Better Forest Management Through Better Adaptation

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Adaptation, in the forest genetics context, is a process of evolutionary adjustments that fit individual trees or stands to better survive, grow, and reproduce in their environments. The idea and the principle are scarcely new. In history and literature we find evidence that primitive forest dwellers already recognized and understood the importance of adaptation, of putting the right tree in the right place. Perhaps the earliest record of adaptation of forest trees is found in the beginning stanzas of the Finnish epic poem Kalevala, dating back to 900 B.C. In this poem the bard recounts a project undertaken by the hero Pellervoinen (possibly a precursor of Paul Bunyan) who set out to perform a direct seeding operation with a keener awareness of species adaptation than perhaps is exhibited by many highly trained foresters of our times. To quote in part from Kalevala:

" . .. On the firm soil he plants acorns,
Spreads the spruce seeds on the mountains,
And the pine seeds on the hill-tops,
In the lowlands he sows birches,
On the quaking marshes alders,
And the basswood in the valleys,
In the moist earth sows the willows,
Mountain ash in virgin places, . . .
Junipers on knolls and highlands,
Thus his work did Pellervoinen."

In the intervening centuries since Pellervoinen's heroic direct seeding operation, many silviculturists have, by trial and error, acquired a considerable degree of sophistication and awareness concerning adaptation and its significance in forest management, at least as regards a few major species. For example, in the South today, in fewer and fewer instances are loblolly pines being recommended or planted on deep sand sites, and possibly only a very few million slash pines annually are being set out much above latitude 34° N. These signs of restraint indicate the beginning of real progress in an area of primary importance to sound forest management.

Adaptation in forest trees involves adjustment to two major environmental factors, climate and site. Climate includes such variables as range, level, and duration of temperatures, length of frost-free growing season, amount, intensity, distribution, and character of precipitation, and hours of sunlight. Site is construed to include such variables as soil moisture, depth and texture of surface soil, total soil depth, chemical and physical characteristics of surface and subsoil, topography and hydro-geology, depth to water table, and drainage.

Progress toward fuller understanding of adaptation, and especially of its significance and practical employment in forest management, has not been spectacular or rapid. Research in this area represents the efforts of many investigators in many lands over a long period of time. No attempt will be made here to review the very large number of studies that have been published on this subject, but it may be of interest to mention a few; also it may be relevant to note that a rather large number of past investigations have dealt mainly with provenance in relation to climatic factors.

Some Lessons from Study of Provenance

Species occupying a wide geographic range or wide variety of habitats have been the main objects of provenance studies in the past, and, in general, have been the ones exhibiting the most pronounced racial diversity. The Frenchman Vilmorin is generally credited as the first to prove the heritability of racial characteristics of pines. During the years from 1820 to 1830 he conducted extensive experiments in the Loiret Department of France, using seeds from French, Scottish, German, and Russian (Riga) sources of Scotch pine. Interestingly enough, the seed source from the Riga region produced the finest trees, which he described as having straight, beautiful cylindrical stem and "slight boughs" (Engler 1905). Moreover, he noted that the second generation of the Scotch pines from the Riga source grown from seed harvested from the Loiret plantings possessed the same fine qualities as the first generation.

In the United States one of the earliest studies of adaptation was a ponderosa pine provenance experiment begun in the fall of 1911 in Idaho (Weidman 1939). In the 22 progenies under investigation, marked differences in both height and diameter growth were observed, along with differences in several foliage characteristics. One of the more important findings from this study was the observation that a source making the best growth at first was later overtaken by a source showing a steadily sustained growth rate and greater resistance to extremes of climate at the planting location.

In the South, the pioneering study of loblolly pine provenances established in 1926 in Bogalusa, La., has served to dramatize the enormous influence that geographic source of seed may exert on the success of planting this species (Wakeley 1944). Subsequently, striking differences among provenances of loblolly pine in survival, growth, or drought hardiness have been demonstrated by such studies as that of Zobel and Goddard (1955), and similar results have been reported for shortleaf pine, for example, by Auganbaugh (1950).

