

WHAT MIGHT BE USEFUL MEASURES OF GENETIC VARIABILITY FOR ADAPTIVE TRAITS WITHIN POPULATIONS OF SCOTS PINE?

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SUMMARY

There is large genetic variation in Scots pine, both within populations for both neutral and selective markers and between populations particularly for adaptive performance. The pattern of genetic evolution of Scots pine over time and space is of major concern when sustainability of European forests is discussed. The genetic diversity available within populations of Scots pine has been intensively studied by biochemical markers. Unfortunately, genetic diversity measured by isozymes or molecular markers is a poor indicator of genetic variability for adaptive traits. Potential measures of general and specific adaptation of Scots pine populations are discussed for different genetic tests (provenance, progeny). Only a few precise estimates of genetic variability for adaptive traits are available today. Simulations of Scots pine population dynamics under natural or artificial selective pressures require new evaluation of genetic variability, especially for populations at the limits of the range which are sometimes endangered.

KEY WORDS: Population differentiation
Genetic variability
Adaptation
Genetic tests.

INTRODUCTION

Why is within population genetic variability in Scots pine of interest?

In the continuous part of Scots pine natural range, most of genetic variability detectable with allozyme markers is within populations (Mejnartowicz, 1979; Gullberg *et al.*, 1985; Prus-Glowacki and Bernard, 1994; Goncharenko *et al.*, 1994). However, numerous provenance studies have demonstrated clinal adaptation to climatic conditions or even more local adaptation of these populations (Giertych and Oleksyn, 1992). Most Scots pine

forests in the natural range have been reforested with planting stock of local origin when natural regeneration failed. However, in addition seed transfer and genetically improved material have been used for more than 50 years. Definition of management practices respectful of Scots pine ecosystem biodiversity requires knowledge of changes in Scots pine genetic diversity under different climatic (frost or drought stress, global change), biotic (pests, grazing, browsing) and human pressures (intensive management, pollution).

In the southern and eastern parts of the natural range, isolated and sometimes endangered populations of Scots pine exist (Prus-Glowacki and Bernard, 1994; Catalán, 1991; Alía *et al.*, 1999). A precise inventory of the genetic variability still present in these mainly naturally regenerated populations is a prerequisite for genetic conservation programmes.

What are adaptive traits for Scots pine?

Adaptation of Scots pine populations is often measured by survival rate and growth potential. Death can be explained by different adaptive components not acting together (frost, drought, pollution, pest or insect attack). Reduced growth is linked to a sub-optimal growth rhythm (e.g. bad synchronisation of genotype's growth rhythm and seasonal conditions, a conservative strategy to escape drought effects), to a low nutrient efficiency, or to poor allocation of resources between different organs in the case of competition effects. Other characters linked to fitness such as reproductive potential (flowering ability, seed maturation) have a low economical value but play an important role in the evolution of within population genetic variability.

Plasticity of Scots pine populations over time and space is of major concern when sustainability of European forests is discussed:

- plasticity over time is important for long term management of natural populations: how could these populations react to unpredictable bioclimatic events? What is the minimum amount of genetic diversity required to prevent gene losses under these natural pressures?
- plasticity over space is important for definition of seed transfer rules of both natural populations and improved material. Whether plasticity in forest tree species is a property of the genotype or one of heterozygosity *per se* is today a matter of controversy. Examples of positive relationships between heterozygosity and fitness measures as well as negative relationships can be found in different *Pinus* species (Bush *et al.*, 1987; Bush and Smouse, 1991; Linhart and Mitton, 1985; Strauss and Libby, 1987). It is thus not known what level of genetic variability is required in improved material to provide optimum buffering capacity of these artificial populations.

What is an optimal measure of genetic diversity for adaptive traits?

An optimal measure of genetic diversity must describe as precisely as possible not only structural genetic diversity (inventory of all kind of alleles) but also functional genetic diversity in order to simulate evolution of Scots pine forests under climatic, biotic or human pressures.

The purpose of this review is to compare different measures of genetic diversity and to gather the different estimations obtained for Scots pine populations in Europe. Limitations of current knowledge will be discussed.

