NONOPTIMALITY OF LOCAL RACES

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For many years it was recommended that selection for vegetative vigor be limited to trees naturally grown near their intended planting sites. The assumption was that local genotypes always survive better and are more vigorous than genotypes evolved more distant from the test site. In recent years, however, evidence of the nonoptimality of local sources in many areas has been mounting. One explanation is that natural selection is for rapid reproduction, while tree breeders are concerned with vegetative vigor. This paper outlines some evidence of nonoptimality of local sources and proposes another explanation.

Traditional Theory

Strong support for the theory of optimality of local races was presented by Clausen et al. (1948), who found that local populations of _Achillea lanulosa_ Nutt. are well adapted to local variants in environment. Their model leads to the conclusion that natural selection continually eliminates all migrants and segregants not suited to local environments. Thus, in a wide-ranging species, the homogenizing effects of migration are often overcome, and a series of locally adapted populations evolves on all sites. Regardless of whether a species extends over discrete sites (Fisher 1950; Hanson 1966) or over environmental clines (Langlet 1936), almost any restriction on migration would be expected to produce clines of genotypes reasonably well adapted to local environments. The relative effectiveness of migration rates and selection advantage would determine the strength of clinal variation.

The problem for tree breeders in utilizing any information on natural variation is imperfect correlation between vegetative vigor and rapid reproductive success. The correlation can often be expected to be high among species which normally undergo population reduction due to severe vegetative competition. In such species, early growth rates can be critical to successful reproduction and selection. Thus, Clausen et al. (1948) found in the perennial weed A. _lanulosa_ that the measure of reproductive success could as well have been vegetative vigor as seed set because the two were highly correlated. It was not unreasonable to assume that natural selection in forest tree species has been effective in maximizing vegetative vigor, at least in broad environmental regions. Hence, the recommendation that selection be limited to trees naturally grown near their intended planting sites often seems reasonable (Langlet 1936).

Contrary Evidence

As early as 1962, Jonathan Wright pointed to several exceptions to the general rule that local seed sources are superior. He noted that local provenances

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of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest were not optimal in several tests. Since that time, more exceptions have appeared in print. They suggest that a new generalization would better fit the data. In fact, the general concept that static optima generally exist should be reexamined in light of newer theories on evolution in variable environments. Since the environments of species exhibiting racial variation range widely in space and time, such reexamination might suggest new breeding procedures.

Studies too numerous to mention individually have demonstrated the existence of optimal growth provenances of *Pinus sylvestris* L. and *Picea abies* (L.) Karst. in northern Europe. In some widely distributed species growing in milder climates, local provenances do not generally grow best outside of ecological zones which seem to provide optimal conditions for high vigor.

For example, evidence is mounting with the age of tests that an optimal growth zone exists for loblolly pine (*Pinus taeda* L.) along the southeastern border of its range. Wells and Wakeley (1966) find that vigor can be improved up to 10 or 20 percent by moving seed up to 200 miles to the north and west. Their measurements probably are from old enough trees and represent enough yearly variations to reflect a true difference in growth.

On tests with young materials of black walnut (*Juglans nigra* L.), Bey (1968) found a similar trend; i.e., growth potentials were highest for sources from moderate climates. Also with young materials, Squillace (1966a, 1966b) found that slash pine (*Pinus elliottii* Engelm.) possesses an ecological development peak in the interior of its range coincident with an optimal combination of climatic factors. Genotypes from this region are more vigorous than local sources in Olustee, Florida.

Probably, tests with ponderosa pine (*Pinus ponderosa* Laws.) provide the most definitive long-term examples of genotypic sources from optimal ecological zones outgrowing local sources in more marginal areas. In the Northwest, Squillace and Silen (1962) found that races from milder climatic regions had greater growth potentials than those from the harsher environments more inland and at higher elevations. More recently, in California, Conkle (personal communication) has found clear evidence of the existence of an ecologically optimal growth zone in the middle of an elevational gradient. In this zone, where soils are deepest, rainfall distribution is best, and climate is mildest, all seed sources, including the midelevation source, reach their best development. When planted on upper and lower slopes, the midelevation source still consistently grows considerably more vigorously than local genotypes. This pattern was evident at 10 years of age, and at 25 years it is accentuated. A close examination of the data of Clausen et al. (1948) also reveals that for A. *lanulosa* performance in the high elevation, plants from more moderate elevational climates did better than those from the nearest seed sources.

