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Early Testing of Adaptedness to Temperature and Water Availability in *Pinus sylvestris* and *Picea abies*

Johan Sonesson

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Abstract

Long-term climate changes have been evident in the past. In the future an increase in the rate of climate change is predicted owing to man-made emissions. Studies of adaptedness to different climatic conditions are of great importance for the design of appropriate breeding and gene conservation programmes. This thesis presents studies of adaptedness to temperature and water availability in *Pinus sylvestris* and *Picea abies* and explores the possibilities of utilising differences in adaptedness to obtain juvenile-mature (J-M) correlations strong enough for efficient early testing.

Offspring from clones in two Swedish *Pinus sylvestris* seed orchards and one *Picea abies* seed orchard were grown in growth chambers for one and two growth periods respectively. Two temperature regimes and two irrigation regimes were applied in a factorial design.

Both species expressed high phenotypic plasticity and additive variance for height growth and biomass traits. This implies that these populations should be able to adapt both to short-term and to long-term climate changes. Genotype by environment (G×E) interaction indicated strong differences in adaptedness to temperature and lower differences in adaptedness to water availability. Parent rank changes between treatments indicated that climate change could seriously alter the ranking of clones in breeding populations and thus decrease the genetic gain obtained in previous selections. Differences in stability among parents suggested that culling of unstable genotypes could be a way to reduce the negative effects of G×E interaction.

Genetic correlations between growth chamber and 14-30 year old field progeny trials with the same parents were mainly weak for both species. The correlations were improved by the drought treatment in the *Picea abies* experiment suggesting that further development of early testing methods for this species should include treatments with limiting water availability.

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Appendix

Papers I-IV

The present thesis is based on the following papers which will be referred to by their roman numerals.

I. Sonesson, J. & Eriksson, G. Genotypic stability and genetic parameters for growth and biomass traits in a water × temperature factorial experiment with *Pinus sylvestris* L. seedlings. (Accepted for publication in *Forest Science*).

II. Sonesson, J., Jansson, G. & Eriksson, G. Retrospective genetic tests of *Pinus sylvestris* L. in growth chambers with two irrigation regimes and two temperatures. (Accepted for publication in *Scandinavian Journal of Forest Research*).

III. Sonesson, J. & Eriksson, G. Early genetic testing of *Picea abies* in a water by temperature factorial experiment: I. Genetic variation and genotypic stability. (Submitted to *Canadian Journal of Forest Research*).

IV. Sonesson, J. & Eriksson, G. Early genetic testing of *Picea abies* in a water by temperature factorial experiment: II. Juvenile-mature correlations. (Submitted to *Canadian Journal of Forest Research*).

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Introduction

Geographical range and population structure of *Pinus sylvestris* and *Picea abies*

Pinus sylvestris and *Picea abies* have a wide and continuous distribution in Europe and Asia. They are dominant species in boreal and mountainous forests from the European West Coast to the Asian East Coast. In Sweden they are the two main tree species and *Pinus sylvestris* and *Picea abies* constitute 38% and 44% of the growing stock respectively (Anon 2000).

Pinus sylvestris is a pioneer species naturally occupying dry and mesic sites with frequent forest fires. It has a low water demand and is the tree species occupying the driest forest sites in Scandinavia. *Pinus sylvestris* has a low demand for nutrients, which makes it the most common tree species on infertile peatlands. *Picea abies* is a shade-tolerant species naturally growing on forest fire refuges and as a secondary species emerging under a canopy of *Pinus sylvestris* or broadleaf species on wet and mesic sites. *Picea abies* demands more water and nutrients and grows poorly on infertile and dry sites. In plantation forestry *Pinus sylvestris* is used on dry to mesic and infertile sites while *Picea abies* is used on fertile mesic to wet sites.

Pinus sylvestris and *Picea abies* are wind-pollinated, predominantly outcrossing species capable of long distance pollen dispersal (Lindgren & Lindgren 1996). These features together with their continuous distributions on the Scandinavian Peninsula give the two species their population characteristics. Both species express large-scale clinal variation for adaptive traits, mainly along the latitudinal temperature gradient. This has been demonstrated for *Pinus sylvestris* growth cessation (Langlet 1936), damage and mortality (Eiche 1966) and height growth (Remröd 1976). These studies confirm the mainly latitudinal cline but they also report evidence for some clinal variation with altitude. Clines in critical night-length for growth cessation in *Picea abies* have been reviewed by Ekberg et al. (1979). They concluded that there is a strong latitudinal cline in Scandinavia but also presented evidence for a longitudinal cline from interior Finland to the Norwegian coast and an altitudinal cline in the Austrian Alps. Altitudinal and latitudinal clines for critical night-length in *Picea abies* have also been reported for Norway (Kohmann 1996). Large within- and among-population genetic variation for adaptive traits is evident for both species (review by Eriksson 1982).

Plasticity and stability

Phenotypic plasticity is a specific response to a certain range of environments for a particular trait or set of traits (Bradshaw, 1965). A genetic entry that expresses very different phenotypes in different environments is considered to have a high plasticity. Finlay & Wilkinson (1963) introduced the concept of stability. They define a genetic entry as stable if its performance has a slope less than 1.0 when regressed against the average performance on a series of test sites and unstable if the slope is steeper than 1.0. This definition of stability is closely related to the concept of phenotypic plasticity.