MEASURES OF GENETIC DIVERSITY AND GENETIC VARIABILITY IN SCOTS PINE POPULATIONS

What do we call genetic diversity and genetic variability?

Genetic diversity is a fashionable word with broad or narrow meanings according to its use in strategic research policy or as a specific parameter of genetic models. For a given species, genetic diversity is often used to refer to the richness of natural and artificial genetic resources available in given areas.

Within the community of geneticists, Rieger *et al.*, (1991) defined *genetic diversity* as *a function of the number and frequency of alleles per gene* in a certain gene pool. This interpretation, also called *gene diversity*, has been widely used in population genetics and conservation biology and is mostly based on neutral markers such as isozymes, RAPDs, RFLPs of rDNA or microsatellites.

When adaptive traits such as survival or growth are concerned, the term *genetic variability* is preferred to genetic diversity as the diversity measure used. This derives from decomposition of the observed or *phenotypic variance* according to the sampling structure used (provenance, mother-tree, full-sib crosses or clone).

Measures of genetic diversity with neutral markers

Three major parameters are used to describe allelic richness of a given population (Hartl and Clark, 1989):

- A , the coefficient of allelic richness defined as the number of alleles in the population at a given locus
- $H_e = 1 - \sum p_i^2$, the *Nei genetic diversity* or expected *Heterozygosity* within population which gives the probability that two alleles randomly sampled in a population are different
- $N_e = 1 / (1 - H_e)$, the mean effective number of alleles per locus in the population
- $G_{ST} = 1 - H_S / H_T$, the *Coefficient of Genetic Differentiation* between populations where H_S corresponds to the average genetic diversity coefficient over all populations and H_T measures genetic diversity in all populations considered as a single population. This parameter gives an indirect and average estimation of genetic diversity within population.

All these parameters are often averaged over several loci. Multilocus measures of differentiation taking into account gametic disequilibrium have also been recently developed (Kremer *et al.*, 1997).

Comparison of gene diversity measures obtained in different Scots pine studies is presented in table 1.

TABLE 1
GENE DIVERSITY STATISTICS ESTIMATED FOR SCOTS PINE
Estimaciones de varias estadísticas de diversidad genética para Pino silvestre

Geographical area	No population	No. loci	N _A	H _e	G _{ST}	References
Sweden	9	11 isoz.	4.36	—	0.008	Gullberg <i>et al.</i> , 1985
Finland	4	10 isoz.	—	0.34	0.002	Karhu <i>et al.</i> , 1996
	5	3 RFLP	3.0	0.49	0.02	Karhu <i>et al.</i> , 1996
	4	8 rDNA	—	—	0.14	Karvonen and Savolainen, 1993
	2	2 Cp SSR	8.5	0.77	0.014	Karhu <i>et al.</i> , 1996
Scotland	14	16 isoz.	2.60	0.309	0.028	Kinloch <i>et al.</i> , 1986
East and Central Europe	16	7 isoz.	2.74	0.363	0.025	Prus-Glowacki and Stephan, 1994
Latvia, Ukraine, Russia	18	21 isoz.	4.00	0.282	0.030	Goncharenko <i>et al.</i> , 1994
Ukraine, Western Siberia, Turkey	13	8 isoz.	3.50	0.357	0.076	Prus-Glowacki and Bernard, 1994
Spain	7	7 isoz.	2.86	0.325	0.040	Prus-Glowacki and Stephan, 1994

N_A: average number of alleles per locus.

H_e: nei genetic diversity.

G_{ST}: genetic differentiation coefficient.

As a general result for most *Pinaceae* species, the absolute amount of genetic differentiation of Scots pine populations is quite small, with more than 90 % of genetic diversity present within populations (Gullberg *et al.*, 1985; Goncharenko *et al.*, 1994; Prus-Glowacki and Stephan, 1994; Karhu *et al.*, 1996). When molecular markers are used with cytoplasmic genomes, these values are usually higher. However, if several studies indicate low differentiation in Scandinavia as a whole, higher subdivision of Scots pine natural range is found in Central and South-eastern Europe. The most striking differences are observed with Spanish or Turkish populations which are considered as Scots pine Tertiary relicts that have survived as isolated populations (Prus-Glowacki and Bernard, 1994; Prus-Glowacki and Stephan, 1994).

