeten larch (European larch from the Sudeten Mountains) in Denmark often has been based on practical experience gained during the last century by foresters managing the intensive forests of northern Europe. Sometimes the worth of the sources has been further established in experimental plantings in which a number of sources have been compared under relatively uniform conditions, but in most cases the statistical design has been poor. The results, therefore, were limited in scope and the conclusions rarely went beyond simply stating that certain sources were superior to others. Some attempts were made to delineate variational trends within the range of some of the more important species, but here again the conclusions were often sketchy and based on too few observations.

Only in the last 50 or so years have we begun to understand the distribution of the races, ecotypes, and clines within our more important timber species.

These three terms are well enough defined, but as often happens when we try to classify the multiplicity of nature, our classifications clarify some things, but muddle others. Even so the terms are useful..

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1. By a race we understand a population within a species range which exhibits general similarities within itself, but varies distinctly and discontinuously from the characteristics of other populations. The variation may be qualitative as well as quantitative, but the differences between the populations are relatively minor and are not sufficient for the different populations to be distinguished as separate taxa.
2. When the distinguishing characteristics of a race are adaptive, the term is synonymous with ecotype. Distinguishing characteristics are either quantitative, qualitative, or both. Often the differences between the ecotypes show up only when they are grown together in a uniform environment. Ecotypes may show adaptation to climatic, edaphic, or perhaps biotic conditions. They may be described accordingly as climatic or edaphic ecotypes, etc. By definition variation between ecotypes is discontinuous.
3. Where the variation is gradual it is described as a cline. Clines follow geographic or climatic gradients. Although the accepted definition does not specifically state so, clinal variation is usually adaptive and often results from environmental gradients. Genetics glossaries emphasize that the variation considered in connection with the term cline is phenotypic. This connotation seems unnecessary; newer studies have shown clearly that adaptive genotypic variation also may follow geographic, climatic, or other gradients.

The majority of the commercially important tree characteristics such as vigor, resistance to spring or fall frosts, resistance to winter injury or diseases, and even straightness of stem and crown form are examples of adaptive variation and, therefore, may be ecotypic or clinal variations. In some cases - and this in part is where our concepts become muddled - they may be both. The two terms are not mutually exclusive.

We shall discuss that in more detail after first considering why adaptive variation is important in forest management and tree genetics.

The Importance of Adaptive Variation in Forest Management and Tree Genetics

The planting stock set out on a given site must be adapted to the climatic extremes in the area, or death follows. Furthermore, unless the stock is able to utilize the environment with maximum efficiency, yields will be below maximum. In spite of this, millions of trees are planted annually by individuals who know nothing about the seed source and adaptive value of the stock they plant. This is due partly to lack of interest, partly to lack of available knowledge. We need much additional information on the adaptive variation within our important species before our seed distribution policies can be fully developed.

The local seed source is generally the best grower; however, we know of cases where seed sources (ecotypes) planted outside their own environment have grown better than the native sources. Outstanding as an example is the use of German sources of Norway spruce in southern Sweden. German spruce is entirely hardy in southern Sweden, and it yields considerably more wood than the native spruce. Thus, a thorough knowledge of the adaptive variations within a species may lead to a direct increase in yields.

Some of the goals in our tree improvement programs are fast growth and disease resistance. Among the breeding methods available for their attainment are species hybridization, ecotype crossing, and selective breeding of individual plus variants. If by these methods we are to reach our goals rapidly and efficiently and get the best possible development of the different types of hybrids, we need a complete understanding of the adaptive variation within the parent species.

The majority of the species hybrids made in the past were produced in arboreta on a few specimens of doubtful origin, which probably did not represent either the best adapted ecotypes or the best ecotypes of the exotic parents. In spite of this, a surprising number of promising hybrids have been made. This has been good luck. For reasonable assurance that the best species hybrids will be developed, both parents should be of seed sources adapted to the environment to be planted. In addition the hybrids should be tested under a variety of conditions to ascertain that they indeed are grown under the conditions for which they are best suited.

