

Review paper

Genetic variation within European tree species

G. MÜLLER-STARCK^{1,2}, Ph. BARADAT³, and F. BERGMANN¹

¹ Abteilung Forstgenetik und Forstpflanzenzüchtung, Universität Göttingen, Büsgenweg 2, D-3400 Göttingen, Germany; ² Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland; ³ Institut National de la Recherche Agronomique, Centre de Recherches de Bordeaux, Pierroton, F-33610 Cestas, France

Received 7 December 1990; accepted 23 December 1991

Key words: genetic markers, isoenzymes, terpenes, polyphenols, heterozygosity, geographic differentiation

Application. Genetic variation is a fundamental requirement for the maintenance and long-term stability of forest ecosystems since amount and pattern of genetic variation determine the ability of forest tree species to adapt to the variability of environmental conditions.

Abstract. This paper reviews results of studies on genetic variation in various European coniferous and angiosperm tree species, with emphasis on *Picea abies* and *Pinus sylvestris*, *Abies alba*, *Fagus sylvatica*, and *Castanea sativa*. Most of the studies employ enzyme gene markers, but terpenes and other markers are also used. The comparison of data is complicated due to the variety of measures of genetic variation that are reported. Nevertheless, substantial differences in intra- and interpopulational genetic variation can be observed among and also within species. Causes for such heterogeneity are briefly discussed. The necessity for monitoring genetic variation and for standardizing measurement of genetic variation is emphasized.

Introduction

During recent decades, forest ecosystems and forest resources in Central Europe have been threatened particularly by air pollution-induced environmental changes. These and other man-made deteriorating effects on forest ecosystems severely challenge the ability of the constituent forest tree populations to adapt to and to survive in spatially and temporally heterogeneous environmental conditions. This ability to adapt to change is a fundamental requirement for the maintenance of forest ecosystems. Within each tree species, the amount and pattern of genetic variation determine its adaptability and are consequently essential parameters of the long-term stability of forest ecosystems.

The objective of this paper is to review the present state of knowledge on genetic variation within native European forest tree species and to point out causes of heterogeneity in intra- and interpopulational variation. We cite studies which aim at the utilization of biochemical markers, which are expressed environmentally independent. The majority of the studies employ enzyme gene markers detected by means of various electrophoretic methods. Low molecular weight substances such as terpenes and polyphenols are also considered. DNA restriction fragment length polymorphisms have not been applied to date to studies on intrapopulational genetic variation in European tree species.

In reviewing the publications on forest tree species, three major problems arise. Firstly, in many studies an appropriate genetic analysis is missing so that the genetic control and mode of inheritance of markers are not proven unequivocally. Secondly, methods of measuring genetic variation differ among studies, so that direct comparison of results is difficult. Thirdly, in many studies the gene and/or genotype frequencies are not communicated, so that the original data cannot be reanalysed and subjected to a direct comparison. Consequently, this review of genetic variation within European tree species can only describe major trends without detailed characterization and interpretation of differences in genetic structures within and among species.

Brief survey of biochemical and molecular markers in use

(a) Terpenes and polyphenols

Terpenes and polyphenols, as secondary metabolites, have a less obvious genetic control than isozymes and they are often used without precise information about their mode of inheritance. The first class of compounds is the more widely used, with the limitation that only coniferous forest species are concerned. They are generally extracted from cortex oleoresin. Improvement of gas-liquid chromatography (GLC) techniques with automatic integration of peak areas considerably enhances the number of hydrocarbons which can be separated and reduces the analytical cost. Polyphenols, which are found in both conifers and broadleaves have been investigated much less. Analytical techniques for monitoring polyphenols are paper chromatography, thin layer chromatography or high performance liquid chromatography (HPLC).

(b) *Immunoproteins*

Immunological techniques can be efficiently used to study chemotaxonomic problems (for review see Prus-Głowacki 1982). Also clinal trends in immunoproteins (“antigenic” proteins) have been found among populations of *Pinus sylvestris* L. (Prus-Głowacki and Rudin 1981; Prus-Głowacki et al. 1985). Since the genetic control and the mode of inheritance of immunoproteins have not yet been elucidated, these substances are not suitable for monitoring genetic variation among individuals and populations, and will not be discussed further in this review.

(c) *Enzyme gene markers*

Isoenzymes quite frequently are found to be controlled by single gene loci, and thus, are very useful for monitoring genetic (allelic) variation. Certain enzyme systems often reveal considerable variation and are detectable in various plant tissues. Usually, alleles at isoenzyme loci are codominant. Occasional lack of isoenzyme banding as a consequence of “null alleles” is equivalent to recessive expression and results in underestimates of heterozygosity.

