



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 do-

mestic 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 successional 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 successional 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 successional 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 germ-

plasm 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 successional 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 successional 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 successional 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 coadaptation is not likely to be the primary integrative agent.

It should be noted, however, that the possibilities for relational intrachromosomal coadaptation 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; successional advanced species must be specialized whereas pioneer species should be flexible. Perhaps tightly integrated systems characterize successional 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 successional advanced *B. maximowicziana* REG. STERN observed high variability within populations of both species, but closer adaptation of populations of the successional 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 successional 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 successional 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 successional advanced species, genetic variance within populations may be relatively limited, and gene action may be predominantly epistatic. For successional 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 com-

plexes characterize the germplasm of forest trees. Following selection, a reintegration of the gene pool must occur; extreme selection pressures which greatly upset the co-adapted system must not be imposed, and greatest gain can be expected from characteristics which are only secondary to fitness (LERNER, 1958).

#### Acknowledgements

The authors gratefully acknowledge critical review of the manuscript by Dr. K. STERN, University of Göttingen, Federal Republic of Germany; Dr. E. C. FRANKLIN and Dr. A. E. SQUILLACE, U. S. Forest Service, Olustee, Florida; and Dr. R. J. HOFF, U. S. Forest Service, Moscow, Idaho.

#### 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. Successional 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.

#### Literature Cited

- ALLARD, R. W.: Principles of plant breeding. Wiley and Sons, New York, 1960, 485 pp. — ALLARD, R. W.: Genetic systems associated with colonizing ability in predominantly self-pollinated species. pp. 49—75. In: BAKER, H. G. and G. L. STEBBINS (ed.): The genetics of colonizing species. Academic Press, New York, 1965, 588 pp. — ALLARD, R. W., and BRADSHAW, A. D.: Implications of genotype-environment interactions in applied plant breeding. *Crop. Sci.* 4: 503—507 (1962). — BEARDMORE, J. A.: Developmental stability in constant and fluctuating temperatures. *Heredity* 14: 411—422 (1960). — BENSON, L., PHILLIPS, E. A., WILDER, P. A., et al.: Evolutionary sorting of characters in a hybrid swarm. I. Direction of slope. *Amer. Jour. Bot.* 54: 1017—1026 (1967). — BODMER, W. F., and PARSONS, P. A.: Linkage and recombination in evolution. *Adv. in Genet.* 11: 1—100 (1962). — BONNIER, G.: Experiments on hybrid superiority in *Drosophila melanogaster*. I. Egg laying capacity and larval survival. *Genetics* 46: 9—24 (1961). — BONNIER, G., JOHNSON, U. B., and RAMEL, C.: Experiments on the effects of homozygosity and heterozygosity on the rate of development of *Drosophila melanogaster*. *Genetics* 44: 679—704 (1959). — CLAUSEN, J.: Gene systems regulating characters of ecological races and subspecies. *Proc. X Int. Cong. Genetics* 1: 434—443 (1959). — CLAUSEN, J., and HIESBY, W. M.: The balance between coherence and variation in evolution. *Proc. Nat. Acad. Sci.* 46: 494—506 (1959). — DAMMAN, A. W. H.: Some forest types of central Newfoundland and their relation to environmental factors. *For. Sci. Monog.* 8, 62 pp. (1964). — DARLINGTON, C. D.: Evolution of genetic systems. Oliver and Boyd, Edinburgh, 1958, 265 pp. — DAWSON, P. S.: Genetic homeostasis and developmental rate of *Tribolium*. *Genetics* 51: 873—885 (1965). — DOBZHANSKY, T.: A review of some fundamental concepts and problems of population genetics. *Cold Spring Harbor Symp. Quant. Biol.* 20: 1—15 (1955). — DOBZHANSKY, T., and LEVENE, H.: Genetics of natural populations. XXIV. Developmental homeostasis in natural population of *Drosophila pseudoobscura*. *Genetics* 40: 797—808 (1955). — DOBZHANSKY, T., and