Measures of genetic variability for adaptive traits in provenance tests

Historically, the first description of genetic resources of forest tree species was based on large multisite provenance tests where populations sampled all over the natural range of the species were represented by 50 to 500 individuals. For Scots pine, field experiments have been established since 1907 (Giertych, 1991). Measures of genetic variability reported in literature concern mainly frost resistance (Mikola, 1982; Aho, 1984; Nilsson and Andersson, 1987), growth potential (Krusche *et al.*, 1980; Haapanen *et al.*, 1997), resistance to pests (Johnsson, 1976; Martinsson, 1987) and exceptionally reproductive potential.

Most of adaptive traits measured in provenance tests show continuous distribution. Therefore, the observed variance is split according to a nested linear model into a between-population component (V_{between}) and a within-population component (V_{within}) which averages phenotypic tree variation within population. Differentiation between provenances is then measured by:

$$t = V_{\text{between}} / (V_{\text{between}} + V_{\text{within}})$$

The two parameters G_{ST} and t can be linked under the assumptions of Hardy-Weinberg equilibrium and absence of dominance effects (Rogers and Harpending, 1983). In order to compare t and G_{ST} , Kremer (1994) suggested the use of t' as a coefficient of differentiation with quantitative characters:

$$t' = t / (2 - t)$$

As V_{within} does not correspond exactly to the additive genetic variance, t and therefore t' could often be underestimated from evaluation in provenance tests. If available, individual heritability estimations could be used to approach additive genetic variability (Kremer *et al.*, 1997, Yang *et al.*, 1996).

Unfortunately, few studies on Scots pine give an estimation of this differentiation coefficient t or t' , or enough information to calculate them. For the rare Scots pine studies from which t' could have been estimated, values range from 0.25 to 0.70 and are considerably higher than G_{ST} estimations. Many adaptive traits such as budset phenology, frost or drought resistance or resistance to disease show steep climatic gradient or more local adaptation.

Direct evaluation of genetic variability for adaptive traits within populations of Scots pine is necessary

For Scots pine, neutral markers (isozymes, RAPD's, microsatellites) can not substitute direct measures of quantitative variation for adaptive traits (Muona and Harju, 1989; Karhu *et al.*, 1996). Variation at neutral loci may be governed mostly by mutation and drift (Kimura, 1983). Even low levels of migration will equalise gene frequencies among populations at such loci. Genetic variation for adaptive characters depends on a balance between mutation and selection, or between different selective pressures. While migration rates are equal for all genes, selection acts differently on different parts of the genome. Balance between the two forces can result in considerable genetic differences among populations. That is why molecular markers and adaptive performances can be considered as contrasted sampling of the entire genome of Scots pine.

SPECIFIC MEASURES OF GENETIC VARIABILITY FOR ADAPTIVE TRAITS WITHIN POPULATIONS OF SCOTS PINE

Most components of fitness in Scots pine are usually assessed in common environment experiments. Thus, specific adaptation of Scots pine individuals to local conditions such as frost or air pollution is evaluated in field or laboratory tests with discriminant descriptors.

As far as sustainability of Scots pine forests is concerned, measures of general adaptation of populations in varying environments has become a major objective of genetical studies. A precise evaluation of general adaptation, also called plasticity, requires genetic experiments replicated in many environments (more than 10) representative of climatic, edaphic and silvicultural management ranges. Several statistical methods are now available to describe adaptive pattern with few parameters (Namkoong *et al.*, 1992; Piepho, 1998).

We examine below parameters associated with the measurement of specific and general adaptation and present estimates available for Scots pine in Europe.

