SELECTING TREES FOR ADAPTATION TO THE MINERAL ENVIRONMENT[1]

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ABSTRACT. The need for improving the adaptation of trees to the soil mineral environment may be underrated because of a tendency to overlook deficiencies or toxicities unless foliar symptoms are present. Maximum gains in yield will not be obtained until breeders exploit the large variation in response to mineral stresses that potentially exists. Literature on differential response of forest tree species to mineral levels is reviewed with emphasis on the importance of genotype x soil fertility interaction in identifying superior adaptation. Based on results of studies with pin oak and what is known in general about the edaphic environment, it is predicted that genetic variation in adaptation to mineral levels will tend to be higher within populations and lower among populations than is often true for variation in adaptation to climate.

INTRODUCTION

It is almost an axiom of forest genetics that wherever adaptive characters exist they exhibit genetic variation (Stern and Roche 1974). A corollary is that environmental factors affecting adaptedness do so through genetically variable mechanisms of plant response. Variations in the mineral environment affect tree growth and survival, but tree breeders have largely ignored the possibly large amount of genetic variation that may exist as a consequence of this environmental heterogeneity. Adaptations to climate have received much more attention--perhaps because they are easier to study.

Mineral deficiencies (or toxicities) in forest plantations are common and often pass unnoticed because they are only subtly expressed as reduction in growth

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(Kozlowski 1961). Unfortunately, there is a tendency to think of deficiencies only in terms of easily observed foliar symptoms that are either present or absent. A similar mistake lies in categorizing sites as either fertile or infertile, as if those descriptions have meaning apart from the nutritional requirements of plants. Fertility must, of course, be measured on a continuum, and fertility must be defined only in relation to the genetic potential of the crop. A site that is infertile for one genotype may be very suitable for another. If maximum yield is to be obtained, it is the breeder's responsibility to insure that improved varieties are highly adapted to the soil mineral environment--even if they are to be planted on "fertile" sites.

Expectations of finding genetic variation in adaptation to the mineral environment have been confirmed by a number of studies on forest trees. However, this subject has attracted interest only within the past few years, and there is still much to be learned about methodology. The following thoughts were stimulated by our research on the genetics of resistance to iron-deficiency chlorosis and aluminum toxicity in pin oak and other species.

MEASURING DIFFERENTIAL ADAPTATION

Any proof of variation in adaptation to an environmental factor requires the presence of genotype x environment interaction under different levels of the environmental factor in question. Statistical interaction need not be computed if its presence is implicit under the conditions of study. But, interaction must be explicitly demonstrated if plant response is not otherwise solely attributable to the environmental factor in question. Genetic differences in growth rate under nitrogen stress are not a good measure of differences in adaptation to this stress because genotypes may vary in growth rate even without the stress. Similarly, variation in growth and survival on an adverse site is not necessarily indicative of variation in adaptation to that site because the same variation could occur on a favorable site. This point of logic is occasionally overlooked, and it may be of more than academic interest--as we will illustrate later.

Several studies have demonstrated significant genotype x soil fertility interaction in forest tree species. Curlin (1967) studied 22 clones of eastern cottonwood under unfertilized and nitrogen-enriched conditions. Fertilization increased the growth of all clones, but some clones significantly more than others. Goddard et al. (1976) reported that family x fertilizer interactions have usually been non-significant in loblolly pine field trials, but that interactions have been found in slash pine (see also Pritchett and Goddard 1967 and Jahromi et al. 1976b). Van Buijtenen and Isbell (1970), however, reported significant family x nutrient level interactions in loblolly pine grown in sand culture. Steinbeck (1971) found that four clones of sycamore responded in growth differently when the concentrations of all nutrients was increased in solution culture. One clone responded only slightly to the increase while others grew much faster in the more fertile solutions.