In this thesis genotypic stability is defined as the absence of rank changes between environments. If a genotype is considered as stable or unstable is based on its contribution to the genotype-by-environment interaction sum of squares. Wricke (1962) and Shukla (1972) have developed methods for estimation of stability. Studies of rank changes between environments are of major interest for the understanding and estimation of the effects of selection in breeding programmes as well as in nature. It should be noted that stability defined in this way is a relative estimate that depends on the population studied. A genetic entry with high phenotypic plasticity in a population of entries with low plasticity is likely to cause rank changes and thus be considered unstable. If the same entry were tested together with a population of equally plastic entries it would more likely be considered as of average stability.

Climate change and adaptation

Trees are long-lived and must endure shifting weather and even climatic trends during their lifetime. Weather changes considerably between years mainly with respect to temperature and precipitation. Long-term climate changes have been evident in the past. In the future an increase in the rate of climate change is predicted owing to the increase of anthropogenous greenhouse gases in the atmosphere (Houghton et al. 1995). Predictions for Sweden include an increase in mean annual temperature of 2-3 °C over the period up to year 2050, a slight increase in precipitation and a lower humidity in South and Central Sweden (Mattson & Rummukainen 1998). The predictions for future climate in northern Europe are uncertain, however, and the effect of greenhouse gases on the North Atlantic ocean current may counteract the temperature rise or even create a cooler climate (Weaver 1995).

There is no principal difference between evolution with and without climate change induced by human activities. The difference is the higher speed of change predicted due to human activities. Individual trees are long-lived and thus have to rely on phenotypic plasticity to ensure survival in a rapidly changing climate. Tree species normally have large phenotypic plasticity for many adaptive traits but for long term species survival in a changing climate this will not be sufficient (Eriksson 1999). Species have to adapt or migrate to survive long-term climate changes. For a species to adapt to a changing climate, additive variance for adaptive traits is needed (e.g. Lynch & Lande 1993). Species with long generation turnover time, such as trees, will need higher additive variance than annual species to be able to adapt rapidly. A low additive variance can be compensated for by rapid migration through high propagule dispersal ability. In a rapidly changing climate the adaptation and migration processes in nature may be too slow to assure species survival (eg. Davies 1988). Human intervention with well-managed breeding populations and transfer of regeneration material will then be the only solution (Eriksson 1999).

Effects of climate change on *Pinus sylvestris* and *Picea abies* populations

Effects of non-optimal adaptedness in a changed climate have been studied at the provenance level in series of provenance tests for several species. Schmidtling (1994) estimated the growth reduction at 5-10% *for Pinus taeda* and *Picea abies* owing to non-optimal seed sources in a climate with an average temperature 4°C higher than the present. Growth reductions of less than 10% have been estimated for *Pinus sylvestris* in Sweden by Persson (1998). Studies of provenance trials have however suggested that the general effect of a warmer climate in Northern Europe will be increased growth for the economically important species *Pinus sylvestris* and *Picea abies* (Kellomäki et al. 1988, Beuker 1994, Persson, 1998). Climate change would thus not negatively affect the wood supply for human needs. These studies do not consider the fact that provenance transfers are accompanied by changes in photoperiod as stated by Matyas (1994) neither do they take account of the effect of changes in precipitation and humidity. Persson and Beuker (1997) have distinguished between the effects of temperature and photoperiod in provenance trials of *Pinus sylvestris* in Sweden. They concluded that projections of the effects of a warmer climate on the total yield of *Pinus sylvestris*, based on latitudinal transfers in provenance trials, would underestimate the actual effects of an increasing temperature sum.

The effects of climate change at the provenance level is buffered by large within population genetic variation and the effect on breeding populations where individual selection is practised may be larger. To counteract the negative effects of climate change it would be wise to maintain high genetic diversity in the breeding population, to test progenies in a broad span of environments and to select for generalists (stable genotypes) as suggested by Ledig & Kitzmiller (1992).

Another effect of climate change that may cause larger problems for forest management is the predicted increase in risks for frost damage, windthrow, fungi and insect damage (Cannell & Smith 1986, Kellomäki et al. 1988, Grace et al. 1991). This implies that the principal trait for breeding may change from growth to traits related to pest resistance and early survival.

The Swedish breeding program

The Swedish breeding programs for *Pinus sylvestris* and *Picea abies* are based on long-term recurrent selection with a multiple-population breeding strategy (Danell 1993). The objectives of the programs are to conserve adequate genetic variation, prepare for possible climate changes and breed for growth, adaptation and quality.

The programs for *Pinus sylvestris* and *Picea abies* each have a meta-population of about 1000 trees selected in each generation. The meta-population is divided into 22-24 sub-populations with about 50 trees each. The sub-populations are allocated to different adaptation targets defined by photoperiod and temperature climate (Fig 1.).

The distribution of adaptation targets covers an area that is broader than the current temperature climate range of Sweden today. When future climate changes occur, whether they are towards warmer or colder climates, there will be improved material ready to be propagated for reforestation purposes (Danell 1993). The generation time in the breeding populations is estimated at 15-35 years, which is considerably shorter than the generation interval in most natural stands. The managed breeding populations thus have the potential for faster adaptation to a changing climate than wild populations. This will also contribute to the effectiveness of the breeding program to buffer the negative effects of climate change.