Evaluation of specific adaptation in common environment tests

Potential measures in provenance and progeny tests

As mentioned previously, provenance research focuses on population differentiation rather than on evaluation of within population variability. The question is whether geneticists can benefit from the numerous experiments established over Europe with common collections of Scots pine populations to assess within population genetic variability for adaptive traits. For traits not much influenced by micro-environmental variations and for provenances or populations represented by more than 60 trees, phenotypic approximation of within population genetic variability could be estimated through the three following parameters:

V_{wp} , the within provenance variance of design-adjusted individual performances,

$CV_{wp} = 100 \times \sqrt{V_{wp}} / X$, the corresponding coefficient of variation, where X = mean value based on individual tree data,

$R_w = t_{90} - t_{10}$, the 80 % range of design-adjusted individual performances

With current technology, we cannot measure directly the genetic value of a tree in a stand free of the confounding influences of the environment in which it is growing. Furthermore, as few adaptive traits in forest trees are inherited in a pattern that can be attributed to the effects of major genes alone, prediction of genetic variability through phenotypic observations is reached through the quantitative genetic model:

$$V_P = V_A + V_{NA} + V_E \text{ with } V_G = V_A + V_{NA}$$

V_P , the total variance among phenotypic values observed in the population,

V_G , the variance associated with the genetic differences among all trees in the population,

V_A , the genetic variance associated with additive effects. Genetic effects are called additive when progenies performances are exactly intermediate between parent performances. They can be estimated when identity of one of the 2 parents is controlled (e.g. open pollinated progenies).

V_{NA} , the genetic variance associated with non-additive genetic effects. This component express the gap between the observed genetic value and the genetic value predicted from only additive effects. Their estimation requires control of the identity of the two parents according to specific mating designs.

V_E , the portion of variation associated solely with environmental effects.

Difficulties linked with production of controlled crosses in forest tree species often limit genetic variance estimation to the additive genetic variance especially when vegetative propagation is not available. This estimation for a given population is based on com-

parison of performance of numerous open-pollinated progenies randomly chosen in the population in a common design.

An additional description of genetic variability expressed for quantitative traits is given by the heritability concept:

$$h_s^2 = V_A / V_p \quad \text{and} \quad h_L^2 = V_G / V_p$$

Heritability values h_s^2 or h_L^2 express the proportion of variation observed in the population that is attributable respectively to additive genetic (h_s^2) or genetic differences (h_L^2) among individuals.

Limits of provenance tests in Europe for evaluation of Scots pine genetic variability

Comparison of measures of genetic variability in provenance and progeny tests for three Scots pine populations is presented in table 2.

TABLE 2
GENETIC VARIABILITY ESTIMATIONS FOR HEIGHT INCREMENT AND
SUSCEPTIBILITY TO *Melampsora pinitorqua* FROM PROVENANCE AND
PROGENY INFORMATIONS COLLECTED ON THREE SCOTS PINE
POPULATIONS, IN ONE FIELD TEST IN FRANCE AND TWO FIELD TESTS
IN SPAIN

*Variabilidad genética en el crecimiento en altura y susceptibilidad a *Melampsora pinitorqua* estimadas en ensayos de procedencias y progenies para tres poblaciones de *Pino silvestre**

		Test 24721 Orléans forest				Spanish field tests	
		French population Haguenau		Polish population Taborz		Spanish population Valsain	
Trait		Provenance Seedlot (n=92)	65 Open pollinated progenies (n= 2342)	Provenance seedlot (n=89)	60 Open pollinated progenies (n= 2172)	Provenance seedlot	plus-trees-open pollinated progenies
Increment Height (cm)	mean	48.23	51.68	44.61	45.05	64.2	75.3
	CV _{wp}	24.05%	6.41%	24.6%	5.43%	23.5%	7.3%
	CV _A		0.253		0.141		0.350
	hs ²						
		CV _{wp} *h > CV _A 12.10% > 6.41%		CV _{wp} *h > CV _A 9.24% > 5.43%		CV _{wp} *h > CV _A 13.9% > 7.3%	
<i>Melampsora</i> Susceptibility	mean	0.875	0.881	0.212	0.224		
	CV _{wp}	18.48%		34.43%			
	CV _A		9.21%		21.52%		
	hs ²		0.695		0.724		
		CV _{wp} *h > CV _A 15.41% > 9.21%		CV _{wp} *h > CV _A 29.3% > 21.5%			

CV_{wp} is calculated from the provenance seedlot, CV_A and hs² are calculated from the progenies seedlot through quantitative genetic model (French data from INRA, C. Bastien, unpublished data, Spanish data from INIA Climent *et al.*, 1997 and unpublished data).