Teich and Holst (1974) have shown that genetic differences in nutrient response may be attributed to the environment of origin. Their results demonstrated that white spruce populations collected from calcareous and granitic sites differed in their ability to grow on calcareous and granitic soils. Populations from calcareous sites grew better on calcareous soil and populations from granitic sites grew better on granitic soil. Similarly, Jenkinson (1974) found that ponderosa pine progenies from ultramafic sites had better growth and survival on ultramafic soil then progenies from granitic sites. Differences between progenies in growth rate appeared to be related to ability to accumulate calcium from soils low in available concentrations of this nutrient.

The most abundant evidence for genetic variation in mineral utilization comes from measurements of nutrient accumulations in the foliage of different clones, families, or populations (Baker and Randall 1974, Fober and Giertych 1970, Forest and Ovington 1971, Gerhold 1959, Jahromi _et al_. 1976a, Lee 1970, Scott et al. 1975, Steinbeck 1965). Epstein (1972) pointed out that when two varieties differ in foliar levels of some elements but not others, the differences are probably caused by genetically controlled mechanisms of mineral nutrition. Nevertheless, it is difficult to interpret the adaptive (and practical) significance of genetic differences in foliar mineral accumulations, even when they interact with environment, because the physiological meaning of foliar mineral levels is usually unknown (Durzan 1974). They usually have no obvious and consistent relationship with direct measures of survival or growth.

Lacking a physiological interpretation of foliar mineral levels, it is difficult to even identify the proper way to express them. Steinbeck (1965) found variation among Scotch pine populations in foliar accumulations, expressed as percentage of dry weight, of several nutrients. However, these differences corresponded roughly with geographic variation in needle length and growth rate, and they disappeared for all but one nutrient when expressed as total content per needle. Similarly, Jahromi et al. (1976b) found a nearly exact relationship between total phosphate accumulation and growth rate when compared across families of slash pine, but the relationship was less exact and of the opposite sign when accumulation was expressed as percentage of dry weight. Forest and Ovington (1971) found that two clones of Monterey pine differed markedly in potassium concentration in young leaves but had nearly identical concentrations for the whole crown.

Since mineral accumulation expressed as concentration in tissue is a function of dry weight, and hence growth rate, it is not certain whether accumulation causes increased growth or *vice versa.* Furthermore, particularly in provenance studies, an association between mineral accumulation and growth rate may actually represent genetic rather than physiological linkages. If that is the case, the association is a spurious one and would be transitory under the recombination involved in a breeding program. An additional possibility that must not be excluded is that mineral accumulation in the foliage and efficiency of mineral utilization may not be related at all. Lee (1970) showed that foliar accumulation of nitrogen varied among populations of European black pine both before and after fertilizer was applied. However, fertilizer x population interaction was not significant for either nitrogen accumulation or growth rate. As pointed out above, interaction would be expected if genetic differences in nitrogen accumulation, or growth rate, truly reflected differences in adaptation to nitrogen levels in the soil.

Vose (1963) concluded from a review of the literature that of many examples of differential nutrient accumulation only a few were related to varietal differences in production. The significance of foliar mineral levels to characters other than growth rate is also problematical. Wallace and Lunt (1960) stated that much work has failed to show relationship between iron levels in leaves and degree of iron-deficiency chlorosis. Grime and Hodgson (1969) found in a study of several species that calcicoles were much more resistant to iron-deficiency chlorosis on alkaline soils than calcifuges, but both groups of plants accumulated equal amounts of iron in their foliage and both accumulated more when grown on acidic soil.

It appears that most studies of mineral accumulations in the foliage of different genotypes have been merely suggestive that variation in adaptation to the mineral environment exists. They have been of little use in discovering the nature of the adaptation and its practical consequences for tree improvement. These benefits must await a better understanding of the physiological significance of mineral accumulations. In the meantime, the best measure (and only proof) of differential adaptation remains the demonstration of genotype x soil fertility interaction.