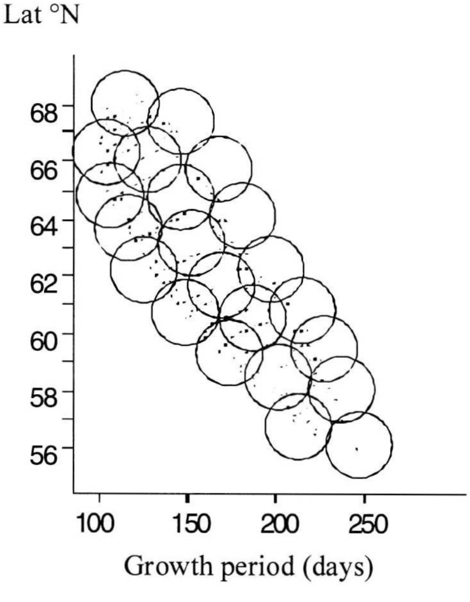

Figure 1. Principal design of the Swedish breeding programs *for Pinus sylvestris* and *Picea abies*. Subpopulations are represented by circles, each with a target climate described in terms of photoperiod (Lat °N) and temperature (length of growth period). The shaded area approximates the present climatic range of Sweden.

Early genetic testing in controlled conditions

Selection in tree breeding is normally made at tree ages considerably lower than the rotation age. In Scandinavian conifer breeding, field trials are normally measured and evaluated at 3-5 m height (10-15 years) as recommended by Lindgren (1984). The possibility of increasing the genetic gain per unit time by early tests in controlled environments has been considered for many species. The efficiency of early testing depends on the juvenile-mature (J-M) genetic correlation, the heritability for the juvenile trait and the selection intensity. If these values are high the possibilities for efficient early selection improve, especially if the heritability and/or the selection intensity for the mature trait are low. The potential for efficient early selection is also improved if the possible gain in time is high, i.e. if the difference in test time between the early test and the mature age is high.

Repeated assessments of field trials have revealed high J-M correlations between height growth at early and late ages in many conifer species (Lambeth 1980, Bentzer et al. 1989, Li et al. 1993). This demonstrates that selection within a trial can be made at an early age without serious loss of genetic gain.

When J-M correlations between field trials and experiments in controlled conditions, such as nurseries or growth chambers, are estimated the correlations are often weak. Weak J-M correlations were found in studies on *Picea mariana* (Mullin & Park 1994, Mullin et al. 1995), *Picea abies* (Danuscevicius et al. 1999, Hannerz et al. 1999), *Pinus contorta* (Wu et al. 1997) and *Pinus sylvestris* (Abraitis et al. 1998, Jansson et al. 1998). However, there are some examples of strong and significant J-M correlations from studies of *Pinus sylvestris* (Eriksson et al. 1993, Jonsson et al. 2000). Reviews of early testing studies (Eriksson et al. 1993, Jonsson 2000) confirm that very differing J-M correlations are obtained depending on the treatments applied and the experimental design. The high genetic correlations between heights assessed on the same plants in the same environments and the weak correlations obtained between controlled environment experiments and field trials suggest that G×E interaction between the juvenile and mature environment can be an explanation for the low J-M correlations.

The hypothesis that J-M correlations can be improved by mimicking the field environment in the early test environment has been supported by a few experiments. Cannell et al. (1978) studied one-year-old *Pinus taeda* seedlings and found strong correlation between growth in a water stress nursery environment and in well-drained field trials as well as between a well-watered nursery environment and poorly drained field trials. Tan et al. (1995) studied two-year-old *Picea mariana* seedlings and found significant correlation between the drought-stressed nursery environment and a field trial at a dry site. The correlations between the drought-stressed as well as well-watered nursery treatments and field trials on moist sites were low. In a study with *Picea abies* (Larsen & Wellendorf

1990) there was a significant correlation between water-use efficiency (WUE) of the seedlings in a nursery experiment and older field trials with the same families.

The environmental factors that would be of major interest to mimic in the early test environment are the growth-limiting ones. Besides climatic factors, such as temperature and growth period length, the main growth-limiting factor for conifers on most sites in Sweden is nitrogen availability (Tamm 1991). Even water availability is sometimes growth limiting, as is evident for *Picea abies* in southern Sweden (Alavi 1996, Bergh et al. 1999a) but not in northern Sweden (Bergh et al. 1999a). There are also indications of limiting water availability for *Pinus sylvestris* in some years (Jonsson 1969, Ciencialia et al. 1998).

Aims

The main objective of this thesis was to study adaptedness to temperature and water availability in *Pinus sylvestris* (L.) and *Picea abies* (L.) Karst. and to explore the possibilities of utilising differences in adaptedness to obtain juvenile-mature correlations strong enough for efficient early testing.

The following questions were addressed:

How large is the genetic variation in growth, biomass and phenology traits between families grown in growth chambers at varying temperature and water availability? (I & III)

How large is the genotype by environment interaction and are there differences in stability among families? What are the implications for breeding programmes in a changing climate? (I & III)

Can the genetic correlations between juvenile traits assessed in growth chamber experiments and adult growth traits in field progeny trials be improved by mimicking the field environment in the growth chamber? (II & IV)

Material and methods

Plant materials

Offspring from clones of three Swedish seed orchards, two with *Pinus sylvestris* and one with *Picea abies* (Fig. 2) were included in this study. The clones in the orchards are plus-trees selected in stands of unimproved stock. The number of clones used in the study was 28 and 35 for the *Pinus sylvestris* orchards and 36 for the *Picea abies*. Progeny tests of the orchard clones were established 1966-1971 and assessed for height and diameter at ages 14-30 years.

