Specialization and Flexibility in Genetic Systems of Forest Trees[1]

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The concept of the gene pool is fundamental to ecology and to population genetics. Ecologists recognize that the gene pool determines species tolerances to environmental conditions, and differences in tolerance of species form the basis for the philosophy of successional replacement. To population geneticists, the structure of the gene pool is basic to theories of selection and evolution. Since species of forest trees occupy different successional positions, the concept of the gene pool in forest trees must be considered from both genetic and ecologic viewpoints.

Recent interest in the genecology of forest trees is reflected in a review by Tigerstedt (1967) and genecological studies with birches (Stern, 1964 a, b) and several European hardwood species (Galoux, 1967). These papers point out the significance of genetic structure of populations in studies of genetic variation and in tree breeding as well as emphasizing the relationship between ecologic and genetic variation.

The present paper attempts to relate genetic and ecologic theory in order to develop testable hypotheses of genetic structure for forest tree populations, populations being here envisioned as any natural grouping of trees which are genetically semi-discrete. Consideration is given to the fitness-flexibility compromise, to methods by which species meet the conflict between fitness and flexibility, and to the action of natural selection.

Fitness-flexibility Compromise

Genetic variation within the gene pool of natural species is subject to a compromise between fitness in contemporary environments and flexibility (Mather, 1943; Darlington, 1958). Fitness is necessary for survival and reproduction of individuals in their immediate environment; flexibility is necessary for the production of progenies preadapted to environmental change (Heslop-Harrison, 1964). Species lacking genetic variability are doomed to extinction. for they cannot become adapted to changing conditions (Thoday, 1953). Conversely, species that express a high degree of genetic variability within their germplasm are unable to consistently produce specialized progenies that are highly adapted to a particular set of environmental conditions, and, therefore, may not survive because of an inability to compete successfully with better adapted species (Mather, 1943). Thus, the advantages of recombination through sexual reproduction are balanced against the disadvantages of segregation. A segregation load is imposed on the species; actual fitness is a compromise and does not approach the maximum.

Since the fitness-flexibility compromise is universal to all species, it is not surprising that both unique and general methods for resolving it have evolved. Unique methods include production of true breeding heterozygotes in *Oenothera* (see Heslop-Harrison, 1964), alternation of apomictic with sexual reproduction (Thoday, 1953), and alteration between self and cross pollinations (see Allard, 1965). General methods may involve the subdivision of species into genetically distinct breeding units, developmental homeostasis, and coadaptation of genetic systems. It is the general methods that are of major relevance to forest trees, and even though the methods are not mutually exclusive, they will be considered separately.

Breeding *Units*

The genetic consequences of subdivisions of a species into genetically discrete breeding units have been theoretically explored by Sewall Wright. Wright (1965) envisaged a complementary process for current adaptability and future evolution which results from the combined effects of polygenic inheritance, selection for phenotypes intermediate with respect to numerous traits, pleiotropism, and lack of overdominance in creating surfaces of adaptive values. Within breeding units, inbreeding or random genetic drift combined with mass selection allows breeding units to attain the highest adaptive peak which is compatible with local environmental conditions (Wright, 1960). Migration among breeding units promotes diffusion of adaptive genetic combinations throughout the population and generates genetic variability necessary to meet changing conditions (Wright, 1965).

The concept of breeding units, as developed by Wright, has not been systematically explored for forest trees. Limited genetic data indicated discontinuous patterns of variation for two populations of western white pine (Pinus monticola Dougl.) which were located on contrasting exposures less than one-half mile apart in northern Idaho (Squillace and Bingham, 1958). Morphologic observations suggested an edaphic basis for discontinuous variation among adjacent populations of northern white cedar (Thuja occidentalis L.) in northern Wisconsin (Habeck, 1958) and for species of Quercus in Texas (Muller, 1952). Moreover, Benson, et al. (1967) have shown that segregation toward parental types in introgressants between species of Quercus in California varied with exposure on single hills, and that the degree of introgression was interpretable from the ecologic requirements of the parental types; they concluded that even on a local scale, evolutionary sorting is rapidly adjusted by the environment.

Developmental Homeostasis

Developmental homeostasis, defined by Lerner (1954) but also noted by Thoday (1953) and Dobzhansky and Wallace (1953), is the ability of individuals to respond to a variety of environments with a moderately constant morphology and physiology. According to this concept, the genotype is balanced to such an extent that development is buffered and similar adaptive phenotypes result from a variety of genotypes in a range of environmental conditions (Thoday, 1953).