IDENTIFYING SUPERIOR RESPONSE

When comparing varieties, agronomists tend to speak of "efficiency" of nutrient utilization measured by yield at single levels of fertility. Some tree breeders, on the other hand, have focused on the magnitude of response, or yield increase, when fertilizer is added--apparently assuming that fertilizer will always be used or that only fertile sites will be planted. However, a complete description of genotype x soil fertility interaction must include measures of both relative yield among genotypes and slope of change in yield between fertility levels. Either measure may be insufficient for comparing varieties if used alone.

Some of the kinds of genotype x soil fertility interaction that may occur are illustrated by the performance of hypothetical families in Figure 1. These examples are based on results reported in the literature on genetic variation within tree species in adaptation to nutrient conditions (Curlin 1967, Goddard et al. 1976, Jahromi et al. 1976b, Pritchett and Goddard 1967). No distinction is made between response to the addition of one nutrient and response to the addition to several, and of course the pattern of responses among genotypes may depend upon the range of fertility levels used in the test. Furthermore, response to changing fertility is actually curvilinear rather than linear. However, these graphs serve to illustrate some of the possibilities. They may apply also to response to mineral toxicities.

Family A in Figure 1 is clearly superior to all others because it has the greatest yield at both low

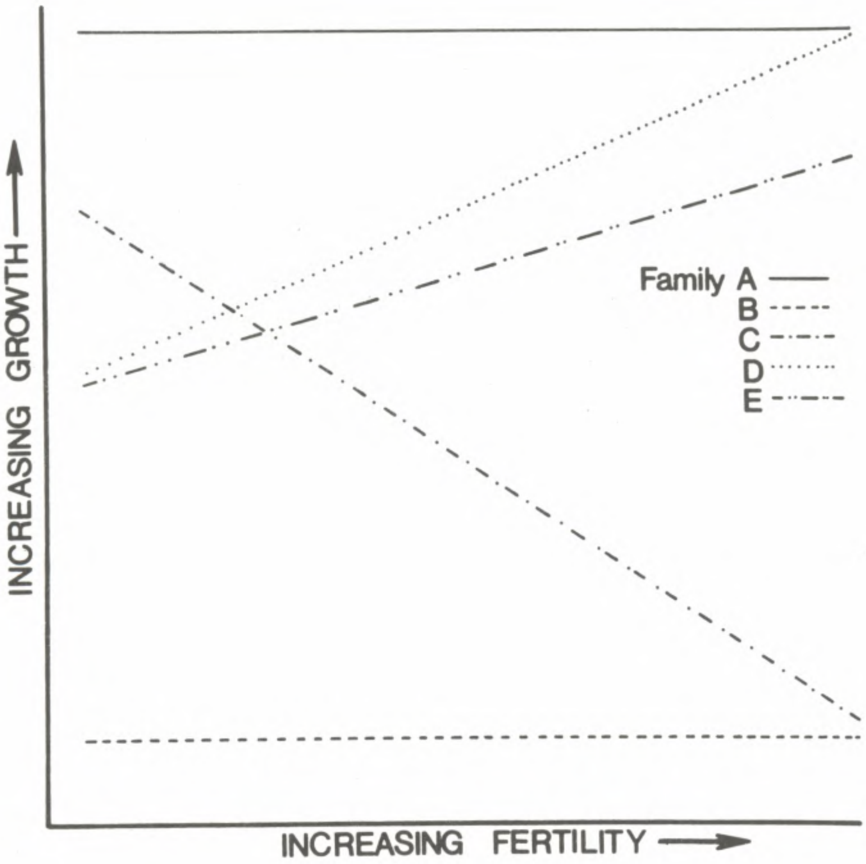

FIGURE 1. -- Examples of response of families to increasing fertility.

