

Challenges for forest geneticists

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As regards long-rotation-time forest trees, only partial economic gains of today's breeding will be obtained until 60 years or more ahead. Some or all of today's breeding goals may be obsolete at that time. When there is such great uncertainty it is wise to concentrate research on basic understanding of the genetic variation in the processes determining complex characters. The phenotypic plasticity of individual trees as well as the plasticity that may be achieved by tree populations should also be studied. It is hoped that research along these lines will enable us to respond rapidly and precisely to any changes in our environment. A better physiological understanding will probably be achieved if plant materials are exposed to more than one environmental variable at a time. Strong efforts should be devoted to a determination of the curves for hardiness and degree of dormancy during the annual cycle of different genetic entries. The impact of light, temperature, nutrient, and water on growth ought to be studied in different genetic entries. Previously forest geneticists may have concentrated too much on single character studies without estimating the genetic correlations between different characters. We urgently need to start studies to reveal the relationship between several characters since breeding rarely comprises only one character. An understanding of the phase change from juvenile to adult and vice versa might be most helpful for a rapid generation turn-over in breeding.

Uncertainty requires basic research

One great problem in the breeding of long-rotation-time tree species is the uncertainty in future demands for wood products. Thus traits given high priority today may be obsolete at the end of the rotation. Therefore it cannot be taken for granted that the same traits will be bred for in future. This does not mean that we shall totally refrain from looking into the future. In a recent publication by Gemmel and Remröd

(1991), several scientists and decision makers have made predictions for the future. Thus the former head of the Swedish National Board of Forestry, Hägglund, predicts that we shall have three types of forest in Sweden in 2030:

- farmlike plantations mainly with birch and hybrid aspen
- multipurpose forests
- nature reserves

As regards the first type it will be located close to the industry and be heavily dependent on sophisticated fertilization programs like the ones described by Linder (1987). The role of amenity forests is missing in Hägglund's prediction and personally I believe in a more diversified forest in future (cf. Eriksson 1990). Other scenarios (Elliot 1985, Pöyry 1988) have still shorter time perspectives, which make them less suitable for breeding goal decisions for long-rotation-time species like temperate and boreal zone forest trees.

Another great uncertainty is how large the impact of global warming will be in different parts of the world. Based on present knowledge I take it for granted that we shall have global warming unless other types of man-made pollutions occur on such a large scale that the effect of the greenhouse gases is counteracted.

The rapid technical development of all kinds of forest operations during the last decades (cf. Fryk 1990) speaks against an attempt to predict future reforestation and silvicultural concepts which might have genetic implications.

A strategy for university research in a world with great uncertainty requires properties like 1) the ability to plan for the future, 2) the ability to change and 3) the ability to redirect research tasks when required (Skarp et al. 1989). In essence this means concentration on basic research, (cf. Eriksson 1990). In basic research we do not try to get answers to questions related to one specific applied situation; rather we try to get answers for an array of potential future situations. This can be illustrated as is done in Fig. 1,

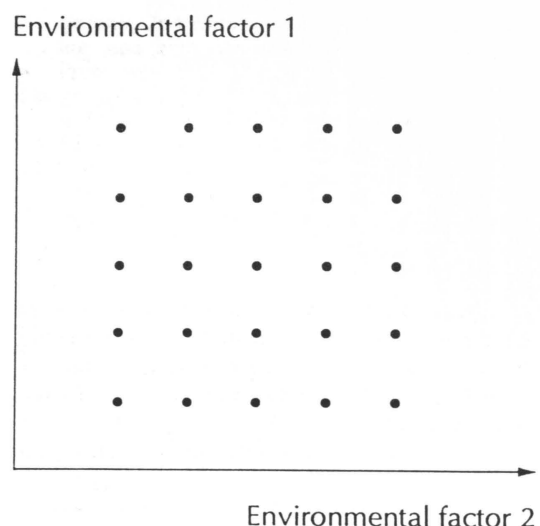


Fig. 1. Combinations of two environmental factors to be used in genic tests to determine dose-response surfaces of a series of genetic entries.

in which we study genetic entries in a series of combinations of two environmental factors. Today we do not know which combination is the most likely in the future. If we run the physiological-genetical research in this way we shall be better prepared to respond faster and more precisely to changes in the environment as regards these two factors. Rarely do we have two environmental factors only, but the reasoning might be extended to more than two environmental factors. Such a research design will simultaneously give us estimates of the *phenotypic plasticity* which according to Gause (1947) and Bradshaw (1965) is *the extent to which the environment modifies a phenotype*. It will also give us information on the broad adaptability of a genetic entry. By broad adaptability is meant good performance over a variety of environmental conditions. It must not be forgotten that the environment contains biotic factors. As regards the environmental factors that should be included in such basic research we have to consult plant physiologists and ecologists.

By crosses between different *Solanum* species and back-crosses Palta (1991) showed that different genes are probably responsible for frost hardiness components in these species. Breeding for hardiness in *Solanum* might therefore be carried out more effectively. The opportunity to create new trait combinations to improve hardi-

ness has risen considerably thanks to this increased understanding.

A basic understanding of the interaction between genes and physiological processes may also be crucial for tree breeders working with long-rotation tree species. In such species we cannot measure or assess all the target traits. Yield at the end of the rotation constitutes such a trait, which is estimated from stem volume at a quarter or a third of the rotation time. If we knew the basic processes determining growth and assessed them instead of the complex trait, *stem volume*, we might overcome the problem with different target and assessment traits (cf. Danell 1990).

In summary, basic research, if carried out properly, will give us possibilities to respond faster and more precisely in a changed situation and to generate genotypes with new and desired trait combinations.

Before the state of knowledge as regards forest genetics research is analyzed I shall give a brief comment on how to cope with the great uncertainty in breeding. Namkoong et al. (1980), Namkoong (1984), Gullberg and Kang (1985), Kang and Nienstaedt (1987) have all argued in favour of multiple population breeding, which means that the breeding population is split into subpopulations and each population can have a separate breeding goal. This will enable future breeders to rapidly respond to new breeding goals. This will avoid the situation several cereal breeders faced some ten years ago when farming with high nitrogen fertilization was no longer possible for various reasons (Hagberg 1985). Moreover, multiple population breeding takes care of gene conservation without extra cost.

Have we addressed the right questions?

