Forestry Commission, Research and Development paper No 76. London WIX 2AY, 16 pp., 1970. — DIETRICHSON, J.: The Geographic Variation of Springfrost Resistance and Growth Cessation in Norway Spruce (*Picea abies* (L.) KARST.). Medd. Det Norske Skogforsøksvaesen Nr. 96, Bind XXVII: 94–106 (1969). — LANGLET, O.: Några data från det internationella granproveniensförsöket av 1938 i Sverige (Some data from the international provenance experiment in spruce of 1938 in Sweden). Skogen 40: 238–239, 244 and 245. For. Abstr. 15, No 1269 (1953). — LANGLET, O.: Mellaneuropeiska granprovenienser i svenskt skogsbruk (Central European spruce provenances in Swedish forestry). K. Skogs- og Lanbr. Akad. Tidskr. 99: 259–329. For. Abstr. 23, No. 1837 (1960). — LANGLET, O.: Practical results and current problems in provenance research in Sweden. Wld Consultn Forest Genet. Tree Improv. Paper FAO/FORGEN 3/1: 1–10, 1963. — LANGLET, O.: Proveniensvalets betydelse för produktion och skogsträdsförädling av gran. Svenska Skogs. For. Tidskr. 62: 145–155 (1964 a). — LANGLET, O.: Skillnader mellan granprovenienser. Skogen 22: 426–428 (1964 b).

The application of ecological genetics principles to forest tree breeding

By P. M. A. TIGERSTEDT[1])

Department of Plant Breeding
University of Helsinki, Finland

(Received March 1974)

Definitions

Ecological genetics, a synthetic discipline, is difficult to define. It draws heavily on population genetics, quantitative genetics, population biology (itself an interdisciplinary science) and ecology. It is, however, justifiable to breed plants on an ecological genetic basis as the ecological basis is a model example of the interdisciplinary approach so essential in almost all fields of modern biology. Applied biology, in this case forest tree breeding, just does not advance if not approached wisely. It seems as though ecological genetics has finally advanced to a point of refinement which makes it imperative for all kinds of plant breeding. Forest trees with their long generation intervals, and often quite complicated natural ecosystems, stand out as particularly interesting organisms for ecological genetic studies. Emphasis has changed in recent years form more orthodox quantitative genetic approaches to ecological genetics. Heritability studies and the like are, of course, important components in the design of breeding programs but they are quite unreliable if not studied within a wider ecological framework. All these statements can of course be met with a laconic "so what" and it is our intention to penetrate a little the smooth surface into the maze of the ecosystem (food web) beneath.

Self-organizing systems relying largely upon feedback effects are inherent in all phenomena constituting our present world, be it mechanical or biological. These systems occasionally go astray — the results: severe distortion of the balance and input-output nonlinearity. The difference between a mechanical and a biological system is basically one of adaptation. To quote DOBZHANSKY (1956 and later) adaptation is the process of becoming adapted, adaptedness is a status of being adapted, i.e. of being able to live and reproduce in a given environment, while adaptability is an ability to become adapted to a certain range of environments.

A new situation in a biological system causes gradual genetic change in that system until a new optimum condition is attained. This change occurs gradually and almost unnoticed as it is accompanied by invariant reproduction (MONOD 1970). Adaptation in a strictly mechanical system does not in fact occur. At the most such a system adjusts itself through feedback. This, however, does not bring the mechanical system closer to optimality, but merely protects it against damage caused by adverse operating conditions. An optimal yield system in biology is a system in which a certain input, in terms of energy gives a maximum return through growth. An ecosystem is by definition a community of plants (and animals) and its environment treated together as a functional system of complementary relationships, and transfer and circulation of energy and matter (WHITTAKER 1970). The balance of an ecosystem depends on the details of birth, growth, reproduction and death of individuals in the system, i.e. on its demography. Generally, ecosystems follow the diversity-stability rule which means that stability increases with diversity. This rule is valid not only when concerning ecological food-webs but also when diversity is measured as heterozygosity within populations. Just as a last introductory remark we can conclude that biological systems which function adaptively may adjust themselves in basically three different ways; they may tend towards maximum yield within time limits, they may tend towards maximum sustainable yield or they may tend towards yield optimality. It is a matter of species strategy (r- and K-strategists) and ecological succession which of these ways is chosen. A system close to yield uptimality, however, ist most reliable. It is ecologically stable, it operates under conditions of low energy dissipation and it is highly diversified both inter- and intraspecifically. It is precisely this optimality principle that form the basis for new thinking in forest tree breeding. Ecological genetics gives answers to the many aspects involved in this interdisciplinary science.