and high levels of fertility. This pattern of response is uncommon, and its occurrence may depend somewhat on the particular levels used for testing. However, the potential existence of families with such consistent superiority should not be ignored. The pattern of consistently inferior response exemplified by Family B is also uncommon, but not unknown. Although families with this kind of response curve should undoubtedly be selected against, it is questionable whether they should actually be labelled nutrient-inefficient (Gabelman 1976). Since Family B, like Family A, does not show increasing yield with increasing fertility, its low vigor probably has little to do with poor adaptation to nutrient conditions. In fact, Family B is very well adapted to infertility within the limits in adaptation of grasses to extreme soil conditions over distances as short as one meter. Low hillocks in frequently inundated bottomlands, alluvial soils next to calcareous embankments, and muck or peat soils adjacent to glacial till are some obvious examples among many of local site variation that could lead to variation in adaptation to soil stresses.

As part of a provenance/progeny study of pin oak in progress at Pennsylvania State University, we collected soil samples from below the trees from which seed was collected to learn something of the edaphic variability to which the species is exposed. For each parent, samples of mineral soil were bulked from three points within the drip line of the tree but kept separate according to horizon (0-15 cm. and 15-30 cm.). Each population was represented by four parent trees located not less than 300 feet apart, and populations from most parts of the natural range were sampled. Analyses for several chemical characteristics of the soil were performed, and an analysis of variance was calculated for each characteristic using data from the different horizons to estimate experimental error.

As Table 1 shows, the greatest variation in all characteristics except soil phosphorus was associated

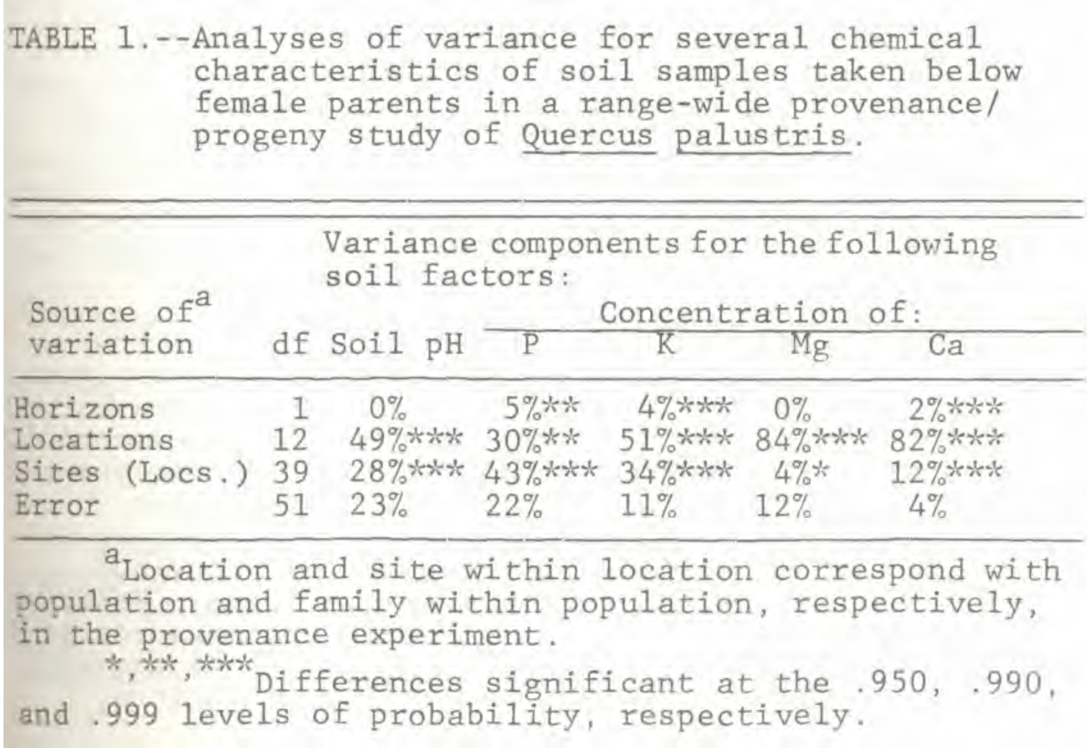

TABLE 1.--Analyses of variance for several chemical characteristics of soil samples taken below female parents in a range-wide provenance/progeny study of _Quercus palustris_.