This does not mean that hybridization on available arboreta material is useless. Far from it; such crosses do yield valuable information on affinities within a genus and on crossability patterns, and may yield very valuable new combinations of parent traits. Very likely, however, several generations of selection in filial or backcross generations will be required for the characteristics to become established in sufficient frequencies in the progenies to make them suitable for field planting.

Stebbins (1950) has discussed a somewhat similar problem as follows:
"If the adaptation of the species to its environment is of such broad general type that many different gene combinations are equally adaptive, then the chances are good that some of the segregates from interspecific hybridization will have selective value... But if certain of the adaptations possessed by the species are very exact and specific,...then the products of hybridization will almost certainly be nonadaptive."

Our growing understanding of the variation within species has made it increasingly clear that a species is a complex of ecotypes or clines in relatively delicate adjustment to a variety of environments. If the above statement is viewed on this background it can perhaps be interpreted as follows: In order for species hybridization to be successful, either the exotic parent must be of broad general adaptation or we must use a specific type of the exotic parent adapted to the environment where the hybrid is to be grown.

Another method of improvement is the crossing of ecotypes. This method also can be used to obtain increased vigor or to develop new strains combining desirable traits of two parent types. Generally speaking, the F₁ generation is intermediate between the parent types, with the segregating types manifesting themselves primarily in the F₂ generation. Here again it is clear that for the first-generation hybrids to have adaptive value suitable ecotypes must be used. Undoubtedly the F₂ generation will also have more desirable types if the parent ecotypes have been chosen with care.

Finally, one may ask how the ecotype concept affects our development of seed orchards based on individual tree selections. We cannot hope to obtain the greatest possible benefit from the seed orchards unless we restrict the distribution of seed to the limits of a particular ecotype or to a restricted portion of a cline. It goes without saying: until we have proof to the contrary, parent clones must be selected within the same areas.

It is possible that we may overcome the problem also by mixing clones from different ecotypes in the orchards thereby broadening the adaptation of the progeny. However, little or no concrete information is available and much research is needed to clarify this subject.

Methods of Studying Ecotypic Variation in Forest Trees

You are all familiar with the conventional seed source studies - field plantings of stock from many seed sources under relatively uniform environmental conditions. I will only say two things concerning them:

- (1) A proper statistical design is essential. No amount of care in selecting a uniform test site will substitute for the proper design.
- (2) In the past the accepted procedure has been to use large plots of 49, 64, 121, or more trees. Larger plots are desirable where per-acre yields

are the main objective of a test; they also give a greater number of individuals to observe and therefore a better chance of finding the rare but perhaps highly desirable variants of the populations. As an illustration, we have a planting of exotic spruces, which included 9 plots of 100 trees each of Serbian spruce. Less than 5 percent of the trees survive today, but some of them are of excellent form and reasonably good growth rate. They are perhaps potential parents of highly valuable hybrids. If we had used individual tree plots, with a total of from 60 to 100 trees, we might not have had a single tree combining hardiness, good form, and growth rate.

However, the large plots have many disadvantages and statistically speaking they are very inefficient. This has been shown by Wright and Freeland (1959). They recommend the use of 1- or 2-tree plots with as many as 100 replications depending on the degree of sensitivity desired from the tests. There is no doubt that test designs of this type will give us the answer to the majority of the problems that can be studied in an ecotype study.

Another new approach to the study of adaptive variation is early evaluation in the nursery or under controlled conditions indoors. By such tests it has been possible to evaluate form and resistance to snow damage on the basis of hypocotyl curvature as a response to a unilateral source of light (Schmidt, 1951), and relative growth rate and frost resistance in eastern hemlock (Olson, Stearns, and Nienstaedt, 1959). Ecotypic variation in seed germination responses has been demonstrated in hemlock (Stearns and Olson, 1958) and in ponderosa pine (Callaham, 1959a). Even wood characteristics such as specific gravity have been studied in nursery material and it has been demonstrated that relative values can be obtained from branchwood of seedlings (Zobel and Rhodes, 1956).