Provenance research — the oldtimer in ecological genetics

Genecology is a synthetic discipline combining ideas and methods from genetics, taxonomy and plant physiology (HESLOP-HARRISON 1964). Provenance research means approximately the same, i.e. genecological observations of species variability that are made from a plant breeder's utilitarian point of view. Actually, the term has been

---

[1]) Address of the author: P. M. A. TIGERSTEDT, Department of Plant Breeding, University of Helsinki, SF-00710 Helsinki 71, Finland.

used almost exclusively in silvicultural or forest genetics contexts. HESLOP-HARRISON named his above-mentioned paper "Forty years of genecology", and gave a thorough review of pertinent information in this field, overlooking however, some of the classics in forest tree provenance research. LANGLET (1971), having personally studied questions of genecology for more than 40 years, supplemented the field with his paper "Two hundred years of genecology". His contributions mainly originate from provenance research done in silviculture, but they also emphasize the large number of provenance studies often overlooked by botanists or other biologists. LANGLET's intentions were clearly to establish contacts between different disciplines all working on the same theme: ecologically induced variation in plant species. It is fortunate that this was done, because it has caused a revaluation of the long forgotten works on provenance research in trees. It has also caused a healthy discussion between specialists representing applied and pure sciences, a discussion from which the forest tree breeder has nothing to lose but everything to gain!

Provenance research, being utilitarian and applied as to its ultimate aims, is generally concerned with adaptive traits. Actually genecology, as defined by HESLOP-HARRISON, is but a broader definition of provenance research also to include traits essentially nonadaptive. It can, however, be argued whether any trait is really without adaptive value. Broadly, provenance research could actually encompass all that is usually called ecological genetics be it growth characters, growth forms or any other trait down to isozymes.

Why is it that the term ecological genetics, until quite recently, was confined almost solely to studies on animals? The reason is evidently to be sought in the genetical definition of populations. These definitions have all been introduced by animal geneticists. To mention two of the classical population definitions we can take the "mendelian population" of DOBZHANSKY (1950) and the "local or random mating population" of MAYR (1963). Both are impossible to use in plant communities due to some basic differences between plants and animals in species ecology and genetics. To summarize, these differences depend on the following facts:

1) Plants are sedentary but animals move and can search for and settle on preferred habitats. Plants have to get along on whatever habitat they are initially established.

2) Plant pollination patterns, particularly in anemophilous species, suggest the establishment of pronounced neighboring effects or local subpopulation formation. Some recent investigations have failed to demonstrate such population clusterings however (KOSKI 1970, TIGERSTEDT 1973). Nevertheless it is difficult to believe that anemophilous plant populations are random-mating. Some other selective effect must in this case counteract population clusterings.

3) Plant pollination is stochastic and capricous, varying with wind and weather. Animal populations show greater regularity in this respect.

4) Plants produce larger amounts of gametes and zygotes than animals, probably in this way compensating for their sedentary mode of life.

5) Plants exhibit an array of different genetic systems ranging from monoecy to dioecy, from predominant inbreeding to predominant outbreeding, as well as apomixis and vegetative reproduction.

Classical provenance research has however demonstrated many of the outstanding features of plant populations. It has shown the existence of ecological gradient clines (LANGLET 1936) and later) in many climax species, established the importance of an edaphic basis for discontinuous variation in others (SQUILLACE and BINGHAM 1958, HABECK 1958 etc.) and revealed the dependence of species diversification upon geographical isolation (chance effects?) in yet others (WRIGHT, READ, LESTER, MERRITT and MOHN 1972). In other words it has opened our minds to modern thinking in provenance research; in population biology, ecological genetics, or community ecology or species strategy if you will. Provenance research is ready at this time to take a great leap forward; its results may even become crucial to basic ecological genetics.