Source of[a] variation	df	Variance components for the following soil factors: Soil pH	Concentration of: P	K	Mg	Ca
Horizons	1	0%	5%**	4%***	0%	2%***
Locations	12	49%***	30%**	51%***	84%***	82%***
Sites (Locs.)	39	28%***	43%***	34%***	4%*	12%***
Error	51	23%	22%	11%	12%	4%

[a] Location and site within location correspond with population and family within population, respectively, in the provenance experiment.

*,**,*** Differences significant at the .950, .990, and .999 levels of probability, respectively.

with differences among locations (of populations), but in all factors there were significant differences among sites (of parents) within locations. Variation among locations was considerably enhanced by two that were quite different from others and had been noticed as such when the seed collections were made. A population from Auglaize County, Ohio, was unusual for this species in being associated with species such as *Quercus muehlenbergii* and *Xanthoxylum* americanum that are typically inhabitants of calcareo [illegible] tes. The unusual nature of this location was borne out by soil data: its soil had the highest average pH, next to highest calcium content, and next to highest magnesium content of all locations. Another population was collected from an exceptionally sandy site in Kankakee County, Illinois, whose soil was distinguished by having the lowest average pH, highest phosphorus content, lowest calcium content, lowest potassium content, and lowest magnesium content of all locations.

However, differences among sites within locations accounted for a substantial portion of total variation in most soil factors, and within-location variation was larger than among-location variation in phosphorus content. Furthermore, it is possible that the effects of within-location soil heterogeneity on selection may be underestimated by these data. Nutrient levels and other soil factors are highly complex and seldom act independently, either in the soil or in plant nutrition. Our soil data show relationships among some factors, as indicated by the two locations discussed above, but there were many exceptions to the relationships and other factors were unrelated. Independently varying levels of nutrients and other soil factors, and their complex interactions in the plant, could create a mosaic of environments that is more complex on a local basis and less so on a geographic basis than is indicated by the variance components for any single factor in Table 1.

These soil data and these speculations suggest that within-population genetic variation could be large for plant responses to the soil factors that were measured. We have not tested our pin oak progenies for response to varying levels of these particular factors, but results of studies by graduate students Paul Berrang and Nelson Foose on resistance to chlorosis and aluminum toxicity in pin oak support the expected trend. Relative resistance to iron-deficiency chlorosis was measured as degree of chlorosis development in solution culture with only 0.2 ppm iron. Relative resistance to aluminum toxicity was measured using an index based on reduction of root growth in solutions containing 100 ppm aluminum vs. solutions containing no aluminum. Nearly all of the genetic variation in both experiments was associated with differences among families within populations (Table 2). Differences among populations were not statistically significant.

It appears that within-population variation in adaptation to mineral levels is important in pin oak. Genetic gains in resistance to chlorosis or aluminum toxicity could have been achieved more efficiently by intensive testing of a few populations than by the range-wide provenance test that was conducted. We believe that similar situations may prevail for other species and other soil mineral responses. However, to guide improvement strategies it is important that more information of this nature be collected through studies of the genetics of mineral adaptation in combined provenance/progeny experiments.