As expected genetic variability evaluated from provenance test information (CV_{wp}) is overestimated especially for characters with low to medium heritability values. However for traits with high heritability such as susceptibility to *Melampsora pinitorqua*, differences of genetic variability amount detected in provenance tests correspond to true differences of additive genetic variances. Nevertheless, precise evaluation of relative difference of genetic variability can be obtained only through progeny testing. In Scots pine, only weak non-additive genetic effects could be demonstrated for both growth traits, wood density traits and even pest susceptibility (Gerhold and Park, 1986; Hannrup and Ekberg, 1998, Quencez, unpublished data).

Estimations of genetic variability measures in Scots pine progeny tests in Europe

The current state of genetic variability estimates within population of Scots pine is presented in table 3 for different adaptive traits and descriptors of wood production (volume production, stem form and wood density).

TABLE 3

ESTIMATES OF GENETIC VARIABILITY WITHIN POPULATION OF SCOTS PINE IN DIFFERENT PROGENY TESTS IN EUROPE

Estimaciones de la variabilidad genética dentro de las poblaciones de Pino silvestre, en diferentes ensayos de progenie en Europa

Adaptive and production Traits	Age	Population Progenies	h^2	References
Frost resistance	1	"+" trees Full-Sib progenies	?	Nilsson and Andersson, 1987
Frost hardness	1	"+" trees Full-Sib progenies	?	Norell <i>et al.</i> , 1986
Bud-set phenology	1-3	"+" trees Full-Sib progenies	?	Mikola, 1982
Twist rust susceptibility	3	"+" trees OP ¹ progenies	0.55	Bastien, 1998, unpubl.
	7	"+" trees OP progenies	0.08-0.18	Andersson and Danell, 1997
Height growth	6-11	"+" trees OP progenies	0.24-0.38	Krusche <i>et al.</i> , 1980
	7	"+" trees OP progenies	0.35	Climent <i>et al.</i> , 1997
	13	random trees OP progenies		Pöykkö, 1982
	16	random trees OP progenies	0.33	Bastien, 1998, unpubl.
Diameter growth	30	random trees OP progenies	0.21-0.42	Eriksson <i>et al.</i> , 1987
	11	"+" trees OP progenies	0.15	Krusche <i>et al.</i> , 1980
	16	random trees OP progenies	0.26	Bastien, 1998, unpubl.
	30	random trees OP progenies	0.10-0.35	Eriksson <i>et al.</i> , 1987
Branch angle	13	Random trees OP progenies	0.12	Pöykkö, 1982
	16	"+" trees Full-Sib progenies	0.20	Velling <i>et al.</i> , 1984
Stem straightness	30	random trees OP progenies	0.13-0.23	Eriksson <i>et al.</i> , 1987
Wood density	33	"+" trees Full-Sib progenies	0.50	Hannrup <i>et al.</i> , 1998

¹ Open pollinated.

h_s^2 corresponds to individual heritability.

Only a few estimates of genetic variability expressed as coefficient of variation CV_A are available in the literature. Even if geographical patterns of Scots pine population differentiation are explained by natural selection effects, there is still a high amount of ge-

netic variability (20-30 %) present within populations from central and northern Europe for all traits related to climatic adaptation and growth performance

Lessons and gaps

From the literature we can conclude that most natural populations of Scots pine form important gene stocks for many adaptive characters. However, genetic variability estimates are available mostly for Scots pine populations from the continuous range covered by ice during last glaciation (Giertych, 1991). Only a few incomplete recent studies include populations from the southern range of the species (Climent *et al.*, 1997; Alía *et al.*, 1999). Differences in the evolutionary history of these populations and in their reproductive behaviour in the mountain areas where they are found, might have structured the genetic variability between and within populations differently. Furthermore, some populations are considered endangered and no exact inventory of the remaining genetic variability for adaptive traits is available.