Modern refinement of provenance research

Using the tools of ecological genetics in provenance research means that a completely new vocabulary has to be adopted by forest geneticists and tree breeders. To the outspoken breeder this may seem superfluous and may even be interpreted as an indication of snobbery or extravagance more harmful than beneficial for tree breeding. Such thinking is deplorable since it does not accept the scientific development so imperative if breeding success is the ultimate goal. The most penetrating of modern biological thinking takes a fresh look at ecology and advances along lines leading to a better understanding of whole ecosystems. Yield maximization has fallen to second place, ecological stability has taken over.

The ecological niche

A species occurs in a geographically restricted area. Its distribution can be plotted on a map. A species is usually further characterized by specifying its habitats demands. A habitat is an environment described in physical and chemical terms. Humidity, temperature, elevation, latitude, pH, mineral composition etc. are parameters that describe a habitat. There are species that, owing to their great ecological tolerance or genetic variability, can occupy a number of different habitats. Others are confined to narrow habitat limits. These two categories differ in species strategy.

The environment of a population can best be thought of as its niche. To describe a niche we use HUTCHINSON's (1965) set theory approach: "The niche of a population (or species) is conceived as a set of points in an abstract hypervolume defined by coordinates each of which represents an environmental factor such as temperature, humidity, salinity etc." Each population or species has an upper and lower absolute value for each environmental factor beyond which it cannot exists. In a two-dimensional system with environmental variables X and Y a niche would hence theoretically have a rectangular form *(fig. 1)*.

Similarly in a 3-dimensional coordinate system a niche could be represented by a cube. Expanded to n environmental variables a niche becomes a hypervolume within the coordinate system.

There are, however, two important objections to this presentation. (1) Environmental components interact, e.g. at higher temperature there is a rise in minimal humidity requirements. In such a case the niche lies within the hypervolume but is not identical to it.

(2) Population fitness is not identical in all parts of the niche. It is logical to assume that fitness takes on a bell-shaped form across the maximum tolerable niche spacing or, conversely, that the fitness of different phenotypes in the population compared in one environment also has a bell-shaped distribution (LEVINS 1961) *(fig. 2)*.

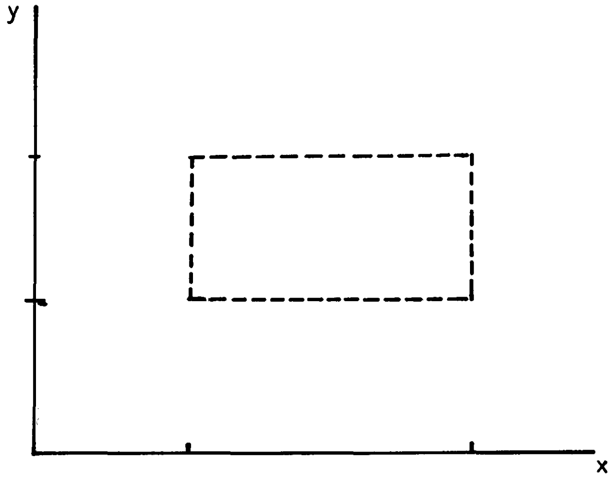

Figure 1. — The 2-dimensional ecological niche.

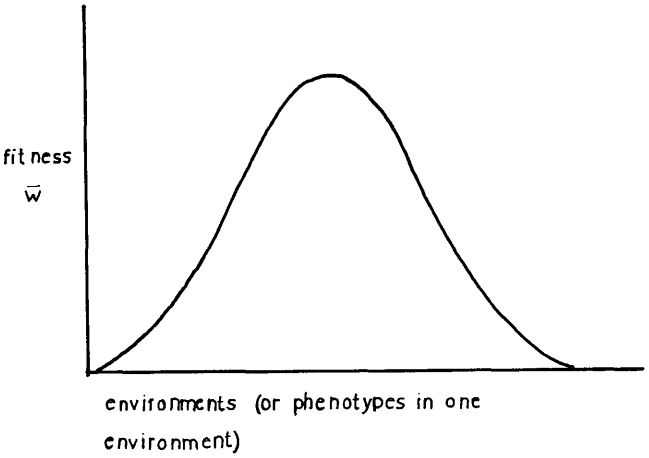

Figure 2. — Population fitness over environments.