In a recent study of 188 origins of Scotch pine, Wright and Bull (1963) recognized 14 ecotypes, basing differentiation on such characteristics as seed size, height growth, summer foliage color, autumnal coloration, first-year bud formation, second-year growth initiation, second-year leaf length, and type of root system. However, these differences were observed only on 1- to 3-year-old seedlings in uniform nursery beds, hence judgment of their importance needs to be deferred until outplantings have been observed over a sufficiently long time.

At this point I want to emphasize and punctuate the dangers inherent in early decisions based on short-run provenance tests. Many seed origins may appear fully adapted to a new environment at the start, and continue to show promise even for 2 or 3 decades, and then succumb to, for example, a single sudden drop in temperature, particularly if the change is unseasonal. A good example of this was observed in some slash pine plantings in North Carolina during the past year. A one-night freeze when temperatures dropped to approximately 20° F. in October 1962 killed over ninety percent of the slash pine seedlings on an organic loam site situated approximately at latitude 34°30' N. and longitude 77°30' W. In an older planting of slash pine on a deep sand site at about the same latitude, the same freeze killed or damaged most of the saplings (already 8 to 10 feet tall) in depressions and basins throughout the plantation. These instances are minor, but they point to the real possibility of similar occurrences on a large enough scale to knock management plans into "a cocked hat." No introduction of exotics or extension of existing range of native species should be made without careful study of probable adaptability. It is not the average values of temperature, rainfall, frost-free season, etc., that are necessarily important, but the extremes of high and low and the probable duration of such extremes.

Other Ecotypes

Most of the provenance studies of the type mentioned above have been concerned wholly or chiefly with discovery and evaluation of climatic ecotypes. But other adaptations are also important. One of the most vital considerations is that a species or strain must be adapted to the soil as successfully as it must be to the climate of that site. Unfortunately past investigations that have taken account of the interrelationships with quality of site and soil are meager indeed, and the price for this lack or oversight or failure has been high. As one example near home to most of us, we may readily recall that in the middle thirties tremendous quantities of black locust seedlings were planted, hopefully for soil stabilization purposes, on eroding Piedmont upland fields. Today the ragged, riddled remnants, still persisting in places, dismally attest to the failure of foresters to adequately assess the edaphic requirements of this species. Even the heroic Southwide study of pine seed sources (Wakeley 1952) was limited in its major emphasis to latitude and longitude of origin, with soil-site aspects included only in a secondary and incidental way. Considering the size of that study it is understandable enough why the decision to limit variables was made, but it is unfortunate that an assessment of edaphic ecotypes could not be made at the same time on the same heroic scale. This lack in this instance is certainly not unique. More often than not the worth of an ecotype or strain is assessed with only one environmental factor as a criterion. This limitation is dangerous; frequently the interaction of two or more factors may be the decisive one, a point not to be overlooked in the progeny testing programs that are burgeoning in the South right now.

Perhaps the first study in North America that made any attempt to include site quality along with altitudinal and latitudinal influence was undertaken in 1912 on Douglas-fir in the Pacific Northwest (Munger and Morris 1936). This study was not designed to evaluate soil-site effects in a critical way, and at age 17 no differences, indeed, were observed. Other studies have, however, demonstrated that there are such things as edaphic ecotypes, meaning that some species do maintain, among other characteristics, a definite root form or habit, and that such ecotypes may not adapt readily to other environments. For example, in Wisconsin the failure of several red pine plantings on sandy soil was thought attributable to the origin of planting stock raised from seed collected from trees on rich lacustrine clays (Wilde 1954). Extensive deterioration of red pine plantations in Pennsylvania also attests to the hazards of ignoring site quality in assigning species to planting chances.