The amount of quantitative genetics research carried out so far is considerable according to the recent review by Namkoong and Kang (1990). Much information is available on the relative importance of additive and non-additive variances as well as on genotype \times environment interaction. This knowledge has certainly been most valuable to predict gains in different programs, to delineate breeding zones as well as how to propagate improved material for the commercial plantations. Even early tests have been developed or are just about to be developed (Jonsson et al. 1981, 1990, Li, B. et al. 1989) thereby shortening the generation turn-

over time considerably. How important these results may be, they will not suffice in the long run. Without a knowledge of the processes behind the creation of a phenotype we can probably not identify the genes determining a trait. When we have identified the genes, breeding becomes simpler.

Much forest genetics research is characterized by analysis of one trait at a time. Since breeding rarely comprises one trait only we must abandon the single-trait analysis and embark on joint research on several traits with the aid of genetic correlations or multivariate analysis (cf. Namkoong 1967). It is necessary to stress that we need to include a large number of genetic entries in our studies to get reliable estimates. This probably has to be done stepwise, starting with a few genetic entries and continuing with larger materials if the first results are promising.

In this paper I shall treat in some detail creation of phenotypes, plasticity, trait relationships, and research needs for the temperate zone tree species. I shall concentrate on research that might be called physiological genetics. This does not mean that other areas of forest genetics research are of low importance but that great efforts ought to be devoted to physiological genetics research for the reasons given above. Moreover, the possibilities that open up from modern cell and molecular biology will be treated elsewhere in these proceedings and therefore I refrain from discussing them.

How is the phenotype created?

There are many possibilities for illustrating the path from a gene to a phenotype. My notion is built on ideas presented by Kramer (1986), Johnson-Flanagan and Singh (1988), and Li, P. et al. (1989). In a very simplistic model we have a signal from the environment which is captured and causes a gene activation. An activated gene transfers its information into an enzyme which in turn starts specific biochemical and physiological processes. The end product of these processes is the phenotype.

We might envisage that the environmental influences act at different levels during this process. The environmental influences on one specific gene can be either genetic or non-genetic. By genetic is understood the influences of other genes on the gene under study. Non-genetic is the situation when we have influences from the physical environment only and no in-

fluence from other genes. A change of the environment may or may not create another phenotype depending on the phenotypic plasticity of the carrier of this gene. In conclusion the operational limits for all processes leading to the phenotype are set both by the genes and the environment.

With these illustrations I have tried to indicate that there is a need for cooperation between molecular geneticists, plant physiologists, and traditional geneticists to achieve the goal of an understanding of how genes act, which might make the progress in breeding much faster. In a review paper on evolution Scharloo (1989) stated that: "Work must address physiological and developmental background of the quantitative variation. Biologists need to work downward from the phenotype, going from phenotypic variation to the physiological effects of genetical and environmental variation. They have to link the reaction norms from various levels of organization by understanding their function and integrate them into pathways and network... To close the gap between genome variation and genetic variation in fitness, biologists must go upward from the molecular differences via physiological and functional effects to fitness". Similar statements were also given by Barker and Thomas (1987) and Mayr (1988, essay 28) in review articles on adaptive evolution. Breeding is analogous to evolution but usually faster and with defined goals. What is said about evolution is therefore also relevant for breeding.

Plasticity

In a world which is predicted to experience great environmental changes, phenotypic plasticity is of particular importance for the successful survival, growth and reproduction of a long-rotation-time species. Models for predictions of tree species migration after global warming must include both the phenotypic plasticity of the species and its genetic variation to have any reliability. No such models have been constructed owing to the lack of information about either of these variables.

Plasticity can occur at different levels of genetic organisation. The plasticity that is displayed by an individual is called the phenotypic plasticity of that individual. The plasticity that might be obtained by a mixture of genotypes may also be exploited in breeding although the experimental procedures will be rather complex.

During the eighties it has become quite evident among evolutionists that the phenotypic plasticity of a trait must be regarded as a separate trait which evolution may act upon (cf. Schlichting 1986 and 1989, Sultan 1987, Stearns 1989). Therefore, besides efforts to gain more insight into the mechanisms and genetic control of traits like frost tolerance and vigour the phenotypic plasticity of these traits must be carefully studied. Via and Lande (1985) have mathematically described the possible evolution of phenotypic plasticity. De Jong (1990) has presented further quantitative genetics aspects of phenotypic plasticity. Via (1987) has examined the quantitative genetics methods to accurately estimate the phenotypic plasticity of a trait and she suggests that this is done by the calculation of genetic correlations. Genetic correlations may be useful if few environments are included but dose-response curves are preferable if several one-dimensional treatments are included in the study. Dose-response surfaces are preferable if several two-dimensional conditions are studied.

It may be possible to obtain higher yields by mixing genotypes. This matter has been discussed particularly in connection with clonal forestry, disease and pest problems (Heybroek 1982, Libby 1982, Hühn 1987, Prakash and Thielges 1986). If various types of clonal mixtures are studied under a series of environmental conditions, the experimentation becomes extremely complex to carry out. Not surprisingly, research along these lines is scanty for forest trees. In spite of the problems connected with this type of study more efforts must be devoted to them. From such studies we may be able to predict whether we can rely on phenotypic plasticity or must we utilize mixtures of genotypes to cope with future stress or achieve larger improvement. The use of mixtures in space and time can easily be incorporated in the multiple population breeding concept (cf. Namkoong et al. 1988).

Trait relationships

Much of the discussion so far has dealt with one character. During evolution it is the combination of traits (= phenotype) that is exposed to selection. This means that the probability for an optimum phenotype as regards all traits of an individual must be extremely low (cf. Stettler 1986). A fine-tuned dependence between different traits may have taken place (cf. Cheverud

1990) leading to negative genetic correlations between desired traits. If so, there is a phylogenetic constraint both for breeding and evolution. Our own findings of difference in genetic correlations between height and growth rhythm in *Picea abies* at the population level as compared to within populations may also be referred to as a phylogenetic constraint caused by a difference in adaptation at the regional and micro-site levels (Ekberg et al., in preparation).

Another reason for a negative relationship between two traits may be a conflict between physiological processes and can be called a physiological constraint. Such a constraint can hardly be overcome by breeding.

Pollen and seed migration are other reasons for the non-existence of optimum phenotypes. This is particularly true for wind pollinated tree species with light seeds. Still another reason for lack of optimum phenotypes as regards breeding is that the breeders' optimum phenotype for reforestation and silvicultural methods may be quite different from the optimum phenotype for natural regeneration (cf. Eriksson and Lundkvist 1986, Matyas 1989). It must be remembered that man creates the environment for all kinds of forest operation. In addition in small populations genetic drift may have led to the disappearance of some combinations of traits.