Now the abscissa of the bell-shaped figure above can also be conceived as a one-dimensional niche, a temperature niche if you will. The niche just sets the limits to the population; it cannot live and survive in environments more adverse than the extreme ends of the niche. The situation becomes more complicated if the temperature niche width has to be measured, while several other dimensions vary simultaneously and interact. Under such circumstances niche width has to be measured in a quantitative way. We present some of LEVINS' (1968) suggestions in this context. If there are k different environments and we can estimate the proportion p_k with which the species is represented in each environment, then niche width is defined by

$$\log B = -\Sigma p_k \log p_k$$

or similarly as

$$B = 1/\Sigma p_k^2$$

Both formulae, when applied to experimental material have given similar results for niche width.

If the fitness of a genotype is measured over a range of values of some environmental variable, in our case temperature sum, the result will normally be a bell shaped curve. The flatter the curve the broader is the environmental optimum and the greater is the ecological tolerance of the population.

The dualism of the curve for a fitness component over environments is shown below where for two fixed environments fitness of a range of phenotypes is plotted *(figs. 3 and 4).*

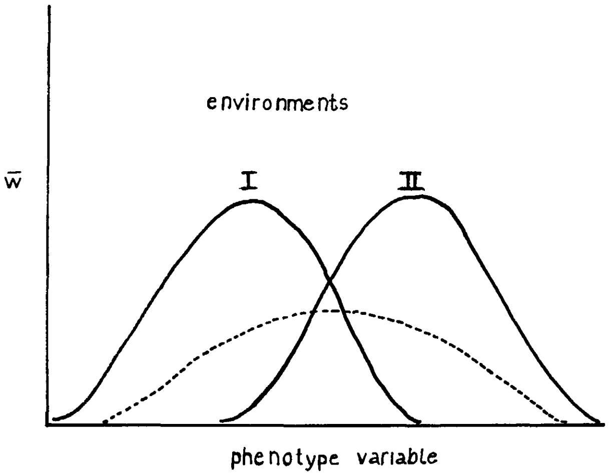

Figure 3. — Fitness as a function of phenotype in two ecologically close environments.

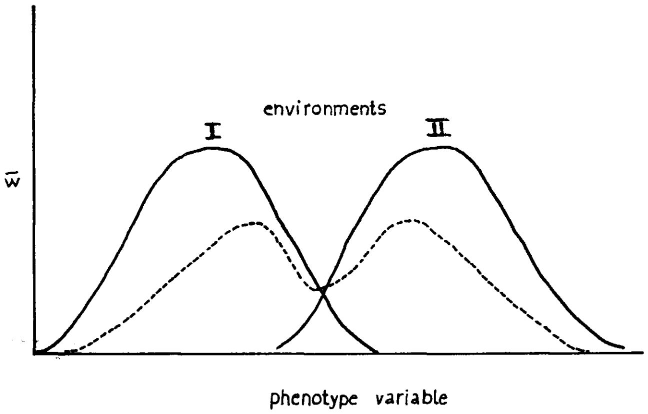

Figure 4. — Fitness as a function of phenotype in two ecologically diverse environments.

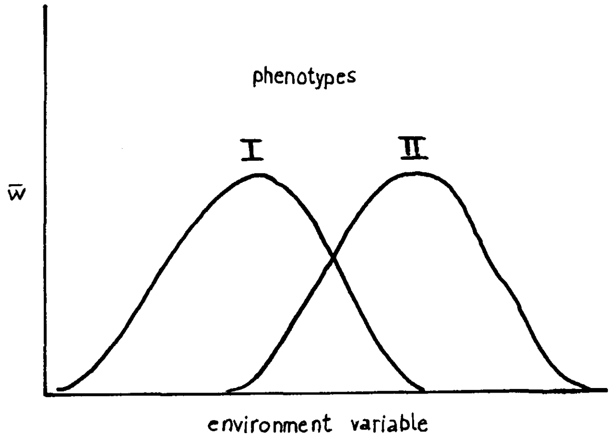

Figure 5. — Fitness as a function of environment for two phenotypes.