The third, least used, but oldest method of study is the taxonomic, i.e. morphological studies on samples collected on endemic trees growing throughout the distribution of a species. This method is the least effective. Because the data are based strictly on phenotypic observations and since many characteristics are highly modifiable by the environment, they cannot give an adequate basis for an evaluation of genetic variation. However, such studies undoubtedly can give much valuable information quickly and cheaply, and can help interpret the results of other experiments.

What is needed to assure the best possible evaluation of the adaptive variation within a species may be a combination of all three methods (Callaham, 1959b). Perhaps the procedure can be outlined as follows:

1. Indoor evaluation of adaptive responses and morphological traits of a large number of seed collections well distributed over the range of the species. The relative response to temperature in terms of rate of elongation and growth duration and to photoperiod

in terms of growth duration, the effects of temperature on germination, and the responses to drought conditions and low temperatures could be studied under indoor conditions. Such studies could be followed up with nursery studies over a 2- to 4-year period to help convert relative to absolute values. The plots in the nursery could be replicated single rows with bulk sowing of stock for field testing.

2. Field plantings of only a limited number of sources to make possible long-term observations of the most promising ones, to allow conversion of early development in terms of mature growth, and to let the sources be exposed to climatic extremes, which they might not experience during 4 short years in a nursery.

Such studies could be 2-tree plots with many replications. In addition, large unreplicated plantings may be included to permit observation of many individuals for selection purposes and to be able to make observations under stand conditions.

3. Observations in endemic stands throughout the range of the species. Such observations, usually morphological and anatomical, have been of considerable value in interpreting variation patterns.

One problem we have in interpreting the results of our field tests is the fact that they can be applied directly to a very limited environment only - ideally only in environments identical to the particular one under which the test is made. The tests must be performed under many diverse environmental conditions in different parts of the range of a species in order for us to evaluate the plasticity of a species unless we can devise methods by which we can sample growth in endemic stands and use the data in interpreting field and indoor tests. Perhaps such an approach will enable us to close the gap between actual behavior in the native habitats and the data we obtain under the artificial conditions which we ourselves create, indoors or in the field.

These then are the methods that can be used in studies of adaptive or nonadaptive variation within the species. Next, let us try to illustrate by selected examples what kinds of adaptive variation have been demonstrated, and finally let us see if we can draw some helpful general conclusions about ecotypic variation within our forest tree species.

Results of Studies of Ecotypic Variation of Forest Trees

Growth responses in terms of elongation, diameter growth, volume production, and frost hardiness are perhaps the characteristics which have been studied in greatest detail. They usually show very clear clinal patterns of variation, as for example, in eastern white pine (Pauley, Spurr, and Whitmore, 1955), Populus spp. (Pauley and Perry, 1954),

Scotch pine (Langlet, 1936, 1942-43, 1959), eastern hemlock (Olson, Stearns, and Nienstaedt, 1959; Nienstaedt, 1958) and many other species. Highly significant correlations have been demonstrated between different measures of the environmental impact and growth. Particularly the length of growing season measured in terms of frost-free period or the length of the period with a daily average of 6 C. or above has been used by many and, generally speaking, seems to be a better measure of climate than, for example, monthly average temperatures either for a single month or for a combination of two or more. Significant regression of growth responses on latitude and altitude and of growth on daylength have been found. Latitude, of course, is basically a measure of photoperiod. Altitude, and in some regions also latitude, is a measure of the variation in temperature.

Most of the relationships that have been analyzed have been straight-line relationships and have shown that if a source is moved from a short to a long growing season regime - movements from north to south or from high to low altitudes - growth is dwarfed; movements in the opposite directions lead to increased growth. Curvilinear relationships have been demonstrated in some cases (Echols, 1958), but apparently they are much less common.