Recent studies of developmental homeostasis in Drosophila and maize have suggested that phenotypic plasticity is a function of genetic heterozygosity. Phenotypic variance

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in a wide range of environments declined with increasing heterozygosity for five characteristics of *Drosophila* (Robertson and Reeve, 1952; Dobzhansky and Levene, 1955; Mather, 1953; Bonnier, 1961; Thoday, 1958; Bonnier *et al.*, 1959; Dawson, 1965; Rowe and Cockerham, 1963), and F_1 hybrids were more uniform than inbred lines at both constant and fluctuating temperatures (Beardmore, 1960). Shank and Adams (1960) found that in variable environments, maize hybrids performed more consistently than inbred lines for six characteristics. Thus, heterozygotes tended to perform better than homozygotes across a range of environmental conditions, whereas homozygotes tended to be narrow specialists (Dobzhansky and Levene, 1955).

Coadaptation of Genetic Systems

The gene pool is considered by the classical definition to be the totality of alleles distributed among the members of an interbreeding population (Lerner, 1958). The totality of alleles is not considered as individual allelic frequencies, but more as an integrated system (Li, 1967), within which allelic frequencies are interdependent (Lerner, 1958). The gene pool is thus considered as a balanced structure, and its components form a coadapted genetic system (Dobzhansky, 1955).

Coadaptation theoretically exists on two levels, interchromosomal and intrachromosomal (Lerner, 1958). At the interchromosomal level, selection does not act to adjust gene frequencies individually, but acts to coadapt all loci on all chromosomes, so that a unified gene pool is created and maintained (Lerner, 1958). This level of coadaptation is apparently synonymous with the concept of cohesion which developed from observations on joint inheritance of traits within ecological races (Clausen and Hiesey, 1959). Cohesion results from (1) dispersion of genes involved in the same quantitative trait throughout the genome, and (2) linkage between genes involved in different traits.

Intrachromosomal coadaptation is of two types: internal and relational (Lerner, 1958). Internal coadaptation refers to the arrangement of genes within chromosomal segments (Mather, 1943). Natural selection apparently induces close linkage of heterozygous loci which are involved in the same trait (Mather, 1943) and which have alternate plus and minus effects on the phenotype (Allard, 1960). Genetic variability is thus considered to be latent (Mather, 1943). This type of coadaptation results in the formation of supergenes (Turner, 1967), the existence of which has been experimentally shown (see Bodmer and Parsons, 1962).

Intrachromosomal coadaptation of the relational type involves the selective attainment of optimal genic combinations at homologous loci (Lerner, 1958). At each locus natural selection apparently results in accumulation of numerous alleles, each of which combines favorably with the other alleles and into the entire genetic background (Lerner, 1958). Through pleiotropism, polygenic inheritance, and linkage, the entire genetic system becomes integrated (Dobzhansky, 1955). Dobzhansky (1955) emphasized this type of coadaptation as the primary factor in organizing and integrating genetic systems. The existence of relational coadaptation is best exemplified in the concept of genetic homeostasis, defined by Lerner (1954) as the property of a population to equilibrate its gene pool and resist sudden changes. In support of his hypothesis, Lerner (1954) listed indirect evidence which included variability experiments, occurrences of phenotypic deviants, and results of artificial selection experiments. Whether these observations on domestic and laboratory populations are applicable to genetic systems in natural populations remains to be shown.

Action of Natural Selection

The three general methods for resolving the conflict between fitness and flexibility vary in how they are related to two hypotheses on the action of natural selection in shaping the gene pool of species. These hypotheses, designated as the classical and the balance hypotheses, involve alternatives in the genetic structure of populations (see Dobzhansky, 1955; Muller, 1958; Wallace, 1958; Allard, 1960; Bonnier, 1961). According to the classical hypothesis, selection operates by gradual substitution and eventual fixation of the more favorable alleles. At most loci, therefore, individuals tend toward homozygosity. Heterozygosity is maintained by dominant and overdominant gene action, balanced polymorphisms, and fluctuations in selection coefficients. The balance hypothesis, on the other hand, assumes that there are few homozygous loci and a large number of alleles per locus. Natural selection, by favoring intermediate phenotypes, maintains heterozygosity in a balanced condition; the result is a coadapted genetic system with complex integrative properties.