The only way to understand the relationship between different traits is joint analysis in well designed experiments. Data from this type of experiment should be used to estimate genetic correlations or should be evaluated by multivariate analysis. Such studies will give us information if strong selection for one trait is counteracted by the regression of another trait. Such studies will probably also give us a better understanding of the physiological processes determining traits. Thus if the genetic and environmental correlations for a pair of traits have different signs we can immediately draw the conclusion that the genes and the environment act upon these two traits via different physiological processes (cf. Falconer 1981, Ch. 19). To my knowledge most forest genetic experiments have been one-trait experiments in the meaning that genetic correlations have not been calculated even if more than one trait was analyzed. Therefore there is an urgent need in forest genetics to carry out more experiments in which we analyze the interdependence between different traits. Another reason for the need to study trait relationships is the finding by Namkoong (1985) that traits which separately did not show

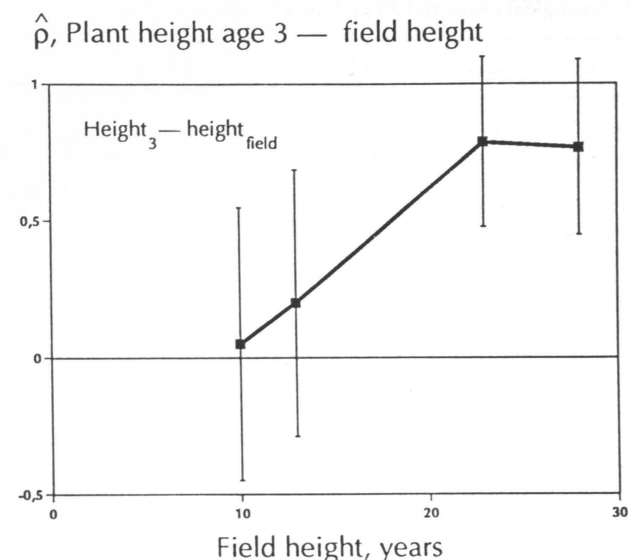


Fig. 2. Estimated GCA correlations \pm standard error for the relationship between height after three growth periods in growth chamber and field heights at various ages in a progeny trial. Number of parents = 11.

any genotype \times environment interaction did so if they were combined in an index.

How desirable it is to estimate genetic correlations, a warning must be raised about the low precision of the estimates of the genetic correlations. One example from our own research on that problem is given in Fig. 2.

Evolutionary guidance for selection of research material

An understanding of evolution will certainly both contribute to a better knowledge of the processes determining a phenotype and give us efficient guidance in selection of research material. To get good starting points for plant biochemists and physiologists it is fundamental that we as geneticists well describe the reactions to various external stimuli of different genetic entries. Such genetic variation constitutes a valuable starting material for studies of biochemical and physiological processes. These in turn might be a gateway to the understanding of gene action and identification of genes responsible for trait creation. A good example of a successful utilization of evolutionary knowledge is the studies of hardiness in *Solanum* species. There

are *Solanum* species that have the following characteristics:

Frost tolerance	Possibility to acclimate to low temperatures
low	+
low	-
high	+
high	-

Crosses between different species have been used in order to estimate the number of genes responsible for each trait (Palta 1991).

For traits with some adaptive significance we can expect to find genetic variation along an ecological gradient. Such traits for some Scandinavian tree species are listed in Table 1. This table is arranged according to Levins' (1963) expectation of a decreasing ratio of within-population genetic variation over between-population genetic variation of adaptive traits. The strategy for selection of material for studies of the genetic architecture of the conifers in the top of the table is quite different from that for *Acer* and *Tilia* in the bottom of the table. This type of ecological difference between species might very well explain the lack of success in plus tree selection in north American hardwoods that was reported by Robison (1989).

Table 1. Ecological characteristics of some Scandinavian tree species.

Species	Pollination	Distribution	Stage in the ecosystem
<i>Picea abies</i>	wind	wide, continuous	climax
<i>Pinus sylvestris</i>	wind	wide, continuous	semiclimax
<i>Betula pendula</i>	wind	wide, continuous	pioneer
<i>Fagus sylvatica</i>	wind	wide, stands	climax
<i>Quercus robur</i>	wind	wide, stands	climax
<i>Fraxinus excels.</i>	wind	scattered	intermedium
<i>Alnus glutinosa</i>	wind	wide, stands	pioneer
<i>Acer platanoides</i>	insect	scattered	intermedium
<i>Tilia cordata</i>	insect	scattered	intermedium

Temperate zone physiological genetics

Hardiness and dormancy

Hardiness is a complex trait and the distinction between hardiness and dormancy/rest is not always expressed clearly. Sometimes avoidance of exposure to frost is referred to as hardiness. To avoid frost injuries both true frost hardiness and avoidance of frost exposure are important breeding goals today. The latter is achieved by entries with an appropriate growth rhythm for the reforestation site.

Hardiness and dormancy must be regarded as traits of high adaptive significance. It is therefore expected that we have genetic variation in these traits along a climatic gradient.

It is important to understand how hardiness and dormancy vary during the year. During the year temperate trees pass through several different stages of frost hardiness. Thus, in *Picea sitchensis* Sheppard and Cannell (1982) identified six stages. Their study was carried out on trees growing outdoors which means that some of the phase changes could be due to parallel changes in ambient temperature rather than a true phase change of frost sensitivity. A hypothetical example of how the degree of dormancy and frost hardiness sensitivity varies over the year is given in Fig. 3. The period when there is no further chilling requirement but the physical conditions are unfavourable and prevent bud flushing is called *imposed dormancy*. The seemingly long phase of imposed dormancy in Fig. 3 is a puzzle to me. Once the curves are well identified a study of the genetic correlation between hardiness and dormancy might be very instructive in understanding how this pattern has developed during the course of evolution.

Below I will mostly refer to Scandinavian tree species. This does not mean that the discussion will only deal with local problems since there are indications that what is true for one temperate tree species is also true for most other species belonging to the same genus (cf. Niens-taedt 1967, Flint 1974, Cannell 1990, Eriksson and Jonsson 1986, Jonsson and Eriksson 1989).

It is well known that avoidance of frost exposure to late spring frosts and early autumn frosts is crucial in *Picea abies* (Dietrichson 1971, Krutzsch 1975). As regards summer frost tolerance we do not know whether there has been some selection for this trait. The mode of natural regeneration of *P. abies* in empty spots within a stand might not have favoured the selection of genotypes with a large frost tolerance during active growth. Information on genetic variation in frost tolerance during active growth is desired. During the phase of highest frost tolerance during the winter there is probably a difference among populations but whether this is true for within-population variation is still an open question.