Most studies presented here have been done with the primary objective of exploiting as quickly as possible this genetic variability to select improved material. Open pollinated progenies have been collected on trees phenotypically selected in the forest for their economical performances. They do not represent a random sample of the population and can underestimate the natural genetic variability available for traits more related to fitness.

Nevertheless, experience acquired from all these experiments offers reliable screening methods for evaluation of frost, drought or pest resistance. They could be easily used in early tests to measure genetic variability present in more isolated and little known populations of Scots pine.

Evaluation of general adaptation in multisite genetic networks in Europe

Potential measures of general adaptation from multisite field experiments

Phenotypic stability or plasticity is of major importance in tree breeding programmes. Therefore, several parameters have been proposed to compare performances of different genotypes (provenances or progenies) in different sites. Among these are:

- a) Stability parameters dependent on the set of populations and on the range of environments tested which include:
 - S_i^2 Shukla variance stability and W_i Wricke ecovalence are closely related measures of the contribution of each genotype to the total mean squares of interaction (Shukla, 1972; Wricke, 1962; Piepho, 1998). They are unfortunately very sensitive to the assumptions of the linear model and to outliers.
 - S_i^4 non parametric measure defined by Hühn is based on the variance of ranks with corrected performance values (Hühn, 1979; Nassar and Hühn, 1987). This parameter is more adapted to genetic selection process in which breeders are mainly interested by rank stability of improved material.
 - $\gamma^1, \gamma^2, \dots, \gamma^r$ the r independent multiplicative terms of AMMI model popularised by Gauch (1988) offer a good explanatory approach of genotype by environ-

ment interactions. The first multiplicative terms capture the major interactive pattern whereas the last ones selectively recover noise. They can easily be connected with available adaptive information.

b) Stability parameters not dependent on experiments and predictive models

A common approach to stability analysis is to regress performances onto an environmental index and to compare the genotypes on specific regression coefficient estimates:

- Finlay and Wilkinson (1963) suggested comparing b_i regression coefficients after linear regression of performance on the mean of all genotypes in the site. In spite of its popularity, the linear pattern supposed for the interaction pattern has often presented a limited effectiveness and the environmental index used could be biased by the subset of genotypes tested (Westcott, 1986)
- The factorial regression analysis developed by Denis (1988) is based on the use of independent covariates referring to the genotypes or to the sites. For genotypes, additional quantitative information may be present from previous tests bearing on some precise adaptive traits such as frost or drought resistance or simply phenological behaviour. For environments, quantitative information can consist simply in geographical data such as latitude, longitude and altitude or in more precise descriptors of natural constraints for Scots pine such as amount of rainfall, drought index, minimum temperature or length of the growing season.
- Extending the simple regression model, non linear regression models can be considered and more than one covariate can be incorporated in the environmental index (Pooni and Jinks, 1980; Gregorius and Namkoong, 1986).

Evaluation of Scots pine plasticity in Europe

Most information on Scots pine plasticity is available at the population or provenance level and concerns material sampled in Scandinavia and the North and Eastern part of the European range of the species.

In Sweden, evaluation of plasticity of local provenances was initiated early in the mid-century in order to build a seed transfer guide for Scots pine in the country (Eiche, 1966; Eriksson *et al.*, 1980). Compared with survival, height or volume growth was less affected by latitudinal transfer demonstrating the high level of plasticity of Scots pine populations. Raymond and Lindgren (1990) confirmed the limit of the linear model proposed by Finlay and Wilkinson (1963). They proposed a curvilinear equation to predict the performance of a given provenance with a site index reflecting the relative severity of the environment for volume production. In their case this severity index is described by latitude adjusted to a constant altitude. Unfortunately, the studies are based on a very limited number of provenances which raises whether they are representative of the wider Scots pine natural range in Europe.