Analogously we can plot the curves for two fixed phenotypes over a range of environments *(fig. 5).*

For any two environments the curves overlap. If they are close enough for their inflection points to overlap, the average of the two curves will have a single peak in the middle *(fig. 3).* If the environments are further apart the average curve has a minimum at the midpoint and two peaks *(fig. 4).* This relationship between tolerance and niche-diversity is decisive in molding population structure, ecological diversification and finally adaptive strategy of species. The reader is referred to the book by LEVINS (1968) for further development of these thoughts and to Rehfeld and Lester (1968) for a study of its application to forest trees. The pertinent information that can be obtained from niche width estimates is of prime importance to the tree breeder. The first attempt to apply these ideas to tree breeding was done by Stern (1964) in a comparison of adaptive strategies in *Betula japonica* and *B. maximowiczii.* This was the introduction of a new way of thinking in forest tree breeding — thinking in terms of adaptive systems, or strategy thinking.

Development of cultivars

There have been alarming signs of genetic erosion and impoverishment in most of the worlds agricultural plants. It has caused severe disease outbreaks, particularly in the United States. This genetic vulnerability of crop plants has unambiguously been ascribed to the narrow genetic basis of the cultivars (NAS publ. 1972). These highly uniform and high performing cultivars have a fitness value close to zero! They do not fit into ecosystems, are highly vulnerable to parasite attacks, they perform well only under the most artificial conditions of cultivation, lack ecological tolerance and are genetically inflexible. Let us not make precisely these same mistakes in modern forest tree breeding. The ecological hazards which destroy short-rotation agricultural plants will hit long-lived tree species with amplified intensity. The situation concerning host-parasite interactions is particularly grave. Under natural conditions the host-parasite relationship has achieved a high degree of stability; the pathogen usually stabilizes at a density level where it does not profoundly distort the growth of the host. To give a simple analogy from economics: the pathogen adjusts its demands so as to live on the interest of the host. This adjustment involves genetic adaptation on both sides. The most simple population simulations have shown that such genetic adaptation takes scores of generations before equilibrium is reached (Pimentel 1961). The pathogen goes meanwhile into damped oscillations in density. In a recent paper Levin (1972) has pointed out the importance of the life cycles of predator and prey involved in systems of this kind. In the case of full "in-phase" conformity between host and parasite, the feedback mechanism may only operate under certain limited conditions. This is the case in Pimentel's example. If however, as is usually the case, host and parasite populations are "out of phase" then the feedback mechanism seems to be more generally operative. Host-parasite interactions between agricultural crops and their parasites have shown that this relationship in many cases depends on a gene-for-gene basis. Plant breeders are then in essence working with an ecological unit which perpetually slips out of their hands if not constantly met by breeding efforts. Varietal changes over a 40 year period (1910—1950) in wheat and oats show that rust resistant cereal varieties ultimately become susceptible to new rust races and that continuous replacement of host varieties has been necessary. On average the breaking of host resistance has taken 5—10 years in races of wheat and oat stem rusts.

One can only hope that tree breeders will not soon find themselves in the same kind of vicious circle. In forest tree breeding we can discern three basic relationships between host and parasite. These are:

1) The relationships between endemic hosts and parasites. Under natural conditions this system has achieved stability.
2) The relationships between endemic hosts and exotic parasites or vice versa. This system is incipient and unbalanced.
3) The relationships between exotic hosts and exotic parasites. This includes natural hosts-parasite systems in new environments or artificial systems also in new environments. Both systems are unbalanced.

At present, when international provenance research is so lively and many species are cultivated far outside of their natural range, it seems particularly justifiable to consider these problems.

An ecological approach is the only relevant one. We have taken a glance at host-parasite systems in order to realize their paramount importance in tree breeding but naturally the forest tree breeder has other motives for his breeding efforts; the breeding of quantity and quality. An ecological approach does not exclude these basic motives, it only looks at problems from a wider, integrated point of view. Heritability studies and generally quantitative genetic achievements in forest tree breeding are not declining in importance, they are only integrated in a wider biological frame.

Breeding for ecological tolerance

There is a simple misunderstanding which is often repeated in discussions on plant cultivars, namely, that genetic heterozygosity in populations or cultivars results in greater crop variability. This is not true; on the contrary, both genic and chromosomal heterozygosity contributes to population buffering which often results in reduced phenotypic variance! Such a reduction of variation in the phenotypes is then basically an ecological phenomenon. It depends on more stable host-parasite relationships, on better niche utilization and on greater flexibility, both developmental and genetic. How can a tree breeder make use of such variation?