If the same sources are grown and compared under different environmental regimes the relationship may or may not be the same. In hemlock, for example, the general trend among 30 seed sources was generally speaking the same on any one of 7 different constant photoperiods and under any one of 14 temperature treatments - both constant and alternating. In all cases long growing season sources grew longer than short season sources. The overall level of growth varies of course; i.e. it increases with increasing photoperiod. In hemlock, however, there is a significant difference in the slope of the curves for elongation as a function of growing season depending on photoperiod. This difference indicates that long growing season sources will show a proportionately greater increase in growth in response to a given increase in photoperiod (Olson, Stearns, and Nienstaedt, 1959). This difference in response to differences in environment is quite uniform in hemlock when a single environmental factor is changed; Langlet (1936) has shown much more complex changes in responses with changing environment and if forest trees behave like herbaceous plants, we might in some cases expect quite drastic changes in response patterns with changes in environment, as has been demonstrated for the milfoils by Clausen (1951).

The relative amount of growth is to a large extent related to duration of growth, and the duration of growth in turn is correlated to frost hardiness. It is to be expected, therefore, that frost hardiness should show the same relationships with latitude, altitude, and climate as have been described above for growth. The most complete study of ecotypic variation in frost hardiness and resistance to winter injury is probably the work by Langlet (1936) on Scotch pine. This and many other studies show that: (1) Long growing season sources have longer growth cycles

than short season sources; therefore, (2) when moved to more severe, short growing season climates they suffer from early fall frost and winter injury. On the other hand, (3) short season sources respond early in the spring in long growing season environments and are therefore apt to suffer from late spring frosts. Finally (4) the variation is gradual and therefore clinal in nature. In Langlet's study it is apparently not a straight-line relationship.

A later study by Langlet (1942-43) has shown the relationship between the growth responses mentioned and photoperiod, and other studies have also shown the dependence between photoperiod and height growth, cessation of growth, and hardiness to early fall frost. That variation in the time of bud-burst also may be an adaptation to photoperiod has been demonstrated with Douglas-fir (Irgens-Moller, 1957). His hypothesis is that higher altitudinal strains break dormancy later in the season when the danger of severe night frosts has passed, because they require a relatively longer photoperiod for bud bursting than low altitude sources.

Most studies of adaptive variation have used fairly widely scattered collections as experimental material. Localized adaptive variation in growth has also been demonstrated. One example must suffice. Squillace and Bingham (1958) have presented evidence of adaptive variation in western white pine from eight pollen sources collected on different watersheds within a 15-mile radius in northern Idaho and western Montana. The pollen was used in pollinating a number of test trees, and the general results were that pollen collected on the best site yielded the better progeny. Undoubtedly the variation is adaptive; whether it is continuous or discontinuous could not be determined from the study.

Other types of adaptive variation have been observed. Callaham (1959a) has shown very definite trends in the response of germinating ponderosa pine seed to photoperiod and temperature. Seed from areas with summer rains requires higher temperature in order to germinate, but shows very rapid germination rates when the required temperature is reached. Seed from areas with spring rains germinates at a slower rate at lower temperatures. In hemlock, southern sources require less chilling when given a favorable photoperiod than do northern sources and a higher optimal germination temperature if sufficiently chilled (Stearns and Olson, 1958; Olson, Stearns and Nienstaedt, 1959). Genetic adaptation to swamp versus upland conditions has been demonstrated in the case of northern white-cedar in Wisconsin (Habeck, 1958). Seed of upland types germinated better and showed much greater plasticity of root development than did lowland types. Adaptive variation in disease resistance also occurs. As an example, northern sources of Scotch pine show greater resistance to *Lophodermium pinastri* and *Phacidium infestans* than do southern sources. Apparent adaptive variation to *Rhabdocline pseudotsugae* and *Phaeocryptopus Gaumanni* has also been shown by Douglas-fir (Bergman, 1954).