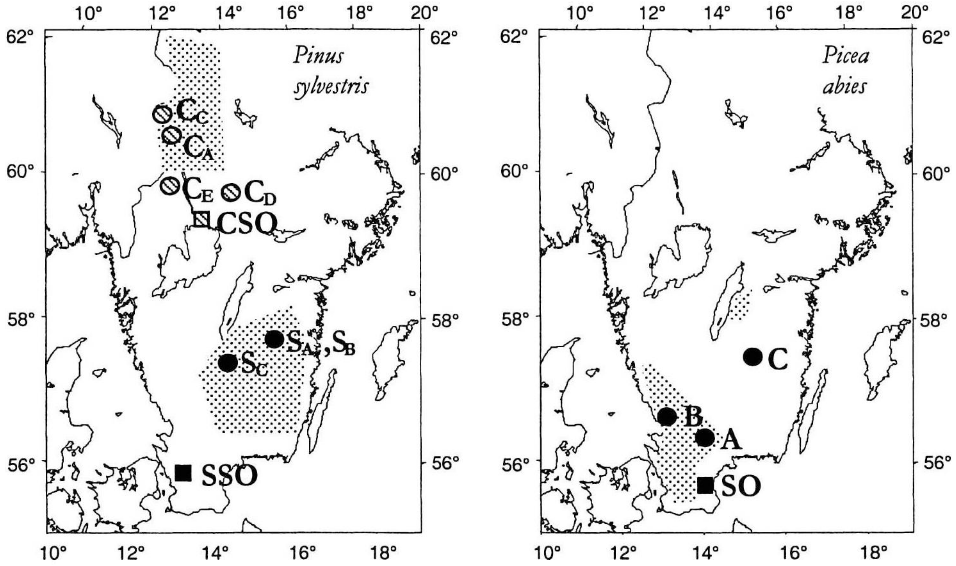

Figure 2. Location (squares) of the two *Pinus sylvestris* seed orchards CSO = Central Swedish and SSO = Southern Swedish orchard and the *Picea abies* seed orchard =SO. Field progeny trial sites are represented by circles and shading indicates the area where the plustrees were selected.

Growth chamber experiments

The seedlings were grown in growth chambers for one (*Pinus sylvestris*) or two (*Picea abies*) growth periods under two different temperature regimes (T25 and T18). Within each temperature regime two irrigation treatments were applied, well-watered (W) and periodic drought (D). The factorial combination of temperature and irrigation resulted in four treatments (T25W, T25D, T18W and T18D). During the growth periods seedling height was assessed at several occasions. Bud-burst and bud-set were recorded in the *Picea abies* experiment. When the growth periods were completed the fresh and dry weights of shoots and roots were recorded separately.

Statistical analysis

Single trait mixed linear models were used to estimate genetic parameters and genotype by environment interaction (I & III). The analysis was performed using the MIXED procedure in the SAS software (SAS 1997) with the restricted maximum likelihood (REML) method.

Phenotypic plasticity for individual parents was calculated as the difference between highest and lowest treatment or trial mean for the parent. Analyses of genotypic stability for individual families were carried out applying the concept of ecovalence (Wricke 1962), using the method by Shukla (1972) for significance testing (I & III).

Two-trait mixed linear models were used to estimate genetic correlations between growth chamber traits and field performance in progeny trials. The softwares used were DFREML (Meyer 1998) in the *Pinus sylvestris* study (II) and ASREML (Gilmour et al. 1999) in the *Picea abies* study (IV).

Main results

Mean height for the seedlings in the most favourable treatment (T25W) was in the same range as commercial container seedlings grown in nurseries. This was observed for both species. The least favourable treatment (T18D) had average heights that were about half the height in the T25W treatment. T25D and T18W treatments had intermediate heights (Figures 3 and 4).

Parental differences in phenotypic plasticity are demonstrated in figure 3 for *Pinus sylvestris* and figure 4 for *Picea abies*. Differences are obvious both in the growth chamber and in the field trials. There was no strong correspondence between phenotypic plasticity in the growth chamber and in the field trials. However, a few exceptions were observed such as the *Pinus sylvestris* parent S3257 which was the most plastic in the growth chamber and was also among the most plastic in the field trials (Figure 3).

Heritabilities for height growth and biomass traits were moderate to high (Table 1) while heritabilies for root-shoot ratio were lower (not shown). For several traits the highest heritabilities were obtained in the T18W treatment. Additive genetic coefficients of variation (CV_A) were high for most traits. The highest values were found for shoot dry weight in the T25W treatment, 36% and 47% for *Pinus sylvestris* and *Picea abies* respectively.

Table 1. Individual tree heritabilities (h^2_i) and additive genetic coefficients of variation (CV_A) in the four treatments. T25W=High temperature and well-watered, T25D=High temperature and periodic drought, T18W=Low temperature and well-watered, T18D=Low temperature and periodic drought.