Environmental variability is either predictable or unpredictable. A species is usually fairly well adapted genetically to cope with regular gross environmental change in climate, soil type and general features of the ecosystem. Within predictable environmental differences there are two kinds; heterogeneity in time and heterogeneity in space. These two are somewhat interdependent. For instance a change in latitude or altitude causes change in the length of the photoperiod. Superimposed on predictable environmental change there is unpredictable variation caused by climatic fluctuations such as drought, heat, cold and wind. A species adopts its strategy by means of adaptation on both levels of ecological variability, but programming of adaptation to regular fluctuations is more profound. The overall pattern of adaptation is revealed in the strategy of the species. Some species are opportunistic, specializing in casual change, while others find their fortune by adapting well to predictable environments. However, these strategies can, to some extent at least, be changed by selection. This has been dramatically demonstrated by Stern (1961) in selection for early flowering in *Betula verrucosa.*

Generally we can conclude that adaptation to regular environmental change is a coadaptation process at the chromosomal level while adaptation to unpredictable environments is largely achieved through heterozygosity on the genic level. A breeding strategy that aims at greater ecological tolerance deals mainly with unpredictable environmental variation. In forest trees, which are predominantly outbreeding, breeding for this purpose means a deliberate effort to preserve population heterogeneity by means of keeping gene pools large enough. However, in the future it may also involve active breeding efforts whereby diversifying selection is applied. In reality this means that genotypes selected must be tested under various environmental conditions, for instance on different soils and under different humidity conditions.

Such programs already exist in agriculture but here they also involve regular environmental fluctuations. Such is the Cimmyt program in Mexico where disruptive selection is applied to knock out photosensitivity in wheat varieties. A most interesting breeding program called "divergent-convergent" selection has been initiated by Lonnquist in Wisconsin. It makes use of ecological tolerance in outbreeding corn (pers. comm. 1972). This is basically a disruptive selection program where selection is applied to a heterogeneous corn population under five different ecological conditions. Selected populations are intercrossed regularly and this eventually builds up wide ecological tolerance.

Breeding multiclone varieties

Recent development in the vegetative propagation of plants opens up new vistas in the use of heterosis. Results in difficult-to-root species such as spruce and other conifers indicate that clonal cultivations are realities (Kleinschmit, 1973). In some easy-to-root species like *Cryptomeria japonica* this mode of artificial reproduction is already in practical use. Here again ecological aspects should be considered. Although it is not adequate always to rely on agricultural experiences and experiments we venture to draw some conclusions from that field as results in forestry are insufficient at the present time.

In predominantly inbreeding species genetic diversity is of course mainly expressed as differences between lines. It is a well known fact that line mixtures show greater stability of yield than pure line cultures. Not only do line mixtures show less variability but over several years such mixtures are also superior in productivity. It is as if "balanced heterozygosity" here were assigned to the mixture of lines of different genotypes. In wheat, for example, the coefficient of variation over several years was 7,3% for line mixtures and 11,6% for pure lines. On average line mixtures yielded 3—5% more that the averages of respective pure cultures and occasionally mixtures exceeded the best pure line cultivars in yield (Simmonds 1962, see same author for summaries).

The forest tree breeder may learn some facts from such experiments. First of all clone mixtures can be expected to show less phenotypic variation than single clone cultivations. Secondly they should be more reliable ecologically, particularly as regards, host-parasite systems. Thirdly they may, if combined optimally, out-perform pure cultures. It is a major task for forest tree breeders to select optimal clone mixes; this may be called selection for ecological combining ability. It is difficult to determine how many clones must constitute such multiclone varieties but their numbers are probably in the tens rather than just a few. This conclusion is, of course, intuitive but it is derived from observations on simple host-parasite ecosystems.

Multiclone varieties in forest tree breeding and in large scale silvicultural applications definitely introduce ecological genetic considerations. Evidently estimation of niche width is one of the most important questions to solve. Competition or its counterpart cooperation or facilitation between clones is another major point for investigation. Investigations on the effect of clonal cultivations on generative genetic systems are of importance from ecological and genetical points of view.