- WALLACE, B.: The genetics of homeostasis in *Drosophila*. Proc. Nat. Acad. Sci. 39: 162—171 (1953). — FEDEROV, A. A.: The structure of the tropical rain forest and speciation in the humid tropics. Jour. Ecol. 54: 1—11 (1966). — FISHER, R. A.: The genetical theory of natural selection. Dover Books, New York, 1958, 291 pp. — FORD, E. B.: Ecological genetics. Wiley and Sons, New York, 1964, 335 pp. — GALOUX, A.: Diversification génécologique régionale chez les espèces ligneuses feuillues. XIV IUFRO Congress, Section 22, 16 pp. (1967). — GEIGER, R.: The climate near the ground. Harvard Univ. Press, Cambridge, Mass., 1965, 611 pp. — HABECK, J. R.: White cedar ecotypes in Wisconsin. Ecology 39: 457—463 (1958). — HARLOW, W. M., and HARRAR, E. S.: Textbook of dendrology. McGraw-Hill, New York, 1958, 561 pp. — HESLOP-HARRISON, J.: Forty years of geneecology. Adv. in Ecol. Res. 2: 159—247 (1964). — JACKSON, M. T., and NEWMAN, J. E.: Indices for expressing differences in local climates due to forest cover and topographical differences. Forest Sci. 13: 60—71 (1967). — KITAWAGA, O.: Interaction in fitness between lethal genes in heterozygous condition in *Drosophila melanogaster*. Genetics 57: 809—820 (1967). — KRIEBEL, H. B.: Parental and provenance effects on growth of red oak seedlings. Proc. 4th Cent. States For. Tree Imp. Conf., p. 19—25 (1964). — LERNER, I. M.: Genetic homeostasis. Wiley and Sons, New York, 1954, 134 pp. — LERNER, I. M.: The genetic basis of selection. Wiley and Sons, New York, 1958, 298 pp. — LEVINS, R.: Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. Amer. Nat. 96: 361—372 (1962). — LEVINS, R.: Theory of fitness in a heterogeneous environment. II. Developmental flexibility and niche selection. Amer. Nat. 97: 75—90 (1963). — LEVINS, R.: Theory of fitness in a heterogeneous environment. III. The response to selection. Jour. Theoretical Biol. 7: 224—240 (1964 a). — LEVINS, R.: The theory of fitness in a heterogeneous environment. IV. The adaptive significance of gene flow. Evolution 18: 635—638 (1964 b). — LI, C. C.: Genetic equilibrium under selection. Biometrics 23: 397—484 (1967). — MATHER, K.: Polygenic inheritance and natural selection. Biol. Rev. 18: 32—64 (1943). — MATHER, K.: Genetic control of stability and development. Heredity 7: 297—336 (1953). — MULLER, C. H.: Ecological control of hybridization in *Quercus*: A factor in the mechanism of evolution. Evolution 6: 147—161 (1952). — MULLER, H. J.: The mutation theory re-examined. Proc. X Int. Cong. Genet. 1: 306—320 (1958). — OLSON, J. S.: Energy storage and the balance of producers and decomposers in ecological systems. Ecology 41: 322—331 (1963). — PAULEY, S. S., and PERRY, T. O.: Ecotypic variation of the photoperiodic response in *Populus*. Jour. Arn. Arb. 35: 167—188 (1954). — PFAHLER, P. L.: Genetic diversity and environmental variability within the cultivated species of *Avena*. Crop. Sci. 5: 47—50 (1965). — ROBERTSON, F. W., and REEVE, E. C. R.: Heterozygosity, environmental variability, and heterosis. Nature 170: 286 (1952). — ROWE, K. E., and COCKERHAM, C. C.: Relation between performance and heterozygosity in *Drosophila*. Genetics 49: 63—66 (1963). — SHANK, D. B., and ADAMS, M. W.: Environmental variability within inbred lines and single crosses of maize. Jour. Genet. 57: 119—126 (1960). — SIMMONDS, N. W.: Variability in crop plants, its use and conservation. Biol. Rev. 37: 422—465 (1962). — SQUILLACE, A. E.: Geographic variation in slash pine. Forest Sci. Monog. 10, 56 pp. (1966). — SQUILLACE, A. E., and BINGHAM, R. T.: Localized ecotypic variation in western white pine. Forest Sci. 4: 20—32 (1958). — STERN, K.: Herkunftsversuche für Zwecke der Forstpflanzenzüchtung, erläutert am Beispiel zweier Modellversuche. Züchter 34: 181—219 (1964 a). — STERN, K.: Die Intensität der natürlichen Auslese entlang eines Altitudinalklins. Pp. 139—146. (In) Forstsamengewinnung und Pflanzenanzucht für das Hochgebirge. BLV. Verlagsgesellschaft, München, 1964 b. — THODAY, J. M.: Components of fitness. Soc. Expt. Biol. Symp. 7: 96—113 (1953). — THODAY, J. M.: Balance, heterozygosity, and developmental stability. Cold Spring Harbor Symp. Quant. Biol. 20: 318—327 (1955). — THODAY, J. M.: Homeostasis in a selection experiment. Heredity 12: 401—415 (1958). — TIGERSTEDT, P. M. A.: Quantitative genetics in provenance research of forest trees. XIV IUFRO Congress, vol. 3: 395—412 (1967). — TURNER, J. R. C.: On supergenes. I. The evolution of supergenes. Amer. Nat. 101: 195—221 (1967). — VAN VALEN, L.: Morphological variation and width of the ecological niche. Amer. Nat. 99: 377—390 (1965). — WALLACE, B.: The role of heterozygosity in *Drosophila* populations. Proc. X Int. Cong. Genet. 1: 408—419 (1958). — WALLACE, B., and DOBZHANSKY, T.: Experimental proof of balanced genetic loads in *Drosophila*. Genetics 47: 1027—1042 (1962). — WALLACE, B., and VETUKHIV, M.: Adaptive organization and the gene pools of *Drosophila* populations. Cold Spring Harbor Symp. Quant. Biol. 20: 303—310 (1955). — WATT, K. E. F.: Systems analysis in ecology. Academic Press, Inc., New York, 1966, 276 pp. — WHITTAKER, R. H.: Recent evolution of ecological concepts in relation to the eastern forests of North America. Am. Jour. Bot. 44: 197—206 (1957). — WHITTAKER, R. H.: Dominance and diversity in land plant communities. Science 147: 250—260 (1965). — WRIGHT, J. W.: Genetics of forest tree improvement. FAO Forestry and Forest Products Studies No. 16. Rome, 1962, 399 pp. — WRIGHT, J. W.: Genetic variation among 140 half-sib Scotch pine families derived from 9 stands. Silvae Genet. 12: 83—87 (1963). — WRIGHT, S.: Physiological genetics, ecology of populations, and natural selection. (In) The evolution of life. Sol Tax (ed.) 1: 429—475 (1960). — WRIGHT, S.: Factor interaction and linkage in evolution. Proc. Roy. Soc. London. B 162: 80—104 (1965).

## Geographic variation in eastern white pine, 7-year results in Ontario<sup>1)</sup>

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(Received for publication March 18, 1968)

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 lammass shoot growth in seedlings of southern origin. Contrary to this,

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