In longleaf pine rather marked differences in root systems have been observed that seem to be related to origin of seed, the more fibrous root systems being associated with moister habitats. In jack and red pine Youngberg (1952) found that seedlings from sand dune sites grew at a much slower rate than those originating from parentage on granitic outwash and other fertile soils. The cited studies and observations, and many others, clearly indicate the necessity of paying heed to soil and site factors wherever and whenever the management situation involves species assignment, racial diversity, or ecotypic variation of any kind.

Beyond Provenance and Site

The problems of adaptation in forestry are not restricted to reactions and susceptibilities that may be encountered in new environments associated with large changes in geography and climate, or in site and soil. In a very real sense, adaptation is also involved when it comes to taking advantage of individual tree variation within restricted local environments.

Fecundity and precocity are two characteristics that are of vital concern in tree improvement, and they are inherent at least to some degree within otherwise apparently uniform populations. But under a different photoperiod or a different thermoperiod, a given source may turn out to be neither fecund nor precocious, or vice versa.

Differences among species in the capacity to tolerate intra-stand competition are so well known as to be taken for granted. But this capacity extends also to strains within species, and to individuals within strains. The rigidity of control in this characteristic has not been adequately determined but its importance in forest management can be appreciated easily enough; it concerns spacing directly in relation to maximum production of fiber, volume, or both per unit area of land.

Variation also occurs among trees, at least in loblolly pine, with respect to their capacity to respond to fertilizer applications affecting wood properties; that is, some trees may show a marked growth response without a concomitant drop in specific gravity or some other properties (Zobel et al. 1961). Some individual trees apparently have greater tolerance to changes in fertility levels of the site, insofar as effects on anatomical characteristics are concerned.

Phenological variations, relating to active periods of shoot elongation and diameter increment, are also observable not only among species and different environments, but within species in the same environment; they may, in fact, account for a very significant portion of dry matter production differences among trees. Variation of this type can also determine how successfully a species can become established in a new environment, particularly one involving higher altitudes or greater latitudes where killing frosts may decapitate, decimate, or destroy the early starters or the late season growers. By the same token, these variations may also be closely associated with apparent resistance to pests; a strain that appears resistant to an infestation, such as tip moth, on average or better sites, may prove to be essentially nonresistant on sites of poor quality. These variations, and similar ones, provide a basis for selection among species and among strains within them for improved adaptation. But to capture the full potential and to make intelligent use of such superior specimens or strains will require rigorous assessment of their adaptation to the environments in which they are to be grown to specified sizes.

What About Hardwoods?

From foregoing examples and observations an impression may have been created that adaptation phenomena are confined to softwood or coniferous forestry. Nothing could be farther from a true picture. Hardwoods in general are even more likely than conifers to exhibit greater sensitivity to large changes in geography and soils, climate and site. (For example, a freezing temperature on the night of May 1, 1963, killed back all new shoot growth on most of the native strains of yellow-poplars in sapling-size plantations on the Hill Forest in Durham County, N. C., but in local sources of loblolly, Virginia, and shortleaf pine plantings of the same age, it appeared to cause no damage.) Local climate, indeed, is likely to have a greater bearing on the outcome of various silvicultural practices in hardwoods than in pines, as is suggested in the studies by Hough (1945) and others. Because many hardwoods regenerate from old root stocks and stump sprouts more readily than from seed, the opportunity for perpetuating given traits or characteristics through hardwood silviculture is greater than in pines, at least in our existing populations. Conversely, the problem of getting rid of undesirable strains may prove more difficult.

Most hardwood species lack the capacity for successful invasion of situations involving primary succession; hence, where hardwood establishment is attempted on open land, extra help in the form of cultivation and fertilization may be almost invariably necessary to assure a successful start. Even on existing forest soils on cutover lands some form of relatively drastic site preparation may be necessary. For example, our studies on yellow-poplar planting have shown that this species when planted into spots where logging slash has been burned will attain an average total height of 18 feet in 6 years, but outside these severely burned spots on otherwise identical soil it will attain a height of only about 9 feet in the same length of time.