Generally, the more refined methods of breeding trees become, the more important will be the conservation of natural tree populations. Whatever the tree breeder undertakes, the awareness of natural populations as a basis for his success must call on great cautiousness.

Summary

Recent development in ecological genetics is briefly reviewed and provenance research, genecology and forest tree breeding methods are scrutinized from an ecological genetic aspect. Particular stress is placed on ecological stability and the general stability-diversity rule is discussed. Special emphasis is laid on host-parasite systems and on the effect of genetic erosion and environmental variation on such systems. Breeding for greater ecological tolerance is discussed and diversifying selection methods are suggested. Multiclone varieties to utilize immediate heterosis are discussed and some suggestions on their composition are made.

Key words: Ecological genetics, ecological stability, niche concepts, adaptive strategies.

Literature Cited

Dobzhansky, T.: Mendelian populations and their evolution. Amer. Nat. **84**: 401—418 (1950). — Dobzhansky, T.: "What is an adaptive trait?" Amer. Nat. **90**: 337—347 (1956). — Habeck, J. R.: White cedar ecotypes in Wisconsin. Ecology **39**: 457—463 (1958). — Heslop-Harrison, J.: Forty years of genecology. Adv. Bot. Res. **2**: 159—247 (1964). — Hutchinson, G. E.: The Ecological Theater and the Evolutionary Play. Yale Univ. Press, New Haven, 1965, 139 pp. — Kleinschmit, J.: A program for large scale cutting propagation in Norway spruce. Paper IUFRO meeting, New Zeeland, 1973, 5 pp. — Koski, V.: A study of pollen dispersal as a mechanism of gene flow in conifers. Comm. Inst. For. Fenn. **70**: 1—78 (1970). — Langlet, O.: Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Ett bidrag till kännedomen om tallens ekotyper. Medd. Stat. Skogsf. Anst. **29**: 219—470 (1936). — Langlet, O.: Two hundred years of genecology. Taxon **20**: 653—722 (1971). — Levin, S. A.: A mathematical analysis of the genetic feed-back mechanism. Amer. Nat. **106**: 145—164 (1972). — Levins, R.: Mendelian species as adaptive systems. General Systems **6**: 33—39 (1961). — Levins, R.: Evolution in Changing Environments. Princeton Univ. Press, New Jersey, 1968, 120 pp. — Mayr, E.: Animal Species and Evolution. Harvard Univ. Press, 1963, 797 pp. — Monod, J.: Le Hasard et la Nécessité. Editions du Seuil, Paris, 1970, 244 pp. — NAS publication: Genetic Vulnerability of Major Crops. Printing and Publ. office, NAS, Wash. D. C., 1972, 307 pp. — Pimentel, D.: Animal population regulation by the feed-back mechanism. Amer. Nat. **95**: 65—79, (1961). — Rehfeld, G. E., and Lester, D. T.: Specialization and flexibility in genetic systems of forest trees. Silvae Genetica **18**: 118—123 (1968). — Simmonds, N. W.: Variability in crop plants, its use and conservation. Biol. Rev. Cambr. Phil. Soc. **37**: 422—465 (1962). — Squillace, A. E., and Bingham, R. T.: Localized ecotypic variation in western white pine. Forest Sci. **4**: 20—32 (1958). — Stern, K.: Über den Erfolg einer über drei Generationen geführten Auslese auf frühes Blühen bei *Betula verrucosa*. Silvae Genetica **10**: 53—64 (1961). — Stern, K.: Herkunftsversuche für Zwecke der Forstpflanzenzüchtung, erläutert am Beispiel zweier Modellversuche. Der Züchter **34**: 181—219 (1964). — Tigerstedt, P. M. A.: Studies on isozyme variation in marginal and central populations of *Picea abies*. Hereditas **75**: 47—59 (1973). — Whittaker, R. H.: Communities and Ecosystems. The Macmillan Co. New York, 1970, 158 pp. — Wright, J. W., Read, R. A., Lester, D. T., Merritt, C., and Mohn, C.: Geographic variation in red pine. Silvae Genetica **21**: 205—210 (1972).