Some characteristics which in themselves can have little adaptive value are closely correlated to growth phenomena which are. As a result they

themselves show apparent clinal variation. I am thinking of wood characteristics. Echols (1958) has shown a close curvilinear regression for tracheid length and wood density on latitude at the point of origin of seed sources of Scotch pine, and Larson (1957) found, on the basis of phenotypic observation, clinal variation in summerwood percentages in slash pine.

Finally, I would like to refer to two studies as a basis for some general conclusions regarding adaptive variation in forest trees. One is a study of lodgepole pine by Critchfield (1957), the other a study of sugar maple by Kriebel (1957). Both studies bring out a number of very important points.

1. Variation patterns within a species range are not the same for all characteristics. Thus clines of one character may be superimposed over a pattern of ecotypes or may occur within an ecotype of another character. In sugar maple, for example, injury from high insolation shows a discontinuous ecotypic variation, while variations in the time of flushing and in fall coloration form definite clines which transect the ecotypes based on sensitivity to high insolation. Moreover, within one of these high-insolation ecotypes a cline in response to insolation manifests itself. Similarly in lodgepole pine each of the principal characteristics - in this case they are morphological characteristics - is unique in its variation pattern: for example, two large areas show distinct differences in leaf width but no corresponding difference in the number of resin canals per leaf; in another large area resin canals show a distinct variation along a climatic gradient while leaf width remains essentially the same.
2. By definition ecotypes are adaptive and evolve in response to variation in environmental factors. Environmental factors vary either continuously as, for example, photoperiod with changing latitude or temperature with changing altitude, or they may vary quite discontinuously as, for example, soil types, which change abruptly with changes in the parent bedrock. It follows that adaptive variation may form clines or ecotypes depending on the variation in environmental factor from which it results.

We still may be faced with an apparent dilemma where discontinuity in a species distribution may cause apparent discontinuities in a climatic gradient. As a result, an apparent cline within the species may be broken into distinct sections, and therefore, one might argue, distinct ecotypes. Personally, I would not favor such an interpretation unless definite discontinuous variation occurred in other traits also.

Lodgepole pine furnishes one example of a distinct ecotype resulting from a sharply delineated environmental factor. This ecotype occurs in an area which is edaphically quite distinct from adjacent

areas occupied by the species. The population in this area is relatively homogeneous (no resin canals, narrower leaves, serotinous cones) and genetically differentiated from the rest of the species; it thus constitutes an ecotype as defined earlier in the discussion. Other characteristics, such as cone type, form inter-regional gradients quite typical for the cline.

3. Both studies bring into focus the problem which I mentioned in the introduction; i.e., are the terms ecotype and cline mutually exclusive? The discussion, I hope, has illustrated that they are not; it was with full justification that Stebbins (1950) used the term clinal ecotypic variation.

When we then consider that the major part of the genetic variation which determines survival value and potential yield is the result of adaptation to gradients of environmental factors and therefore is clinal or clinal ecotypic, it becomes clear that we must avoid subdividing our species into discontinuous races or ecotypes unless our conclusion is based on sufficient sampling and on observations of the responses of not one, but several characteristics under as many different environments as possible.

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Group Discussion

Most questions concerned types of variation. It was pointed out that we may have clines within ecotypes and within races. It is often difficult and hazardous, therefore, to delineate distinct races. Also we have edaphic as well as geographic ecotypes.

A comparison was made of variation in ponderosa pine and in sugar maple, both of which grow over wide geographic ranges. With the former, there is some discontinuous variation and doubtless many distinct ecotypes have developed. In the latter, variation probably is more gradual and the differences between ecotypes are less abrupt. More studies are needed, of course, to clarify variation types and patterns in both species.

Some miscellaneous discussion brought out that: (1) There are now some possibilities of obtaining tree seeds of known origin from Mainland China and North Korea. (2) Poplar cuttings cannot be imported directly from overseas. The plant quarantine organization insists on growing them in test gardens for 1 year before releasing any such cuttings. Those interested should check with their local plant quarantine office for details as to procedure.