From 1974 to 1976, the Forest Research Institute in Pushkino near Moscow initiated the largest Scots pine provenance test network with 113 populations sampled from throughout the range and compared in 33 experimental sites widely distributed over the same area. Shutyaev and Giertych (1998) recently reported partial results on Scots pine variability for general adaptation. This study suffers from the limited effectiveness of the

Finlay and Wilkinson linear regression and would profit by using more informative models such as those mentioned above.

The most important series of Scots pine provenance trials established in the twentieth century at an international level were initiated by The Union of Forest Research Organizations (IUFRO) in 1907, 1938, 1939 and 1982 (Giertych and Oleksyn, 1992). Unfortunately, few succinct joint evaluations of these trials have been made (Giertych, 1979).

Within population general adaptability in Scots pine has also rarely been studied in multisite progeny tests. It was suggested in only one Scandinavian experiment (Gullberg and Vegerfors, 1987) that different Scots pine genotypes might present a range of adaptation to soil fertility through varying nutrient efficiency. However if some genetic variability was revealed for nutrient efficiency, it did not explain plasticity over the planting sites tested (Jiang, 1988; Jonsson *et al.*, 1992).

Lessons and gaps

Studies of Scots pine populations from the whole European range concern general adaptation to some environments tested and not more specific adaptation to climatic, edaphic or silvicultural constraints. Response curves to varying environments are only available for Scandinavian populations with site index defined from latitude and altitude.

The old IUFRO provenance trials could complete information for populations from Central Europe and range of sites with other selective pressures (drought, wind, soil fertility, biotic aggressors). Different statistical methods of analysing provenance by site interaction partitioning could be applied to new datasets provided by all partners involved in the IUFRO series (for most development see Koski and Matyas in the same publication).

However, Scots pine natural forests from the marginal and southern range of the species are rarely represented in these series either as sample provenances or as sites for the trials.

The genetic basis of adaptability of Scots pine populations is still not known. Possible implications of genotypic buffering (number and variability of genetic components of the population) or heterozygosity at the individual tree level must be clarified in specific experiments (Savolainen and Hedrick, 1995).

CONCLUSIONS

Current molecular markers reveal differentiation and structure of Scots pine populations but rarely their adaptive potential over space and time. Direct measures of specific adaptive traits are absolutely necessary. Early tests and screening techniques in climate chambers are now available for most of Scots pine adaptive parameters (growth, frost tolerance, pest or insect susceptibility). They could be applied to new progeny tests in order to estimate more precisely within population genetic variability. Four or five natural populations sampled from contrasted areas in the European range (Scandinavia, Central Europe, Alps, Spain) could serve as model populations. International cooperation could help the establishment of this collection on a wide range of ecological sites and contrasting silvicultural regimes in Europe.

RESUMEN

¿Que parámetros pueden ser útiles para evaluar la variabilidad genética dentro de las poblaciones para los caracteres adaptativos en Pino silvestre?

Existe una gran variación genética en Pino silvestre, dentro de las poblaciones (tanto en marcadores neutrales y selectivos) como entre poblaciones (principalmente para el comportamiento adaptativo). Los patrones de evolución genética del Pino silvestre en el tiempo y el espacio es de la mayor importancia cuando se discute la sostenibilidad de los bosques europeos. La diversidad genética disponible dentro de las poblaciones de Pino silvestre ha sido ampliamente estudiada mediante marcadores bioquímicos. Desafortunadamente, la diversidad genética medida mediante isoenzimas o marcadores moleculares es un pobre indicador de la variabilidad genética de los caracteres adaptativos. Las medidas potenciales de la adaptación general y específica de las poblaciones se discuten para diferentes ensayos genéticos (procedencias, progenies) de Pino silvestre. Solamente se dispone de unas pocas estimas precisas de la variabilidad genética de los caracteres adaptativos. La simulación de la dinámica de las poblaciones de Pino silvestre bajo condiciones de presión selectiva natural o artificial requiere una nueva evaluación de la variabilidad genética, especialmente para poblaciones en el límite del rango de distribución, que suelen estar amenazadas.

PALABRAS CLAVE: Diferenciación de poblaciones
Variabilidad genética
Adaptación
Ensayos genéticos

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