Trait	T25W		T25D		T18W		T18D	
Seed orchard	h^2_i	CV_A (%)	h^2_i	CV_A (%)	h^2_i	CV_A (%)	h^2_i	CV_A (%)
Total height increment								
Pinus sylvestris South	0.55	17.9	0.51	16.3	0.35	12.2	0.49	16.3
Pinus sylvestris Central	0.38	14.8	0.43	15.6	0.80	20.1	0.43	14.3
Picea abies	0.34	15.6	0.37	12.5	0.41	19.2	0.28	12.4
Shoot dry weight								
Pinus sylvestris South	0.19	18.2	0.36	11.7	0.49	23.3	0.33	10.6
Pinus sylvestris Central	0.61	36.1	0.63	18.8	0.82	30.6	0.41	13.9
Picea abies	0.56	46.8	0.39	13.4	0.60	40.3	0.12	9.4

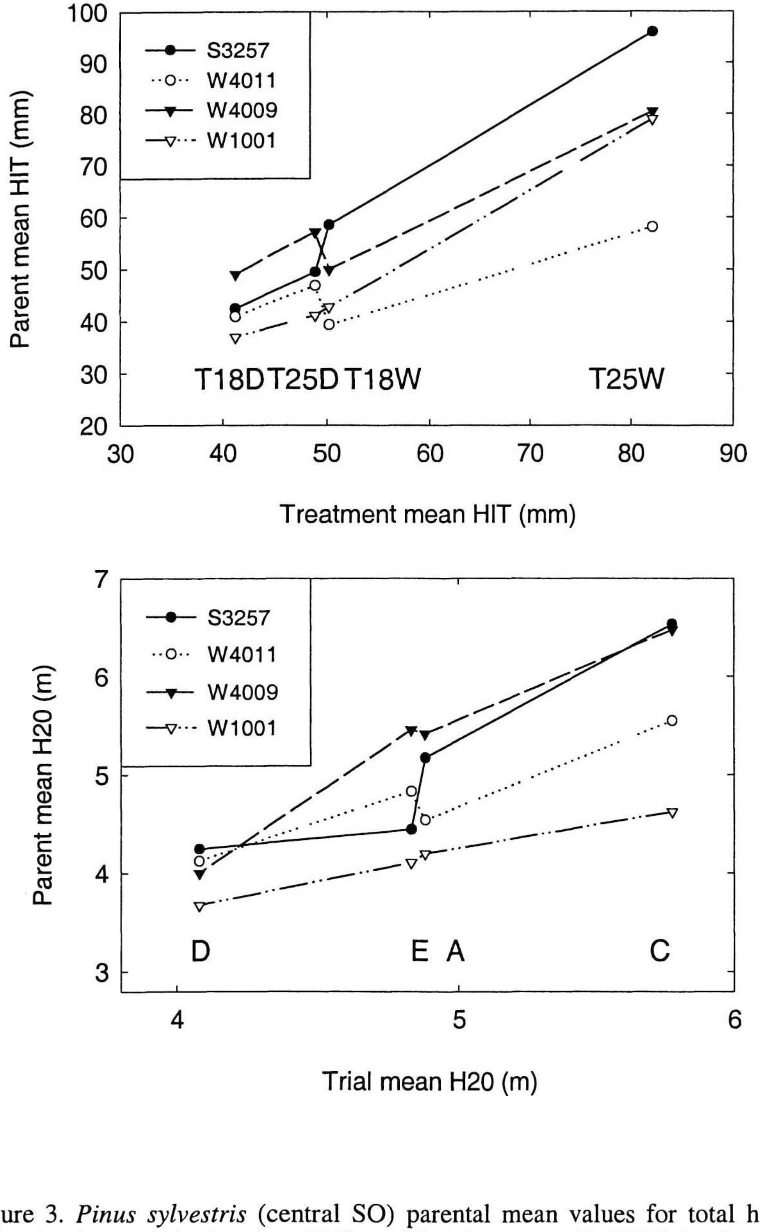

Figure 3. *Pinus sylvestris* (central SO) parental mean values for total height increment (HIT) in the growth chamber (GC) and height at age 20 (H20) in the field trials (FT) plotted on treatment/trial mean values for the same traits. The four families shown are the ones with the highest and lowest phenotypic plasticity (PP) in the growth chamber and in the field respectively. S3257 = highest PP in GC, W4011 = lowest PP in GC, W4009 = highest PP in FT and W1001 = lowest PP in FT.