Although knowledge about hardwood silviculture and hardwood adaptation problems is meager, particularly for species in the South, we are in a better position with this group of species than we were with pines to draw on the considerable backlog of research and experience accumulated over the centuries in the field of horticulture.

What About Breeding and Hybridization?

In striving for better adaptation, we are not limited to selections from superior phenotypes in existing populations. Much improvement may also be achieved from breeding and crossing for specific purposes, as indeed has already been done and is being done, for example, in projects of the Industry-North Carolina State Cooperative Tree Improvement Program. Through such work we may ultimately achieve crosses or strains with greater photosynthetic efficiency, drought hardiness, or other characteristics that make for better utilization of existing resources of soil, water, and air. It is a foregone conclusion, however, that no miraculous outcome is in the offing, just solid, and perhaps sometimes annoyingly gradual, improvement. As an illustration, our study of loblolly pine has indicated a high degree of correlation between certain foliage constituents and usable volume in individual trees. One might loosely assume that some trees are much more efficient than others in extracting the available nitrates, phosphates, and other molecules or elements from the soil. What is more likely is that certain apparently rapid-growing trees have had access to greater amounts of the constituents that appear in greater concentration and amount in the foliage of the larger specimens. It seems very likely also that new strains or new hybrids selected or developed for rapid growth will not attain their full hereditary potential, if at all, unless given an environment of high native fertility, or one made high through intensive culture.

In Peroration

In a general, rambling discourse of this sort, indulging in peroration seems pardonable, justified, and maybe even necessary. I have attempted to show how adaptation in forestry from a genetic viewpoint is vital to sound forest management. Many aspects involving other facets of interactions and susceptibilities of genotypes to their environments have been passed over or mentioned only in passing because others on this program will treat them in detail. But lessons from the past stand out clearly enough even in a general exposition to point out where we have operated stupidly in the past and to suggest how and where we might operate more cleverly in the future. A few specific areas relevant to this southern forest region bear reiteration now.

We have replaced longleaf pine with slash and loblolly on deep sands and other droughty sites.

We have introduced slash pine on loblolly sites on much too large a scale.

We have planted loblolly on "poop-out" spots all over the Piedmont, spots so poor that a demanding species like loblolly will die before reaching marketable size, whereas other species without cultural measures or loblolly with intensive cultural measures would have made the grade.

We have tended largely to ignore or to malign such species as Virginia pine and pond pine, overlooking their splendid qualities such as tolerance, respectively, of infertile sites or wet pocosins; their vegetative vigor, sure-fire regeneration capacities, and the tremendous capacity of pond pine to survive or to recover from severe damage by fire.

We have attempted planting hardwood species on eroding old fields without even the minimum of cultural assistance.

We have brought slash pine too far up from its native botanical range.

We have assumed that shortleaf pine is more drought resistant than loblolly, confusing its capacity to sprout at early ages with its persistance on dry ridges.

We have made many species-site studies using sources of seed or seedlings often with no knowledge of their edaphic or geographic home site.

Additional examples of ignoring or failing to understand the importance of adaptation might be cited, but let this suffice. These past mistakes will haunt us for some time to come, but the experience should be worthwhile, if we learn something solid about adaptation from it. We may even need to unlearn some things from our past mainly of the empirical and frequently uncritical studies. As Sir Thomas Browne said over 300 years ago : "To purchase a clear and warrantable body of truth, we must forget and part with much we already know."

But I should not want to close on so negative a note. We surely know enough about adaptation already to avoid making big mistakes. The first and perhaps the greatest benefit from application of the genetic viewpoint in forest management stems from rigorous use of the growing knowledge about adaptation. The beauty of it is that we need not wait to start reaping the benefits; they accrue from the day we employ that knowledge in forest renewal.