There is little doubt among evolutionists that natural selection acts as a balancing agent on the interchromosomal level. This type of integration would not completely exclude fixation according to the classical hypothesis, for integration would be loose and readily adjusted. The main problem involves whether the balancing action of natural selection can create tightly integrated systems with complete exclusion of the systematic changes in gene frequency envisioned in the classical hypothesis (Dobzhansky, 1955). For example, studies in *Drosophila* have shown conflicting results. Kitigawa (1967) maintained that the interaction between lethal genes is synergistic and genic action conforms more closely to the balance hypothesis. By contrast, Wallace and Dobzhansky (1962) believed that the action of lethal genes conformed to the balance hypothesis.

Although tightly and differentially integrated gene pools might characterize individual breeding units, the significance of the breeding unit organization, as envisaged by Wright (1960), was for an approach to differential homozygosity within each unit through differential selection pressures and random genetic drift. Interchromosomal coadaptation accompanied by allelic substitution and fixation is thus the more compatible view in relation to Wright's theory. The concepts of relational intrachromosomal coadaptation and genetic homeostasis were clearly derived from the balance hypothesis involving complex integration. Developmental homeostasis, with its apparent association with heterozygosity, also would seem more compatible with the balance hypothesis. Internal intrachromosomal coadaptation, on the other hand, appears compatible with all general methods for resolving the fitness-flexibility conflict.

Relationship Between the Genetic System and the Environment

The relationship between the genetic system and the environment was considered from an intuitive and theoretical approach by Thoday (1953) and Levins (1962, 1963, 1964 a, b), respectively. Thoday (1953) reasoned that species living in a variable environment require genetic variability, but species living in a homogeneous environment tend to be relatively genetically uniform. These relationships were further elucidated by Levins in a series of papers on the theory of fitness in a heterogeneous environment. Levins (1964 a) assumed that there is no correlation between environments of succeeding generations and showed that in terms of differentiation along geographic gradients, if niche differences are small compared to homeostasis of individuals, clinal patterns of variation can be expected. If niche differences are large compared to the homeostasis of individuals, and if the environment is stable in time but variable in space, discrete races should develop. For species occupying environments that vary widely in space and/or time, either developmental homeostasis or polymorphism can be expected. Ecological polymorphism is likely to be the optimal form of genetic structure where environmental extremes are lethal for different groups of genotypes (Levins, 1963), or where major genes, supergenes, or chromosome reconstructions govern environmental adaptations (Ford, 1964).

Among the few experimental investigations that pertain to these concepts, Van Valen (1965) reported that phenotypic variability in bird species was directly proportional to the breadth of the ecological niche. Moreover, varietal mixtures of crop species have shown greater productivity than pure lines when grown in a variable environment (Pfahler, 1965; Allard and Bradshaw, 1962; Simmonds, 1962). These results suggest that populations which occupy a variable environment tend to be more variable genetically than populations living in a less variable environment.

Application to Forest Trees

The application of concepts on the fitness-flexibility compromise and the genetic systems in populations to forest trees requires an assessment of the temporal and spatial environmental variability commonly met by individuals of each species. Although precise environmental data of this nature are not generally available, gross assessment of the environment of forest trees can be inferred from the different successional positions occupied by each species. Pioneer species must become established in an environment that is highly variable in time. These species impart a degree of stability to the environment and permit the influx of species adapted to conditions somewhat less variable but more optimal for growth. Succession thus proceeds through a sequence of plant communities on a specific site toward a relatively stable association. Stability is applicable to both vegetation and environment, it implies relative freedom from large environmental fluctuations (see Whittaker, 1957; 1965; Geiger, 1965; Olson, 1963; Jackson and Newman, 1967). Thus, the degree of environmental heterogeneity met by each species is associated with the relative successional position of a species.

The degree of environmental variability associated with particular species on a given site is correlated with the spatial environmental variability common to that species. Pioneer species, which face a variable environment in time, tend to occupy a broad range of sites. Successionally advanced species, which are exposed to rather stable conditions, are found only on mesic sites. Yet, pioneer species also attain their best growth and development on the mesic sites where they are rarely found as natural components of successionally advanced plant communities. For example, jack pine (*P. banksiana* Lamb.) occurs on pine barrens and swamp borders, but it attains its best growth and development on deep, moist, well-drained sites (Harlow and Harrar, 1958). By contrast, it is only on the mesic sites that the successionally advanced sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) are found. In addition, Damman (1964) has shown that greater ranges of nutritional and moisture conditions separate sequential forest associations on the pioneer level than on the terminal level. Pioneer species have a wide adaptability whereas successionally advanced species are specifically adapted. Succession proceeds from species of lesser specialization to species of greater specialization, and it approaches termination with species of maximum fitness for relatively stable conditions.