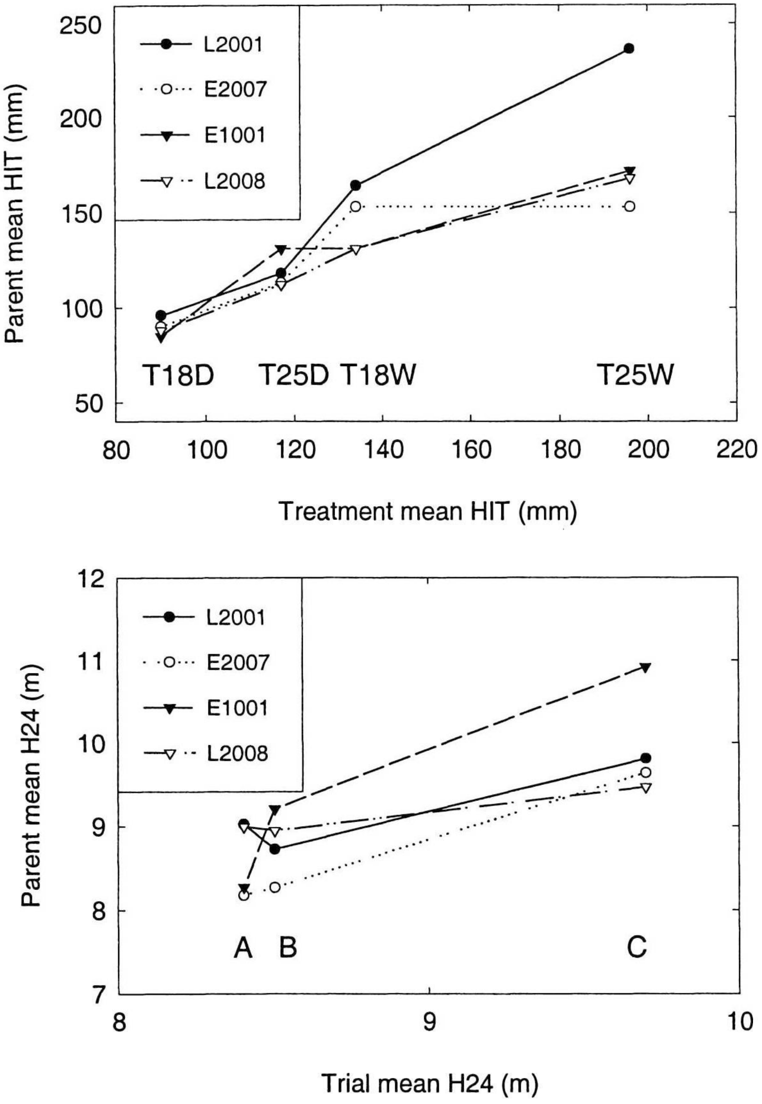

Figure 4. *Picea abies* parental mean values for total height increment (HIT) in the growth chamber (GC) and height at age 24 (H24) in the field trials (FT) plotted on treatment/trial mean values for the same traits. The four families shown are the ones with the highest and lowest phenotypic plasticity (PP) in the growth chamber and in the field respectively. L2001 = highest PP in GC, E2007 = lowest PP in GC, E1001 = highest PP in FT and L2008 = lowest PP in FT.

The joint analysis of variance components based on the four treatments revealed significant interaction variance components for most traits (Table 2). For height growth traits the three-way interaction parent×water×temperature was the highest and it was significant in most cases. For biomass traits significant parent×temperature interactions were found as well as three way interactions. Significant parent variance components were found only for total height increment and budburst (not shown) in *Picea abies*. Parent×water interaction variance components were small and insignificant for all traits in all the three experiments.

Table 2. Results from the joint linear model of four treatments. Variance components for random effects as percent of the total random variation. σ^2_p, σ^2_{pw}, σ^2_{pt}, σ^2_{pwt} and σ^2_e are the variance components for parent, parent by water regime interaction, parent by temperature interaction, parent by water regime by temperature interaction and error respectively. Level of significance is denoted by: * = $0.05 > p > 0.01$, ** = $0.01 > p > 0.001$

Trait	Variance components (%)				
Seed orchard	σ^2_p	σ^2_{pw}	σ^2_{pt}	σ^2_{pwt}	σ^2_e
Total height increment					
Pinus sylvestris South	3.1	0.0	3.8	5.8**	87.2
Pinus sylvestris Central	3.6	3.3	1.0	3.9	88.2
Picea abies	3.4*	0.1	0.0	4.8**	91.7
Shoot dry weight					
Pinus sylvestris South	0.0	2.3	4.8**	0.8	92.1
Pinus sylvestris Central	2.6	0.0	7.0*	4.9**	85.5
Picea abies	1.2	0.0	1.6	4.4**	92.8

The analysis of stability expressed as ecovalence for individual parents revealed that there were only a few (0-4) parents contributing significantly to the interaction variance in the *Pinus sylvestris* South SO and in the *Picea abies* SO. In the *Pinus sylvestris* Central SO there were up to one third (3-11) of the parents contributing significantly to the interaction (Figure 5).

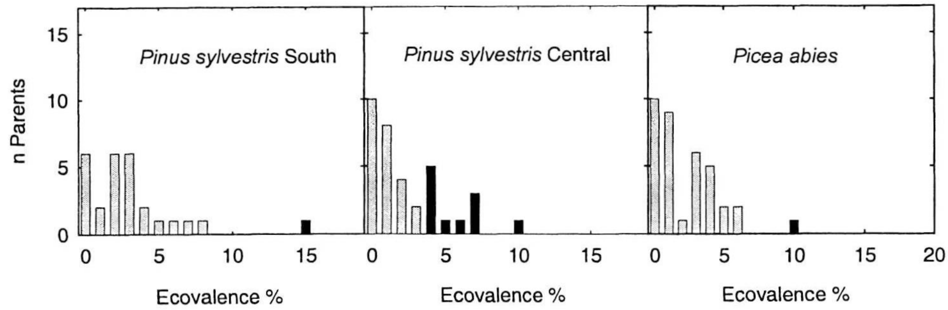

Figure 5. Distribution of parental ecovalence values (in % of total interaction) for Shoot dry weight. Parents that contribute significantly (P<0.05) to the interaction according to Shukla (1972) are represented by black bars.

Additive J-M genetic correlations were generally weak and non-significant (Table 3). Large differences in genetic correlations between different combinations of growth-chamber treatments and individual field trials were observed for *Pinus sylvestris*. However, the treatments did not differ in average J-M correlations. In the *Picea abies* experiment the average genetic correlation with field trials was higher for the drought treatments than the well watered. There were also a higher number of significant J-M correlations in the drought treatments. In both species there was a tendency for height growth traits to have slightly higher J-M correlations than dry weight traits. This was most pronounced in the Central *Pinus sylvestris* population.