As regards *Pinus sylvestris* Eiche (1966) has convincingly proven that the lethal frost injuries are induced during late winter. It therefore might seem somewhat surprising that our group has found good correlations between artificially induced autumn frost injuries and field survival in this species as well as in *Pinus contorta* (Nilsson and Eriksson 1986, Jonsson et al. 1981). Langlet reported a sharp clinal variation of autumn dry matter content of *P. sylvestris* seedlings more than 50 years ago (Langlet 1936). Since dry matter content is a good indicator of frost hardiness this finding, like our own results, on autumn frost hardiness (cf. above and Norell et al. 1986) suggests that time of lignification is im-

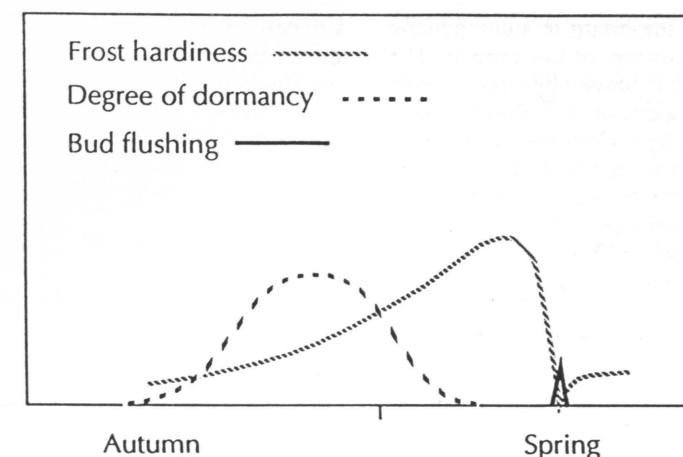


Fig. 3. Hypothetical curves for frost hardiness, degree of dormancy, and bud flushing of *Picea abies* during its annual cycle.

portant for hardiness in these pine species. This could be accomplished by very strong linkage though such a linkage between two sets of polygenes does not seem too plausible. As regards the time for bud break and summer frost tolerance I do not think that there is any adaptive significance in them. Years when frost injuries have been induced during spring or summer in *P. sylvestris* are so rare and the injuries so slight that they cannot have constituted any selection criterion.

Knowledge of the genetic variation in hardiness of hardwoods is limited (Eriksson and Jonsson 1986, Jonsson and Eriksson 1989). However, growth rhythm in both European (Håbjørg 1978) and American hardwoods seems to have played a great role in their adaptation (Flint 1972, Kriebel 1957, Kung and Clausen 1984, Townsend 1977). The adaptive role of growth rhythm is probably of universal importance in hardwoods from the temperate zone. In contrast to the conifers, I assume there is no peak in frost sensitivity during bud break, rather the frost sensitivity might be higher when the fully developed and lush leaves are present. The capacity to recover after a leaf killing frost exposure is probably of adaptive significance.

We ought to concentrate our efforts to reveal the genetic variation of the curves for dormancy and winter frost hardiness as is illustrated in Fig. 3. Much work has been done in Finland to identify these curves for *Betula pendula*, *Picea abies*, and *Pinus sylvestris* (Koski and Selkäinaho 1982, Koski and Sievänen 1985, Repo and

Pelkonen 1986, Hänninen and Pelkonen 1988 and 1989, Hänninen 1990) but much remains to be done for many important tree species (see also Cannell 1990).

Curves of the type shown in Fig. 3 and their dependence on temperature conditions are crucial before we can give any reliable predictions on how trees will respond to a global warming. Hardiness might occur later owing to the absence of low temperatures. For the same reason chilling requirements might not be fulfilled. One consequence may be that the present balanced system of growth rhythm might collapse totally.

Parallel to these studies, assessments of metabolic changes of critical hormones, membrane lipid constitution, Ca^{2+} - and K^{+} -ions as well as enzymes during acclimation and deacclimation ought to be carried out (cf. review articles by Carter and Brenner 1985, Steffen and Palta 1987, Johnson-Flanagan and Singh 1988, Minorsky 1989).

Determinants of wood production

A number of reports indicate that the amount of intercepted light is crucial for wood production in trees (for reviews see Kramer 1986 and Cannell 1989). The early study on the inheritance of branching type in *Picea abies* done by Sylvén during the first decade of this century may be regarded as ahead of its time (cf. Sylvén 1910, Eriksson 1990). The amount of light intercepting needles or leaves is thus crucial for

production and it is important to study genetic variation in the architecture of tree crowns. The size of the tree crown is limited by stress caused by nutrient deficit, water deficit, flooding, and high or low temperature. Kramer (1986) emphasized that growth is mostly limited by such stress factors and little progress is expected from identification of genotypes with better physiological processes such as more efficient photosynthesis. Light during the growth period as well as the duration of the growth period also exert a great influence on the crown size. The need for reduction of the dark respiration as a means of increasing growth was stressed by Kramer (1986). Genetic variation in response to these environmental factors as well as the associations between the traits are key issues for forest geneticists.

Tree responses to nutrients

In a review paper on tree genetics and nutrients Nambiar (1985) suggested that genetic studies ought to concentrate on variation in nutrient acquisition and focus less attention on utilization. *Acquisition* = the ability to take up nutrients; in many cases it is equal to the ability to penetrate a substrate. *Utilization* = the assimilate produced per unit of nutrient in the plant (Nambiar 1985). It is also referred to as *productivity* (Ingestad 1979). There is a third capability that might influence the nutrient efficiency of a plant or tree, the ability to *reallocate* nutrients from low productive sites to sites in the plant or the tree with an efficient dry matter production. Nambiar's statement is analogous to Kramer's disbelief in the possibilities of obtaining improvements by more efficient photosynthesis. Nambiar had greater hopes for identification of genotypes that perform well under stress. It might be questioned whether there has been any room for genetic variation in such a fundamental process as nutrient utilization. In agreement with this Lascoux and Lundkvist (pers. comm.) in our department did not find any genetic variation among 24 *Pinus sylvestris* families in relative growth rate, which were studied according to the concept of Ingestad (1979).

Conclusive evidence of genetic variation in nutrient utilization, nutrient acquisition or reallocation of nutrients are largely lacking in spite of the many indications that there is genetic variation in nutrient response in trees (Cotterill and Nambiar 1981, Mullin 1985, Sheppard and

Cannell 1985, Li, B. et al. 1991). However, for most genetic studies nutrition physiologists raise objections to the way the studies were carried out. I shall therefore treat this topic in some detail. The prerequisite for a study of nutrient productivity is that the nutrient conditions are stable and comparable. This can be achieved by using the technique developed by Ingestad (1979), in which nutrients are supplied according to the demand of the plants. A separate productivity could be distinguished for each nutrient element. Thus the meaning of *nitrogen productivity* is *growth rate per unit nitrogen in the plant*. Only with this technique is it possible to make a correct comparison of the reaction pattern of different genetic entries. The biological interpretation of nitrogen productivity is that uptake and growth are proportional to the protein content in the plant. It has been shown that nitrogen productivity has a most significant influence on the regulation of growth and allocation of biomass (Ågren and Ingestad 1987) as well as on nutrient uptake and nutrient allocation (Ingestad and Ågren 1988).