It is possible that in geographically varying tree species local racial variants from ecologically marginal areas may not be optimal, at least in terms of growth vigor. If it can also be assumed that natural selection among genetic variants is correlated with growth vigor, a nonmaximal growth genotype must also have less than maximal competitive fitness. If a species is evolutionarily successful, some compensatory benefits must accompany the loss of vigor.

Maintaining Vigor Loss

There are probably as many combinations of compensatory factors as there are species. In some cases, the relative loss of vigor may be poorly correlated with reproductive success. This might well be the case when measurements are only taken over a small portion of the life cycle or in a small number of environments. When Scots pine is transplanted over very long distances, temperature and phenological effects make vegetative vigor very poorly correlated with seed set and pollen maturation (Eiche 1966; van Buijtenen and Stern 1967). In tests with young slash pines, transitional climatic cycles may be responsible for the temporary success of nonlocal provenances (Bengtson et al. 1967). However, the prevalence of optimal nonlocal provenances in continuously distributed populations indicates a real and permanent loss of vigor. The large losses of vigor demonstrated in the old materials of local ponderosa pine and loblolly pine provenances also indicate that short-term climatic or other environmental trends do not affect the comparisons.

It is reasonable to expect that, in some cases, vigor is highly correlated with reproductive success and that present forest tree populations in ecologically marginal areas are not maximally fit for their present environment. These populations may be better adapted to more severe environments than those presently available to them. It is clearly better for trees to adapt to present environments and to adjust competition and reproduction for maximum vegetative production. However, since the exact environment of the progeny generation is sensed with high uncertainty in the present generation, errors are to be expected in adjusting the organism. In cases where populations face variable and uncertain environments, a conservative strategy would require good adaptation to poor environments if they are frequent and have a drastic effect on survival.

The question of how populations remain stable under changing environments was considered by Levene (1953). He showed that genetic equilibria can exist if the population is faced with two environments and the alternate alleles partially adapt the genotype to the alternate environments. If the harmonic mean of the loss in fitness caused by possessing the wrong alleles in the wrong environments is less than the arithmetic mean fitness loss, then a stable, optimal, intermediate gene frequency exists. The concept of intermediate, stable, optimal genetic populations evolving under variable environments was considerably extended by Levins (1968), who defined general optimal conditions for stable equilibria. He showed that maximum fitness, when measured over several generations, can be achieved by populations which are not maximally fit in any one environment but are not badly fit for most environmental variations. If future generations face uncertain variations in climatic factors or among soil or elevational gradients, it is advantageous for the population to remain adapted to harsh environments. In tree species--especially for races on ecologically marginal and possibly highly variable sites--it would be advantageous to not respond to selection for what may prove to be transiently favorable site factors. Only in more stable or optimal areas might fine adjustment to environments add to long-term survival of the species.

Since there is some advantage to conservative response to varying environmental factors, some physiological and genetic controls to dampen any overreaction to transient environments may have evolved. However, simpler mechanisms also exist. Since the lack of optimum adaptation seems strongest in ecologically marginal sites, the conservative responses are most obvious in those sites which are most likely to have most recently been subjected to critical stresses. With some restriction on migration, the local population in a marginal area may maintain a lower fitness for better environments simply by constantly fluctuating. Antonovics (1968) has recently shown that, among perennial organisms, even limited amounts of pollen migration can inhibit response to selection and help maintain unfavorable genes in a population. Thus, constant change and less than maximal immediate fitness in marginal populations may be of long-term value.

CONCLUSIONS

The examples cited indicate that a conservative strategy of ecologically marginal populations is common. The breeder must wonder if he may be more audacious than nature has been and use the greater vigor of ecologically optimal provenances on more marginal sites. What nature considers to be transient site improvements may prove permanent enough for the breeder. An answer can be obtained only through tests of plant materials and observations of environmental patterns of variation.

If the correlation between vigor and reproductive success is high, local provenances may have maximal vigor. However, if vegetative vigor is poorly correlated with natural reproductive success, the breeder should consider provenance selection in regions of optimal ecological development and minimal environmental stress. His requirements for reproduction and timber production are separable.

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