We hypothesize that different species of forest trees, as evidenced by their relative successional positions, have met the fitness-flexibility compromise differently. Pioneer species have sacrificed high fitness for specific conditions in order to maintain flexibility or adaptability to a variety of sites. Species living in the highly competitive environments of terminal communities have sacrificed broad adaptability in order to achieve specialization, or a high degree of fitness to specific conditions. Species of intermediate successional positions have met the conflict in an intermediate manner. This hypothesis does not imply, however, that the only difference among genetic constitutions of tree species is in the breadth of the gene pool. The hypothesis is based only on a negative relationship between specialization and flexibility. This relationship should be associated with differences in structure of genetic systems.

In order to apply the concepts of Thoday and Levins, the correlation of environment of subsequent generations must be considered. Autocorrelation of environments between successive generations is visualized as systematic environmental changes from which selection in any one generation will be beneficial to the following generation (Levins, 1964 a). Regeneration of pioneer species requires open conditions resulting from site disturbances; generations are therefore discrete (even aged stands). Barring disturbance, subsequent generations of species from early and intermediate successional stages most often are not established on the site where their parents grew. Environmental correlation for these species thus would reflect spatial elements more than temporal ones. On a given site, however, environmental correlation is temporal with each succeeding species occupying a more uniform environment. Only for species of the terminal stages of succession, however, are successive generations associated with the same site. Since environmental conditions associated with terminal communities approach stability, environmental fluctuations between non-discrete generations would be random. It thus appears that autocorrelations do not characterize environments of subsequent generations of forest trees.

In accord with the proposals of Thoday and Levins, populations of pioneer species, as a consequence of their establishment and development in a highly variable environment, should be characterized by a genetically heterogeneous gene pool. Since the environment is variable in time as well as space, developmental homeostasis should be a property of most individuals. Thus, highly heterozygous trees should compose each population, continuous patterns of variation should be predominate, and additive genetic variance should be common (Levins, 1964)

Developmental homeostasis should be relatively unimportant for species of terminal communities, for the environment of each individual is relatively stable. Successionally advanced species are restricted to specific environmental conditions for which their offspring must be specialized. It seems reasonable, therefore, to propose that the germplasm of these species is subdivided into breeding units, and each unit is largely homozygous with respect to fitness characteristics for each site. As noted by THODAY (1955), when species are placed in a stable environment, selection, in order to retain high fitness, will promote attainment of homozygosity or evolution of apomictic systems. Hence, local differentiation of the successionally advanced species is plausible; the environmental differences between successive generations are probably random, and thus non-additive (epistatic) gene action possibly involving homozygous loci (see WALLACE and VETUKHIV, 1955) can be expected because natural selection must act to create isolating mechanisms under these conditions (LEVINS, 1964 b).

Natural selection in forest trees must act toward fixation of the genotypes which provide maximal fitness on a particular site at a particular time. However, genotypes cannot be fixed for pioneer species since selection favors a degree of heterozygosity and since contiguous generations most often are established under greatly different site conditions. Fixation can occur for successionally advanced species; the environment of these species is rather stable in time and only somewhat variable in space, and subsequent generations are often established on sites on which their parents grew.

Adjustment by forest trees to the fitness-flexibility conflict is visualized as a continuous sequence which parallels increasing environmental stability associated with succession. Under this hypothesis, the evolutionary theories of FISHER and WRIGHT would then appear at opposite ends of a continuous gradient. WRIGHT (1960) believed that evolution would be most rapid with the establishment of small breeding units which become differentiated through random drift and/or selection; variability could be generated by migration between units. This theory appears to apply to successionally advanced species. FISHER (1958) theorized that evolution would be most effective in large heterogeneous populations, for the larger the population, the more genetic variability it may carry, and the less the non-adaptive effects of chance. This apparently applies to pioneer species.

The degree to which coadaptation is involved in genetic systems of forest trees is uncertain. Intuitively, it is improbable that a single balanced system could produce a similar phenotype in the broad range of environments that pioneer species face. Indeed, ALLARD (1965) has shown that single coadapted systems do not endow flexibility in several colonizing species. We therefore suggest that coadaptation of genetic systems of forest trees is primarily of the inter-chromosomal type; gene pools tend to be loosely integrated without exclusion of fixation according to the classical hypothesis. We do not propose that internal intrachromosomal coadaptation (supergenes) is non-existent; we imply only that relational intrachromosomal coadaption is not likely to be the primary integrative agent.