If different genetic entries have different nitrogen productivities it is of interest to study if this can be attributed to their differences in root/shoot ratios (Ingestad and Ågren 1991). If there is a genotype \times environment interaction it is important to establish if this is caused by a difference in capacity to change the root/shoot ratio. Both these conditions might give us an increased understanding of the causes behind genetic variation in nitrogen productivity in the same way as was reported by Li et al. (1990) for 23 open pollinated families of *Pinus taeda*. Some of the families that grew best at low nitrogen had a larger root/shoot ratio. Studies of the allocation of material in the plant and tree must be given a higher priority than done up to now.

Uptake of nutrients might be facilitated by symbiotic mycorrhizal fungi. Ingestad et al. (1986) studied the nitrogen productivity of *Pinus sylvestris* seedlings with and without an ectomycorrhizal fungus. They did not find any significant differences in nitrogen productivity, which means that there was no extra cost of the host plant for the ectomycorrhizal fungus, which is somewhat puzzling.

Temperature and water availability

Larsen (1990) recently stressed the need to switch to breeding for broad adaptability to cope with the anticipated global warming. Global

warming might cause a longer growth period with a higher frequency of more extreme temperature and precipitation conditions than today. For the influence on growth we have to design experiments that inform us about the plasticity and broad adaptability of different genetic entries over a series of temperature and water availability conditions. Only in growth chambers is it possible to carry out such studies with some reproducibility. From such studies we shall obtain dose-response curves and dose-response surfaces when one or two factors are varied. What was said about genetic correlations in the section on evolutionary remarks applies here. The usefulness of estimating dose-response curves was stressed by Parsons (1987) in his review of evolution under environmental stress.

So far only juvenile plant materials can be studied in growth chambers. The value of such studies is sometimes questioned because of the special features of juvenile growth, as is the case in spruce species (Pollard and Logan 1974, Cannell and Johnstone 1978, Ununger et al. 1988, Ekberg et al. 1991). Recent results from pines (Li, B. et al. 1989, Jonsson et al. 1990) and Norway spruce (Larsen and Wellendorf 1990) have been most promising as regards the possibilities of predicting future growth based on juvenile performance. If studies on dose-response curves are carried out as in the investigations referred to, there is hope that they will be of value not only for the juvenile stage. Therefore, it is advised to use so called retrospective studies, i.e. the families studied in long-term field trials are recreated and cultivated in the growth chambers. If the studies are run in this way additional information on genetic correlations between juvenile and adult performance can be obtained. Preferably the correlations with the field performance should be calculated separately for each treatment at the juvenile stage.

As regards light the concept of tree ideotype (Donald 1968) may be discussed. Ideotypes in tree improvement have been discussed among others by Cannell (1978, 1982), Dickmann (1985), Kärki (1985), and Libby (1987). The matter is further discussed by Pulkkinen in this volume. A better understanding of genetic variation in crown architecture and competitive ability would be welcome. However, the long experience in breeding agricultural crops does not support a total substitution of traditional breeding for ideotype breeding (cf. Rasmusson 1987).

Duration of the growth period

Hardly any other trait has been studied in more detail than growth rhythm since the pioneering work of Sylvén (1940). Mostly the studies have dealt with growth rhythm in juvenile plants. It is known that the duration of the shoot elongation period is drastically reduced from the second to the fourth growth period in *Picea abies* (Langlet 1960, Ununger et al. 1988). More important is probably to study the mitotic activity in meristems to have a better understanding of the processes determining growth in trees. This is valid both for root, apical, and lateral meristems. This will help to get a good understanding of which external factors influence the meristem activity most.

Phase changes between juvenility and adulthood

One of the greatest constraints on rapid genetic progress in tree breeding is the long generation time of trees. An understanding of the phase change from juvenility to adulthood may make it possible to manipulate this phase change and overcome the constraint imposed by the long generation time. Another great constraint is the lack of satisfactory early tests for tree volume and stem quality although there has been considerable progress recently (Li, B. et al. 1989, Jonsson et al. 1990). An adult behaviour of young seedlings may facilitate the development of reliable early tests.

As is illustrated in Fig. 4 there are other potentials in breeding and reforestation if we understand the phase change from juvenility to adulthood and vice versa. Thus, a change from juvenile to a more adult performance already during the second growth period might cause a conditioned hardiness which is urgently desired for reforestation with Norway spruce on frost prone sites. This has already been achieved by cultivation of the plants for a long period in continuous light, which resulted in more adult behaviour with a much reduced shoot elongation period (Ekberg 1990). The hypothesis behind the cultivation under continuous light is that the plant carries out several more cell divisions and thus becomes aged. These first results must be confirmed by additional investigations before being applied on a large scale.

In contrast it is sometimes desirable to keep the juvenile behaviour for a longer time as in

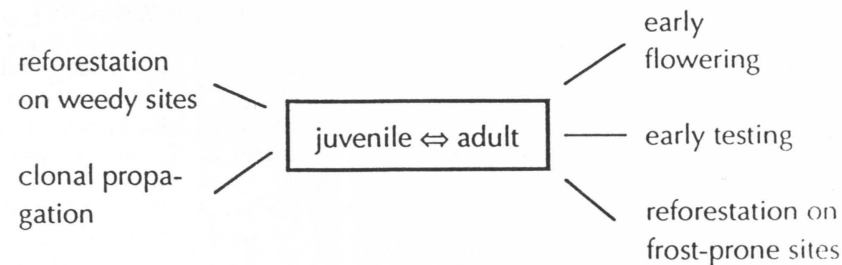


Fig. 4. The potentials if we know the processes determining the phase change between juvenility and adulthood in a tree.

Picea abies plants aimed for reforestation sites with severe competition from weeds. Plants with the juvenile free growth (cf. Pollard and Logan 1974, Cannell and Johnstone 1978, Ununger et al. 1988, Ekberg et al. 1991) can better compete with weeds. Free growth declines with age and is totally lost when plants are about six years old. Juvenility is also desired for easy propagation of cuttings. If the phase change from juvenile to adult is due to the number of cell divisions which a plant has experienced then experiments to keep juvenility should be designed such that cell division is prevented and cell elongation is promoted.