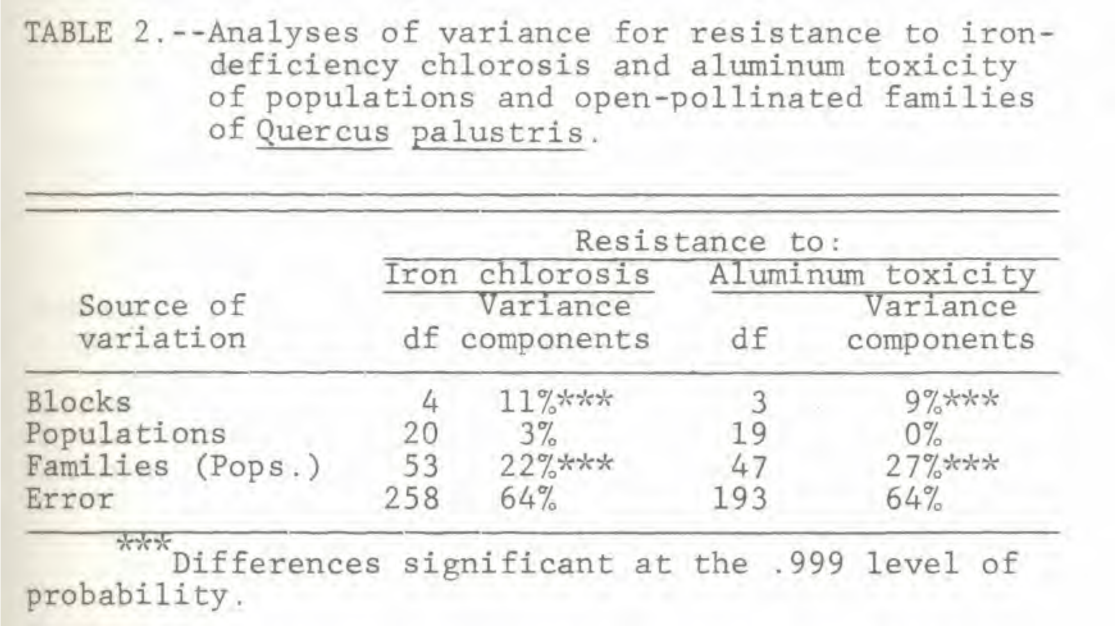

TABLE 2.--Analyses of variance for resistance to iron-deficiency chlorosis and aluminum toxicity of populations and open-pollinated families of *Quercus palustris*.

	Resistance to:			
	Iron chlorosis		Aluminum toxicity	
Source of variation	df	Variance components	df	Variance components
Blocks	4	11%***	3	9%***
Populations	20	3%	19	0%
Families (Pops.)	53	22%***	47	27%***
Error	258	64%	193	64%

***Differences significant at the .999 level of probability.

CONCLUSIONS

Improving the responses of trees to soil mineral environments presents a challenging opportunity for tree breeders. This opportunity has until now received attention in only the most advanced improvement programs, but it will become more important as we proceed in the domestication of trees. The need for improvement in mineral response is most obvious where particular deficiencies or toxicities are common and pronounced--such as iron deficiency of pin oak and some other amenity tree species or aluminum toxicity of many species on coal mine spoils. However, we must also recognize that adaptation to more normal sites may be less than optimum and that sub-optimum adaptation may not be expressed as classic symptoms of deficiency or toxicity.

Differential adaptation can be demonstrated only by the existence of genotype x soil fertility interaction. Both yield and slope of the response curve are necessary for a full description of interaction, and both measures are important in determining the relative superiority of genotypes. Parallel response curves show no interaction; hence relative growth or survival on one particular site is not necessarily indicative of differential adaptation. Furthermore, steep response curves, while perhaps associated with superior performance even on poor sites, may be indicative of problems that could occur under slightly different experimental conditions.

More information regarding genetic variation patterns in adaptation to mineral stresses would be useful in planning improvement strategies. Ecotypic variation has in some instances been shown to occur in response to extreme soil types, but little is known of the kind or amount of variation that may occur where soil differences are less obvious. Our tentative proposition is that adaptation to the mineral environment may show more local variation, and less geographic variation, than is generally true for adaptation to the climatic environment. If so, this means that intensive progeny or clonal testing, with little regard to provenance, will be the most efficient approach for improving response to the mineral environment.

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