(d) *DNA markers*

Like enzyme gene markers, restriction fragment length polymorphisms (RFLP's) or other DNA variants allow for monitoring genetic polymorphisms in cases where appropriate genetic analyses have identified allelic variants (for specific problems in genetic analysis see Gillet 1990). The extremely high information potential will favour DNA markers in the future, although many techniques like “fingerprinting” reveal intrapopulation variation which does not necessarily correspond to allelic variation. To our knowledge, there are no results published to date on intra- or interpopulational genetic variation in European tree species using DNA markers. Chloroplast DNA, however, has been utilized to study phylogenetic relationships among species (e.g., Szmidsztajn 1991) and for solving specific problems, like the classification of seedlots which originate from introgression zones (e.g., Szmidsztajn et al. 1988).

Results of experimental studies

The present survey refers to forest tree species which are commonly considered as to be ecologically and/or economically important and are

managed according to forestry, and not to agricultural regimes. Studies which mainly refer to characterization of components of mating systems are not included. Investigations involving only one population were taken into consideration only if no other information was available for that particular tree species. Studies using terpene markers, are reviewed separately from those which have used enzyme gene markers.

Results of studies using terpenes or polyphenols

Biology and inheritance

Terpenes

Monoterpenes (C₁₀ hydrocarbons) and sesquiterpenes (C₁₅ hydrocarbons) have been intensively studied in forest trees. Recent progress has been made in understanding their biosynthesis (Bernard-Dagan et al. 1982; Cori 1983) and the relationships between intensity of their synthesis and architecture of resin ducts (White and Nilsson 1984). Zavarin (1970) used correlations between expression of terpenes to help in understanding biochemical pathways. Squillace (1976) reviewed methods of evaluating the inheritance of these compounds and focused attention on autocorrelations between relative amounts. Birks and Kanowski (1988) consider that these autocorrelations are an important cause of error in determination of inheritance pattern of terpenic compounds and lead to uncertainty about the number of polymorphic loci involved in their biosynthesis. Strong genetic control of terpenes is well established by broad sense heritabilities close to 1 even when grafts are grown at different localities (Baradat and Yazdani 1988). Segregation data based on full-sib families support monogenic inheritance of terpenes in three European species: 3-carene in Norway spruce, *Picea abies* L. Karst. (Esteban et al. 1976); β -phellandrene, β -pinene, myrcene, limonene and 3-carene in Scots pine, *Pinus sylvestris* L. (Yazdani et al. 1982); 3-carene, myrcene, limonene, longifolene and caryophyllene in Maritime pine, *Pinus pinaster* Ait. (Baradat et al. 1972, 1974; Marpeau et al. 1975, 1983).

Pleiotropy of terpene genes is frequent due to common precursors in biosynthetic pathways. This is, for example, the case for 3-carene and terpinolene (Baradat et al. 1972). Linkage relationships have been reported in Maritime pine: genes which control 3-carene, myrcene and limonene belong to the same linkage group (Marpeau et al. 1983).

Polyphenols

Inheritance studies have been done on Norway spruce (Wellendorf and Kaufmann 1977) and on Scots pine (Thielges 1972; Yazdani and Lebreton

1991). The last named authors found a case of pleiotropy, where one locus controlled two flavonoids, prodelphinidin and taxifolin.

Use in the study of genetic variability

Table 1 summarizes results on intraspecific variability in seven European species of conifers using terpenes or polyphenols. The main field of utilization of terpene and phenolic compounds is chemotaxonomy because they display a strong geographic variation. The corresponding data are usually relative concentrations which are mainly processed with classical statistical methods used for quantitative traits. The most widely spread biometrical technics are analysis of variance, discriminant analysis, and cluster analysis.

Terpenes

Many experimental results (see Table 1) suggest that terpene markers correspond to selection pressure in a similar way as isoenzymes can do. For instance, Li and Adams (1988) found in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) a similar pattern of geographical variation using isozymes than v. Rudloff (1973) found for terpenoid compounds of needles (see also Baradat et al. 1991).

High discriminating power of terpenes at the population level may be a consequence of the fact that different molecular forms correspond to drastic changes of physiological properties of enzymes acting on metabolic pathways. The expected result is a very low effective mutation rate at loci which control terpenes. This property makes these markers useful also for phylogenetic studies (see Table 1).