Conclusions

There are great uncertainties about the future as regards reforestation and silvicultural methods, breeding goals and environmental change. It is therefore a wise strategy to concentrate on basic research that can open up new opportunities and make it possible to respond rapidly and precisely under new conditions. We know something about the genetics of some important composite traits like growth and hardiness. We know little or nothing about the steps from genes to the phenotype. To be able to reveal the sequential events between these two poles it is necessary that we cooperate with molecular geneticists, biochemists and physiologists. The identification of the important steps will give us tools for more efficient breeding.

Studies of phenotypic as well as mixed population plasticities are urgently needed in a world that supposedly experiences a gradual change of its environment.

It is important to realise that man creates his environment for reforestation and silviculture.

This is one of the reasons why for breeding we cannot expect to find optimal phenotypes in nature. Other reasons are the phylogenetic constraints and migration of pollen and seeds, both meaning that natural selection is not the only factor influencing the phenotypes in nature.

Forest genetics up to now is characterized by the study of one trait at a time. There is an urgent need for simultaneous analysis of several traits by the aid of genetic correlations or multivariate analysis. Generally there is a need for inclusion of larger numbers of genetic entries in forest genetic investigations.

For the long-rotation-time species there is a need to determine the curves for degree of dormancy and hardiness during the annual cycle. Information on plasticity in two-dimensional environments like water availability and temperature is needed. Both types of study will give us better possibilities of predicting the effects of global warming on our tree species. Studies on nutrient utilization and acquisition will tell us whether or not we must have different breeding populations for different soil fertilities. An understanding of the phase changes between juvenile and adult opens up many possible applications such as faster generation turn-over in the breeding population via early flowering and early testing as well as better plants for frost-prone and weedy sites. Juvenility will also enhance our possibilities for cutting propagation.

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References

- Ågren, G.I. & Ingestad, T. 1987. Root/shoot ratios as a balance between nitrogen productivity and photosynthesis. *Plant Cell Environ.* 10: 579–586.
- Barker, J.S. F. & Thomas R.H. 1987. A quantitative genetic perspective on adaptive evolution. In: Loeschke, V. (ed.). *Genetic constraints on adaptive evolution*. p. 3–23.
- Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13: 115–155.
- Cannell, M.G.R. 1978. Improving per hectare forest productivity. In: Hollis, C.A. & Squillace, A. (eds.). *Proc. North Amer. For. Biol. Workshop, Gainesville, FLA.* p. 120–148.
- 1982. 'Crop' and 'isolation' ideotypes: Evidence for progeny differences in nursery-grown *Picea sitchensis*. *Silvae Genet.* 31: 60–66.
- 1989. Physiological processes of wood production: a review. *Scand. J. For. Res.* 4: 459–490.
- 1990. Modelling the phenology of trees. *Silvae Carel.* 15: 11–27.
- & Johnstone, R.C.B. 1978. Free or lamma growth and progeny performance in *Picea sitchensis*. *Silvae Genet.* 27: 248–254.
- Carter, J.V. & Brenner, M.L. 1985. Plant growth regulators and low temperature stress. *Enc. Plant. Physiol.* 11: 418–443.
- Cheverud, J. M. 1990. The evolution of morphological patterns. In: Nitecki, M.H. (ed.). *Evolutionary innovations*. p. 133–145.
- Cotterill, P.P. & Nambiar, E.K.S. 1981. Seedling physiology of three radiata pine families with parents of contrasting growth. *Aust. For. Res.* 11: 13–22.
- Danell, Ö. 1990. The forest tree breeder's views on future phytotron research [In Swedish]. *Skogsfakta Konferens* 14: 51–55.
- Dickmann, D. I. 1985. The ideotype complex applied to forest trees. In: Cannell, M.G.R. & Jackson, J.E. (eds.). *Trees as crop plants*. p. 89–101.
- Dietrichson, J. 1971. A summary of studies on genetic variation in forest trees grown in Scandinavia with special reference to the adaptation problem. *Norw. For. Res. Inst., Vollebakk, Norway. Res. Not.* 110. 59 p.
- Donald, C.M. 1968. The breeding of crop ideotypes. *Euphytica* 17: 385–403.
- Eiche, V. 1966. Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden. *Stud. For. Suec.* 36. 218 p.
- Ekberg, I. 1990. Hur kan man lura gener? [In Swedish]. *Skogsfakta, Konferens* 14: 21–26.
- , Eriksson, G. & Nilsson, C. 1991. Consistency of phenology and growth of intra- and interprovenance families of *Picea abies*. *Scand. J. For. Res.* 6: 323–333.
- Elliot, G.K. 1985. Wood properties, and future requirements for wood products. In: Cannell, M.G.R. & Jackson, J.E. (eds.). *Trees as crop plants*. p. 545–552.
- Eriksson, G. 1990. Forest genetics for an uncertain future. *Dept. For. Gen. Swed. Univ. Agricul. Scien.* 45. 14 p.
- & Jonsson, A. 1986. A review of the genetics of *Betula*. *Scan. J. For. Res.* 1: 421–434.
- & Lundkvist, K. 1986. Adaptation and breeding of forest trees in boreal areas. *Proc. Franz Kempe symp. Umeå, 1986.* p. 67–80.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*. Longman House, Burnt Mill, Harlow, Essex, UK. 340 p.
- Flint, H.L. 1972. Cold hardiness of twigs of *Quercus rubra* L. as a function of geographic origin. *Ecol.* 53: 1163–1170.
- 1974. Phenology and genecology of woody plants. In: Lieth, H. (ed.). *Phenology and seasonality modelling*. Springer-Verlag, New York. p. 83–97.
- Fryk, J. 1990. Den nya tekniken och dess möjligheter i skogen. 1. Det storskaliga skogsbruket. *Kungl. Skogs-Lantbr. Akad.* 129: 21–25.
- Gause, G.F. 1947. Problems of evolution. *Trans. Conn Acad. Sci.* 37: 17–68.
- Gammel, P. & Remröd, J. 1991. *Skogen i Sydsverige*. Swed. Univ. Agricul. Scien. SLUInfo/Skog 2. 99 p.
- Gullberg, U. & Kang, H. 1985. Application of a model for tree breeding to conifers in southern Sweden. *Stud. For. Suec.* 170. 8 p.
- Håbjørg, A. 1978. Photoperiodic ecotypes in Scandinavian trees and shrubs. *Meld. Norges Landbrukshøgskole* 57(33). 20 p.
- Hagberg, A. 1985. Genetisk kapacitet – växter. In: *Lantbruksforskare om framtiden, LUI.* p. 166–176.
- Hänninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn.* 213. 47 p.
- & Pelkonen, P. 1988. Effects of dormancy release in Norway spruce and Scots pine seedlings. *Silva Fenn.* 22: 241–248.
- & Pelkonen, P. 1989. Dormancy release in *Pinus sylvestris* L. and *Picea abies* (L.) Karst. seedlings: effects of intermittent warm periods during chilling. *Trees* 3: 179–184.
- Heybroek, H.M. 1982. Monoculture versus mixture: interactions between susceptible and resistant trees in mixed stand. In: Heybroek, H. M., Stephan, B. R. & Weissenberg, K. von (eds.). *Resistance to diseases and pests in forest trees. Proc of the Third Intern. Workshop on the Genetics of Host-Parasite Interactions in Forestry, Wageningen, the Netherlands 14–21 Sept., 1980.* p. 326–341.
- Hühn, M. 1987. Clonal mixtures, juvenile-mature correlations and necessary number of clones. *Silvae Genet.* 36: 83–92.
- Ingestad, T. 1979. Nitrogen stress in birch seedlings. II. N, K, P, Ca and Mg nutrition. *Physiol. Plant.* 45: 149–157.
- , Arveby, A.S. & Kähr, M. 1986. The influence of ectomycorrhiza on nitrogen nutrition and growth of *Pinus sylvestris* seedlings. *Physiol. Plantarum* 68: 575–582.
- & Ågren, G.I. 1988. Nutrient uptake and allocation at steady state nutrition. *Physiol. Plant.* 72:

- 450–459.
- & Ågren, G.I. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* (in press).
- de Jong, G. 1990. Quantitative genetics of reaction norms. *J. Evol. Biol.* 3: 447–468.
- Johnson-Flanagan, A.M. & Singh, J. 1988. Protein synthesis and freezing tolerance in plant cells. *CRC Critic. Rev. Plant Sci.* 7: 279–302.
- Jonsson, A., Eriksson, G., Dormling, I. & Ifver, J. 1981. Studies on frost hardiness of *Pinus contorta* Dougl. seedlings grown in climate chambers. *Studia For. Suec.* 157. 47 p.
- & Eriksson, G. 1989. A review of genetic studies of some important traits in the genera *Acer*, *Fagus*, *Fraxinus*, *Prunus*, *Quercus* and *Ulmus*. *Res. Not. Dept. For. Genet. Swed. Univ. Agricul. Sci.* 44. 50 p.
- , Dormling, I., Eriksson, G., Norell, L. & Stener, L.-G. 1990. Retrospective early tests for growth in *Pinus sylvestris*. *For. Tree Improv.* 23: 115–122.
- Kang, H. & Nienstaedt, H. 1987. Managing long-term tree breeding stock. *Silvae Genet.* 36: 30–39.
- Kärki, L. 1985. Genetically narrow-crowned trees combine high timber quality and high stem wood production at low cost. In: Tigerstedt, P. M. A., Puttonen, P. & Koski, V. (eds.). *Crop physiology of forest trees*. p. 245–256.
- Koski, V. & Selkäinaho, J. 1982. Experiments on the joint effect of heat sum and photoperiod on seedlings of *Betula pendula*. *Commun. Inst. For. Fenn.* 105. 34 p.
- & Sievänen, R. 1985. Timing of growth cessation in relation to the variations in the growing season. In: Tigerstedt, P. M. A., Puttonen, P. & Koski, V. (eds.). *Crop physiology of forest trees*. p. 167–193.
- Kramer, P. J. 1986. The role of physiology in forestry. *Tree Phys.* 2: 1–16.
- Kriebel, H.B. 1957. Patterns of genetic variation in sugar maple. *Ohio Agr. Exp. Sta. Res. Bull.* 791. 56 p.
- Krutzsch 1975. Zwei Herkunftsversuche mit Fichte in Schweden (IUFRO 1938). *Res. Not. Dept. For. Genet., Royal Coll. For.* 16. 93 p.
- Kung, F.H. & Clausen, K.E. 1984. Graphic solution in relating seed sources and planting sites for white ash plantations. *Silvae Genet.* 33: 46–53.
- Langlet, O. 1936. Studier över tallens fysiologiska variabilitet variabilitet och dess samband med klimatet. *Medd. Stat. Skogsförs. Anst.* 29. 188 p.
- 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk [In Swedish]. *Kungl. Skogs Lantbr. Akad. Tidskr.* 99: 259–329.
- Larsen, J.B. 1990. Neue Züchtungsziele unter dem Aspekt der Stabilität von Waldökosystemen. *Schrift. Forst. Fak. Univ. Göttingen und Niedersächs. Versuchsanst.* 98: 14–20.
- & Wellendorf, H. 1990. Early test in *Picea abies* full sibs by applying gas exchange, frost resistance and growth measurements. *Scand. J. For. Res.* 5: 369–380.
- Levins, R. 1963. Theory of fitness in a heterogenous environment. II. Developmental flexibility and niche selection. *Amer. Natur.* 97: 75–90.
- Li, B., McKeand, S.E. & Allen, H.L. 1989. Early selection of loblolly pine families based on seedling shoot elongation traits. *Proc. 20th South. For. Tree Improv. Conf., Charleston, South Carolina June 26–30, 1989*. p. 228–234.
- , McKeand, S. E. & Allen, H. L. 1991. Genetic variation in nitrogen use efficiency of loblolly pine seedlings. *For. Sci.* 37: 613–626.
- Li, P.H., Ryu, S.B., Tseng, M.-J. & Chen, T.H.H. 1989. Induction of plant cold hardiness. *Curr. Top. Plant Bioch. Phys.* 8: 21–40.
- Libby, W. J. 1982. What is a safe number of clones per plantation? In: Heybroek, H. M., Stephan, B. R. & Weissenberg, K. von (eds.). *Resistance to diseases and pests in forest trees*. *Proc. of the Third Intern. Workshop on the Genetics of Host-Parasite Interactions in Forestry, Wageningen, the Netherlands 14–21 Sept., 1980*. p. 342–360.
- 1987. Do we really want taller trees? Adaptation and allocation as tree-improvement strategies. *The H. R. MacMillan Lectureship in Forestry, Jan. 22, 1987, The Univ. of Brit. Col., Vanc., B.C., Canada*. 15 p.
- Linder, S. 1987. Responses to water and nutrients in conifer ecosystems. In: Schulze, E.-D. and Zwölfer, H. (eds.). *Ecological studies*. Vol. 61: 180–202.
- Matyas, C. 1989. Genetic and ecological constraints of adaptation. In: *Forest Genetics, Breeding and Physiology of Woody Plants, Proc. Int. Symp., Voronezh, Sept. 24–30, 1989*. p. 79–90.
- Mayr, E. 1988. *Toward a new philosophy of biology. Observations of an evolutionist*. Harvard Univ. Press. 564 p.
- Minorsky, P.V. 1989. Temperature sensing by plants: a review and hypothesis. *Plant Cell Env.* 12: 119–135.
- Mullin, T.J. 1985. Genotype-nitrogen interactions in full-sib seedlings of black spruce. *Can. J. For. Res.* 15: 1031–1038.
- Nambiar, E.K.S. 1985. Increasing forest productivity through genetic improvement of nutritional characteristics. In: *Forest potentials, Weyerhaeuser Co., Aug. 20–24, 1984, Tacoma, WA*. p. 191–215.