Table 3. Number of significant (P<0.05) and average genetic correlations between stem volume in field trials and growth-chamber experiments. Treatments are: T25W=High temp. and well-watered, T25D=High temp. and periodic drought, T18W=Low temp. and well-watered, T18D=Low temp. and periodic drought.

Seed orchard	Tot.	T25W		T25D		T18W		T18D	
Traits	no. [a]	Sign.	Aver.	Sign.	Aver.	Sign.	Aver.	Sign.	Aver.
***Pinus sylvestris* South**									
Height growth traits	12	3	0.17	0	-0.16	1	0.03	0	-0.19
Dry weights	9	0	0.15	0	-0.38	0	0.14	0	-0.05
***Pinus sylvestris* Central**									
Height growth traits	16	3	0.22	2	0.14	4	0.27	2	0.20
Dry weights	12	0	-0.04	0	-0.28	0	0.15	0	-0.07
Picea abies									
Height growth traits	9	0	0.10	2	0.12	0	-0.20	1	0.32
Dry weights	9	0	-0.01	2	0.16	0	-0.27	1	-0.01
Phenology	6	0		2		1		0	

[a] Total number of correlations for each treatment

Discussion and implications for tree breeding

Validity for field performance

The experiments in this study were performed on very young trees in carefully controlled environments. The strength of the experiments is that in the growth chambers we can reduce the environmental variance and make genetic variances appear more clearly as verified by the high heritabilities obtained in our studies. In the growth chambers we can also control the environment and create conditions that it would not be possible to find in the field today. The weakness of the experiments is that the trees are very young and accurate predictions for full rotation cannot be made. This is to some extent confirmed by the low J-M correlations obtained in the studies. Several studies support the hypothesis that G×E interaction between the juvenile and the mature environment contributes to low J-M correlations (Cannell et al. 1978, Waxler & van Buijtenen 1981, Wu et al. 1997). Since we have found significant interaction effects in our experiments, we should probably not get good J-M correlations for all four treatments. A treatment with low J-M correlations in this study may hypothetically give stronger J-M correlations to a field site climate that is not represented by the field trials in this study.

Breeding for present and future climates

The phenotypic plasticity observed in both growth chambers and field trials indicates that the individual trees in the populations studied will have the ability to respond to short-term climate changes during their lifetime, unless the changes are extremely large. Parent differences in phenotypic plasticity also suggest that some parents will have a higher ability to short-term response to climate change than others will.

High additive variances for growth traits in the growth chamber were found within these populations. This implies that these populations should be able to respond to natural or artificial selection and thus have a high potential for adaptation to future climates.

The significant parent×temperature and parent×temperature×water interaction variance components found for most traits in both species studied indicate strong differences among parents in adaptedness to different temperature climates. There may also be some differences among parents in adaptedness to soil water availability, giving rise to the three way interactions. Similar results were obtained for both *Pinus sylvestris* and *Picea abies.*

Differences in adaptedness to temperature climates support the design of the Swedish breeding programs for *Pinus sylvestris* and *Picea abies*. The programs are designed to cover large variations in temperature climate and photoperiod (Figure 1).

The interactions found in the seed-orchard populations studied are caused by parental rank changes between environments (exemplified in figures 3 and 4). The results imply that a climate change including altered mean temperatures and changes in precipitation pattern could seriously alter the ranking of clones within these populations. If similar rank changes occur in the breeding sub populations as a response to climate change, this would decrease the genetic gain obtained in previous selections.

The Swedish multiple population breeding programme has the possibility to have material prepared for climate change. Having populations tested and selected for both higher and lower temperatures at the same latitude (photoperiod) does this. This strategy can be efficient if good testing methods for temperature climates that are not present today can be developed. Two different ways may be possible. One is to establish field trials in extremely good local climates within the present zone. This would be sites such as wind-protected south slopes at low elevation close to a large lake. To find sites that also fulfil other requirements for a good test site, has a favourable landowner and a new clearcut area at a certain year, will be hard. The other method is to test the populations in controlled conditions, growth chambers or greenhouses. The retrospective approach to method development is not easy since field trials in future climates do not exist. To implement growth-chamber testing for future temperature climates, strong relationships between present field trials, in a range of different temperature climates, and matching temperature regimes in the growth chamber, have to be verified.

Another way to counteract the negative effects of G×E interactions is culling of unstable genotypes. This has been suggested in other studies (Matheson & Raymond 1984, St. Clair & Kleinschmit 1986, Johnson 1992). If only a few families are strong contributors to the interaction, such as the situation for most traits studied in the southern *Pinus sylvestris* seed orchard population and the *Picea abies* population, selection for stability may be useful. However, it remains to be seen whether the families unstable in growth chamber studies also are unstable in the field. If growth chamber selection for field condition stability proves to be useful it can be used as a supplement to the multiple population breeding strategy to reduce negative effects of a rapidly changing climate.

Early testing for breeding and propagation

Early testing in controlled conditions can be used in several ways in the breeding and propagation programmes. Three possible uses can be identified (Figure 6):

1. To replace the field-testing and thus considerably shorten the test time. This would require very strong and stable genetic correlations between the juvenile stage and the adult field performance.