It should be noted, however, that the possibilities for relational intrachromosomal coadaption in forest trees cannot be completely excluded. An unsolved problem in population genetics involves whether natural variability is more dependent on heterosis and coadaptation than on adaptation to different environments (DOBZHANSKY, 1955). It is possible that the effects of different environments on the genetic structure of populations of forest trees have oriented development toward relational integration. In this case, differences in the structure of genetic systems of species from different successional positions apparently would reside in the degree of relational integration. The fitness-flexibility compromise must still be met; successionally advanced species must be specialized whereas pioneer species should be flexible. Perhaps tightly integrated systems characterize successionally advanced species and loosely integrated systems characterize pioneer species. However, at the present time the hypothesis excluding relational intrachromosomal coadaptation appears more plausible.

Little experimental evidence exists to support or refute the present hypothesis. Among the relatively few studies in which within-population variation could be estimated, statistically significant variation among young open-pollinated, one-parent progenies from maternal trees within stands have been found for *Pinus sylvestris* L. (WRIGHT, 1963), *P. elliotii* ENGELM. (SQUILLACE, 1966), and *Quercus rubra* L. (KRIEBEL 1964). Of more relevance, however, is STERN's (1964 a) comparison of genetic structure of populations with open-pollinated progenies from the pioneer *Betula japonica* SIEBOLD and the successionally advanced *B. maximowicziana* REG. STERN observed high variability within populations of both species, but closer adaptation of populations of the successionally advanced species to an expected altitudinal and latitudinal cline than for the pioneer species. From this he concluded that coadaptation was prevalent in the genetic systems of both species, but that the successionally advanced species was more highly specialized. It is uncertain, however, whether reports of significant variation among one-parent progenies reflect the genetic structure of the populations or are an artifact induced by the sampling approaches emphasized in forest genetics.

The present hypothesis relating genetic structure of populations to relative ecologic position must be regarded as a generality. *Pinus resinosa* AIT. and *Picea omorica* (PANČIČ) PURKYNE appear as exceptions to the hypothesis, for both species are apparently rather uniform genetically (see WRIGHT, 1960). Confusion may also arise from the complex ecological terminology, i. e., pre-, post-, sub-, edaphic, or climatic climax. Population structure can only be related to the environmental variability faced by contiguous generations of each species. For example, in the tropics environmental conditions tend to be optimal for growth; the high degree of specialization and speciation in tropical trees may result from genetic drift or inbreeding, promoted by a reduction in population density of individual species (FEDEROV, 1966). Moreover, discontinuous variation may characterize heterogeneous populations of transient species, as suggested for western white pine (SQUILLACE and BINGHAM, 1958). Finally, genes that are not expressed phenotypically but that are arranged in hierarchies of epistatic-hypostatic action are prevalent in several natural species (CLAUSEN, 1959). Similarly complex systems may also be common in forest tree species, regardless of their successional position.

Relevance to Tree Improvement

Implications of a relationship between genetic systems in populations or breeding units and the successional position of species are important for the study of natural variation in forest trees. To date, most studies have emphasized identification of broad geographic variation in experiments using open-pollinated materials. As a consequence of both the potential pollen dispersion between breeding units and the practice of obtaining geographically representative seed collections, it is not surprising that a continuous pattern of variation is commonly reported in provenance tests. Whether the observed provenance tests fairly represent both the sampled population and the geographic area represented by the sampled population is uncertain.

A desirable further step in studies of natural variation would involve disproving null hypotheses that presuppose discontinuous patterns of variation. This would require more detailed studies of variation among and within breeding units in a relatively limited geographic area, particularly for successionally advanced species. Increased intensity of sampling, both in terms of within and among breeding units may result in more evidence of ecotypic differentiation of the type reported by Habeck (1958) for *Thuja occidentalis* L.

Testing of the present hypothesis on the fitness-flexibility compromise in forest trees will require controlled crossing and a careful choice of fitness-related traits. The dimensional characteristics traditionally measured in studies of variation, are generally strongly influenced by environment and hence are likely to indicate continuous variation among progenies. The study of variation in characteristics of growth patterns (e. g., Stern, 1964 a) may offer promise of more clearly demonstrating genetic differentiation especially in those species possessing strongly endogenously controlled growth patterns. Date of terminal bud formation may be the type of characteristic which will provide a more direct view of the genetic consequences of ecological diversity than is now available for most species (Pauley and Perry, 1954).