- Namkoong, G. 1967. Multivariate analysis of multiple regression in provenance analysis. *Proc 14th IUFRO Congr. Sec. 22*: 308–318.
- 1984. Strategies for gene conservation in forest tree breeding. In: Yeatman, C.W., Kafton, D. & Wilkes, G. (eds.). *Plant gene resources: A conservation imperative*. p. 79–92.
- 1985. The influence of composite traits on genotype by environment relations. *Theor. Appl. Genet.* 70: 315–317.
- , Barnes, R.D. & Burley, J. 1980. A philosophy of breeding strategy for tropical forest trees. *Dept. For., Commonw. For. Inst., Univ. Oxford. Tropical Forestry Papers* 16. 67 p.
- & Kang, H. 1990. Quantitative genetics of forest trees. In: Janick, J. (ed.). *Plant breeding reviews*. Timber Press 8: 139–188.
- , Kang, H.C. & Brouard, J.S. 1988. *Tree breeding: Principles and strategies*. Springer-Verlag. 180 p.
- Nienstaedt, H. 1967. Chilling requirements in seven *Picea* species. *Silvae Genet.* 16: 65–68.
- Nilsson, J.-E. & Eriksson, G. 1986. Freeze testing and field mortality of *Pinus sylvestris* (L.) in northern Sweden. *Scand. J. For. Res.* 1: 205–218.
- Norell, L., Eriksson, G., Ekberg, I. & Dormling, I. 1986. Inheritance of autumn frost hardiness in *Pinus sylvestris* L. seedlings. *Theor. Appl. Genet.* 72: 440–448.
- Palta, J. 1991. Mechanisms for obtaining freezing stress resistance in herbaceous plants. In: Stalker, H. T. & Murphy, P. M. (eds.). *Proc. Symp.: Plant Breeding in the 1990's*. In press.
- Parsons, P. A. 1987. Evolutionary rates under environmental stress. *Evol. Bio.* 21: 311–347.
- Pollard, D.F.W. & Logan, K.T. 1974. The role of free growth in the differentiation of provenances of black spruce *Picea mariana* (Mill.) B.S.P. *Can. J. For. Res.* 4: 308–311.
- Pöyry, J. 1988. Demand, production, restrictions, and policies, an economic view of the role and possibilities for agriculture and forestry in Europe, focused on the Scandinavian countries. *K. Skogs Lantbr. Acad. Tidskr. Suppl.* 21: 57–71.
- Prakash, C.S. & Thielges, B.A. 1986. Genetics and breeding for durable resistance to leaf rust in poplars. In: Hatcher, A. V. & Weir, R. J. (eds.). *Conf. Proc. IUFRO Conf. A Joint Meet. Work. Parties Breed. Theory, Prog. Test., Seed Orch.* p. 342–350.
- Rasmusson, D.C. 1987. An evaluation of ideotype breeding. *Crop Sci.* 27: 1140–1146.
- Repo, T. & Pelkonen, P. 1986. Temperature step response of dehardening in *Pinus sylvestris* seedlings. *Scand. J. For. Res.* 1: 271–284.
- Robison, T.L. 1989. Plus-tree selection in hardwoods: A waste of time? *Proc. 31st Northeast. For. Tree Improv. Conf. & 6th Northcentr. Tree Improv. Ass., Pennsylvania State Univ., University Park, PA, July 7–8, 1988*. p. 109–120.
- Scharloo, W. 1989. Developmental and physiological aspects of reaction norms. *BioSci.* 39: 465–471.
- Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. *Ann. Rev. Ecol. Syst.* 17: 667–693.
- 1989. Phenotypic integration and environmental change. *BioSci.* 39: 460–464.
- Sheppard, L.J. & Cannell, M.G.R. 1982. Seasonal changes in the frost hardiness of provenances of *Picea sitchensis* in Scotland. *Forestry* 56: 137–153.
- & Cannell, M.G.R. 1985. Nutrient use efficiency of clones of *Picea sitchensis* and *Pinus contorta*. *Silvae Genetica* 34: 126–132.
- Skarp, S.U., Hjelm, L., Croon, I., Eklind, J.-R., Eriksson, G., Larsson, K., Renborg, U. & Schotte, L. 1989. Research strategies for agriculture and forestry. *Royal Acad. For. Agr.* 57 p. ISSN 0349–1811.
- Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *BioSci.* 39: 436–445.
- Steffen, K.L. & Palta, J.P. 1987. Photosynthesis as a key process in plant response to low temperature: Alteration during low temperature acclimation and impairment during incipient freeze-thaw injury. In: *Plant cold hardiness*. Alan R. Liss, Inc. p. 67–99.
- Stettler, R.F. 1986. The forest as an experiment [In German]. *Z. Forstwes.* 137: 205–220.
- Sultan, S.E. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol. Biol.* 21: 127–178.
- Sylvén, N. 1910. Om pollineringsförsök med gran och tall. *Medd. Statens Skogsf. anst.* 6: 219–228.
- 1940. Long-day and short-day types of Swedish forest trees [In Swedish with English summary]. *Svensk Papp. Tidn.* 43: 317–354.
- Townsend, A.M. 1977. Characteristics of red maple progenies from different geographic areas. *J. Amer. Soc. Hort. Sc.* 102: 461–466.
- Ununger, J., Ekberg, I. & Kang, H. 1988. Genetic control and age-related changes of juvenile growth characters in *Picea abies*. *Scand. J. For. Res.* 3: 55–66.
- Via, S. 1987. Genetic constraints on the evolution of phenotypic plasticity. In: Loeschcke, V. (ed.). *Genetic constraints on adaptive evolution*. p. 47–71.
- & Lande, R. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39: 505–522.

Total of 102 references

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