As basic terpenoid data are quantitative, precise identification of genotypes is possible only when the dominance of a richness allele over a poorness allele, or vice-versa, is not great. Dominance relationships have been determined for β -pinene, 3-carene, myrcene, limonene, longifolene and caryophyllene in Maritime pine (*Pinus pinaster*). These relationships range from high dominance of the poorness allele for caryophyllene to moderate dominance of the richness allele for 3-carene (Bernard-Dagan and Baradat 1977; Baradat and Marpeau 1991b). Most authors describe natural variability for terpenes, without any previous genetic analysis, using percentages of each terpene from individual trees or from mean supplies (one GLC analysis of oleoresin representative of a stand, sampled from series of individuals). Only in a few cases have patterns of variation in terpenes been reported in terms of chemotypes (Gansel and Squillace 1976 for slash pine (*Pinus elliotii* Engelm.), Forrest 1979, 1980 for Scots pine), or gene frequencies (Baradat and Marpeau 1991b).

Table 1. Survey of genetic variation in coniferous tree species on the basis of terpenes (T) and polyphenols (P)

Species and reference	Sampling design	Traits	Levels of variability	Processing of data	Most significant compounds	Genetic conclusions
<i>Abies alba</i> Mill						
Paule et al. 1987	13 prov. (Poland, Czechoslovakia)	T; QT	Within and between prov.	ANOVA	Tricyclene, α -pinene	50% of variance between prov.
Moreau, Pastuska 1991	83 F ₀ , 159 F ₁ trees	T; QT, QL	Within stand	F _{is}	α -Pinene, limonene	F _{is} = 0.77 (F ₀) F _{is} = 0.57 (F ₁)
<i>Abies cephalonica</i> Loud.						
Fady 1991	6 prov., 83 halvesib families	T; QT	Within and betw. famil. (within prov.)	ANOVA	Monoterpenes, longifolene	F _{is} > 0.50
<i>Cupressus sempervirens</i>						
Schiller 1990	22 prov. (Israel)	T; QT	Within and between prov.	Discr. analysis, cluster analysis	Pinenes, 3-carene, phellandrene, caryophyllene	Israel prov. belong to different origins
<i>Pinus halepensis</i> Mill.						
Schiller, Grunwald 1987	22 prov. (Europe, Israel)	T; QT	Within and between prov.	Discr. analysis, cluster analysis	α -Pinene, 3-carene, myrcene	Structure of geographic variability
Baradat et al. 1989	4 prov. (Italy)	T; QT	Within and between prov.	Discr. analysis, cluster analysis	3-Carene, α -terpinene, caryophyllene	High discriminating power of terpenes between prov.
<i>Pinus nigra</i> Arnold						
Arbez et al. 1974	14 prov. (France, Italy)	T; QT	Between subspecies and geographic races	ANOVA	Limonene	Discrimination between 4 subspecies and between Laricio

Table 1. (Continued)

Species and reference	Sampling design	Traits	Levels of variability	Processing of data	Most significant compounds	Genetic conclusions
Fineschi, Grossoni 1981	2 geographical races	T; QT	Between geographical races	ANOVA	Limonene	Discrimination between Laricio from Corsica and Calabria
Gerber et al. 1991	72 prov. (southern Europe)	T; QT	Between prov. and subspecies	Discr. analysis, cluster analysis	β -Pinene, phellandrene, caryophyllene	Revision of taxonomy
<i>Pinus pinaster</i> Ait.						
Baradat et al. 1979	36 prov. 4 geographical groups	T; QT	Within and between stands and zones	ANOVA and principal component	β -Pinene, 3-carene, caryophyllene	Structure of geographic variability; panmictic equilibrium
Baradat, Marpeau 1991a	105 prov. from natural populations	T; QL	Between stands and geographic races	Discr. analysis, cluster analysis	β -Pinene, 3-carene, caryophyllene	Reconstruction of differences among races
Baradat, Marpeau 1991b	105 prov. from natural populations	QL	Within stands	Test of panmixia	6 Terpenes	Panmixia except for coastal stands
Baradat et al. 1991	7 geographical races	T; QT, QL	Between geogr. races	Discr. analysis, cluster analysis	6 Terpenes, 17 loci, 312 spots total prot.	Similar clustering of races with proteins and terpenes
Idrissi-Hassani, Lebreton 1992	4 geographical races, 80 trees	T; QT, QL	Within and between geographical races	Frequency description	Kaempferol	Discrimination of races from Morocco and Landes
<i>Pinus sylvestris</i> L.						
Tigerstedt, Hiltunen 1979	146 clones from N-S range	T; QT, QL	Between stands	Regression	3-Carene	Clinal variation
Forrest 1979	17 prov. (Scotland)	T; QL	Between prov.	Frequency of terpenoid patterns	Pinenes, myrcene, phellandrene	Large variability between prov.