2. To screen candidates prior to field-testing. In the Swedish breeding programs for *Pinus sylvestris* and *Picea abies* a nursery-screening step is included, selecting 10 (*Pinus sylvestris*) or 40 (*Picea abies*) progenies out of 100 in each full-sib family. In *Pinus sylvestris* populations in harsh climates an efficient screening method for hardiness based on artificial freeze testing has been implemented (Andersson 1992). Screening for budburst timing has proven to be efficient in avoiding frost damage in *Picea abies* (Hannerz et al. 1999) and will be used for certain breeding populations. There is still no satisfactory method developed for screening for adult growth capacity.

3. Early testing methods may also be used to select trees for seed orchards or clonal forestry programs. This can be utilised to improve the general breeding traits such as growth and adaptation or to test for specific traits that are not the main long-term breeding goals within the breeding population. These may be traits such as wood properties or disease resistance.

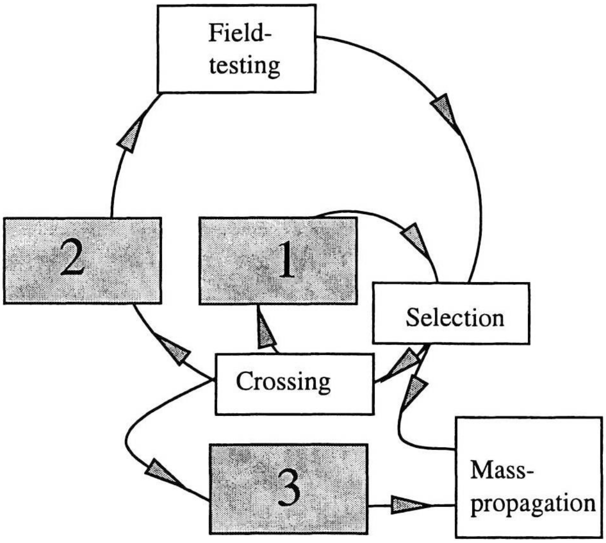

Figure 4. A tree breeding and propagation programme with three different steps of early testing; numbers 1-3 refers to the three different alternatives for early selection described in the text (1=replacing field testing, 2 = screening prior to field testing and 3 = testing for mass propagation).

The J-M genetic correlations obtained in the present study are too weak and unstable to be considered for use in early testing for final selection (alternative 1 described above). However, some of the growth-chamber traits have correlations strong enough to be used in early screening situations (alternative 2 and 3) but they lack the stability over several field trial sites that would be required to allow reliable selection. Some implications for the future development of early testing methods can be concluded from these studies. Height growth traits are potentially more informative than biomass traits. This is an advantage since height can be assessed in a non-destructive way which is necessary for the phenotypic selection screening planned in the Swedish breeding programs. For *Picea abies* it seems likely that methods involving periodic drought will improve the efficiency of the screening.

Further research

Early testing for genotypic stability

It would be of particular interest to study genotypic stability over different temperature climates in field trials, to see if the same pattern, with a few unstable families strongly contributing to the interaction, is also valid for field conditions. It would also be interesting to study if unstable families in the field trials can be identified in stability analyses of growth chamber experiments. However, suitable field trial series are rare and it is uncertain if such evaluations can be performed on existing field trials in Sweden.

Early testing in several temperatures

The studies in this thesis have demonstrated that there are considerable parental rank changes among experiments grown in different temperatures in the growth chamber. Temperature is also one of the two principal factors used to subdivide the Swedish breeding population into sub-populations and reliable methods for testing in warmer climates than the present are lacking. Extended retrospective studies in the growth chambers with several temperature treatments that are designed to mimic the temperature climates on the field trial sites could potentially provide us with important knowledge. Based on the results from earlier studies (Jonsson 2000) and this thesis the seedlings should be grown for more than one growth period and height growth development should be carefully studied.

Selection for water-use efficiency in *Picea abies*

Genetic variation for water-use efficiency (WUE) as determined by carbon isotope composition ($\delta^{13}C$) has been demonstrated for *Picea mariana* (Flanagan & Johnsen 1995) and for *Picea glauca* (Sun et al. 1996). Both studies also reported a positive correlation between WUE and growth capacity. Similar studies on *Picea abies* are lacking at present. In a fibre-farming concept with *Picea abies* as suggested by Bergh et al. (1999b), fertilisers will be applied. This will decrease the growth limiting effect of nutrients and thus likely increase the growth limiting effect of water (Bergh et al 1999a). When selecting genotypes for such fibre-farming forestry, selection for WUE has the theoretical potential to be efficient.

Combining several limiting factors in early tests

Growth is a complex trait that depends on several components such as water-use efficiency, nutrient acquisition capacity, nutrient utilisation, photosynthetic efficiency and duration of growth period. Only for cases, where one of these components dominates as a limiting factor for field growth, can we expect that testing in a controlled environment with simulation of one limiting factor will give strong J-M correlations. Our results from the *Picea abies* study suggest that water is one of several growth limiting factors in the field trials studied, probably with a strong limiting effect only in some periods and years. Studies by our group of other growth limiting factors were carried out with the same genetic entries as in this study. In the near future we shall have the possibility of combining the results from the different studies to better understand the relative importance of the different growth-limiting factors. We suggest that the further development of more efficient early selection methods for *Picea abies* should include periodic drought as one component of an index or a combined treatment.

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