Progress by ecologists in characterizing environment and environmental effects (Watt, 1966), and consideration of the most relevant statistical methods should supplement a more detailed approach to the study of natural variation. In regard to statistical methods, Van Valen's (1965) approach to examining the correspondence of phenotypic variability with the width of ecological niches using combined probabilities from tests of significance may have applicability for forest trees.

In relation to tree improvement, the present hypothesis implies that breeding methods must reflect the natural environment and genetic structure of parent populations. This is a consequence of both the relatively limited degree of genetic manipulation possible within a tree breeder's career, and the relatively minor (in comparison with field crops) degree to which natural environment is likely to be altered for genetically improved forest trees. An effort must be made to define the locality or conditions suitable for propagation of each seed source. Expected genetic gains will not be realized if they are accompanied by degeneration of natural fitness characteristics. Appropriate breeding methods therefore may vary among species. Substantial proportions of additive genetic variance can probably be expected in most of the pioneer species on which, perhaps fortunately, much of the current effort in tree improvement is concentrated. Maintenance of heterozygosity may be one of the most important considerations with pioneer species. By contrast, the present hypothesis and the conclusions of Levins (1963, 1964 a) imply that within breeding units of successionally advanced species, genetic variance within populations may be relatively limited, and gene action may be predominantly epistatic. For successionally advanced species, genetic differentiation among local breeding units may be more pronounced and genetic improvement may have to be based on specific combining ability for relatively specific types of environments.

More restrictive limitations on tree improvement are imposed if relational intrachromosomal coadaptive complexes characterize the germplasm of forest trees. Following selection, a reintegration of the gene pool must occur; extreme selection pressures which greatly upset the coadapted system must not be imposed, and greatest gain can be expected from characteristics which are only secondary to fitness (Lerner, 1958).

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Summary

The genetic structure of populations of forest trees was considered in relation to ecologic and population genetic theory. An hypothesis of population structure of forest trees was proposed after consideration of means by which species adjust to the compromise between fitness in contemporary conditions and flexibility for adaptation to changing conditions. It was proposed that the genetic systems of forest tree species differ among species, and that the differences are manifest in the relative successional positions occupied by each species. Pioneer species have apparently sacrificed high immediate fitness for adaptability to a variety of sites; these species are probably characterized by a highly heterogeneous and largely unsegmented gene pool, and developmental homeostasis is a property of each individual. Successionally advanced species, on the other hand, have sacrificed adaptability for specialization to specific site conditions and may be characterized by a highly segmented gene pool with an approach to homozygosity common within each segment.

The necessity for knowledge on the genetic structure of natural populations to tree improvement is stressed. Estimated genetic gains in economically important traits will not be realized if they are accompanied by a degeneration of fitness characteristics.

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Geographic variation in eastern white pine, 7-year results in Ontario[1]

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Eastern white pine, *Pinus strobus* L., is one of the most valuable timber species of eastern North America. Until the last decade little was published concerning the genetic variability of this species.

In 1955, the U. S. Forest Service organized a range-wide provenance study of white pine to examine some aspects of its genetic variability. Four U. S. Forest Experiment Stations, namely the Northeastern, Lake States, Central States, and Southeastern, and the Research Branch of the Ontario Department of Lands and Forests, co-operated in seed collection and seedling production for this study. Much of the information now available on genetic variation in white pines of different geographic origin has been derived from this co-operative effort.

Seed germination: Mergen (1963) and Fowler and Dwight (1964) reported that white pine seeds of southern origins require longer stratification periods than seeds of northern origins.

Taxonomy: Mergen (1963) found that seedlings of three southern origins had longer needles and fewer stomata per unit length of needle than seedlings of five northern origins, when both kinds were raised in a controlled environment at New Haven, Conn. Wright, Lemmien and Bright (1963) reported that, with the exception of one origin from central Maine, eastern provenances had blue-green foliage in the fall, in comparison with the yellow-green fall foliage of northwestern provenances.

Phenology: Santamour (1960), working with seedlings of 21 origins reported that bud swelling and elongation started at about the same time, but that seedlings of southern origins (Georgia and North Carolina) continued shoot elongation for a longer period than the others. Mergen (1963) found that seedlings from northern areas with a short growing period required less cold treatment to break winter dormancy than seedlings from southern areas.

Santamour (1960) reported slightly greater lammas shoot growth in seedlings of southern origin. Contrary to this,

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