Table 1. (continued)

Species and reference	Sampling design	Traits	Levels of variability	Processing of data	Most significant compounds	Genetic conclusions
Forrest 1980	41 prov. (Scotland)	T; QL	Between prov.	Cluster analysis	Pinenes, myrcene	Clustering of prov. into 4 main groups
Yazdani et al. 1985	26 prov. (Sweden)	T; QT	Between prov.	ANOVA and discr. analysis	β -Pinene, 3-carene, limonene	Clinal variation
Yazdani, Nilsson 1986	10 prov. (Sweden)	T; QT	Within and between prov.	ANOVA and discr. analysis	Limonene, sabinene	Clinal variation; 85% of variance between prov.
Lebreton et al. 1990	16 geographical zones (Sweden, France, Spain); 156 indiv.	P; QT, QL	Within and between stands and zones	Regression and frequency analysis	Prodelphinidin, procyanidin, quercetin	High frequency of chemotypes with procyanidin and quercetin in low altitudes populations

QT stands for "quantitative" and QL for "qualitative" traits, ANOVA for "analysis of variance", discr. for "discriminant", prov. for "provenance(s)", F_0 for parents and F_1 for descendants; F_{is} designates the within population inbreeding coefficient (Wright 1969)

Studies on genetic variability involving terpenes generally use analyses of variance, multivariate analyses (principal components, discriminant analysis), and cluster analyses (see Table 1). They generally bear on comparison of provenances and geographic races and results can also partition the total variance between and within populations (e.g., Yazdani and Nilsson 1986 for Scots pine or Paule et al. 1987 for silver fir, *Abies alba* Mill.). Some studies estimate within stand inbreeding coefficients (F_{is} , see Table 1).

Polyphenols

When HPLC analysis techniques are used, interpretation of genetic variability in phenolic compounds is similar to that employed for terpenes, i.e., the detection of genotypic classes underlying quantitative variation in concentrations. Although there are only a small number of studies and a few discriminating compounds, some flavonoids seem to have good taxonomic value for identifying geographic races. This is the case of

kaempferol in Maritime pine (Idrissi-Hassani and Lebreton 1992) and for prodelphinidin, procyanidin and quercetin in Scots pine (Lebreton et al. 1991; see Table 1).

Studies on intraspecific genetic variation using enzyme gene markers

Studies utilizing enzyme gene markers quantify genetic variation at specified gene loci according to a variety of measures. There are varying concepts and overlapping definitions especially with respect to the terms differentiation, diversity and heterozygosity (Gregorius 1978, 1987; Müller-Starck and Gregorius 1986). When the term heterozygosity is used, most investigators mean actual (observed) heterozygosity, H_a , or expected heterozygosity, H_e (Nei 1973), which is in reality a measure of genetic diversity. The conditional heterozygosity, H_c (Gregorius et al. 1986), is independent of underlying allele frequencies, but is not yet in general use. Tables 2 and 3 briefly characterize degrees of intrapopulational variation by means of a compilation of the average numbers of alleles per locus, A_L , and the heterozygosities H_a and H_e respectively. The most frequently employed measure for interpopulational variation is G_{ST} (Nei 1973), which is equivalent to F_{ST} (Wright 1943, 1951). Recent studies also refer to the subpopulation differentiation, δ (Gregorius and Roberds 1986) which measures for each population its genetic distance from the remaining populations (lumped together). Additional comments in Tables 2 and 3 briefly summarize main conclusion from the respective studies.

The investigations summarized in Tables 2 and 3 reveal considerable variation among species and among studies within species in observed patterns of genetic diversity within and between populations. In the next section, an attempt is made to describe and classify possible causes for this heterogeneity of results.

Causes for heterogeneity in intra- and interpopulational variation as inferred from enzyme gene markers

Specific features of tree species

European forest tree species can be classified as follows:

- (a) Species with large geographic ranges such as *Picea abies*, *Pinus sylvestris* or *Fagus sylvatica* tend to show little genetic differentiation among populations within regions, but greater differentiation among populations derived from different glacial refugia (continuous species).

Table 2. Survey of genetic variation in European conifers based on isoenzymes

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A _L	H (%)	G _{ST} (%)	Main conclusions about intra- and/or interpopulational genetic variation
<i>Abies alba</i> Mill.							
Bergmann and Kownatzki 1988	45 ⁽¹⁾	25 ⁺	5	1.7			Great allelic differentiation among pop. (Europe)
Bergmann et al. 1990	45 ⁽¹⁾	25 ⁺ #	10	1.8			Variation in diversity level and allelic differentiation among pop. (Europe)
Kormuřák et al. 1982	4	22 [#]	9	3.3	56.3 ^(a)		Great intrapop. variation, small interpop. differentiation (Slovakia)
Kormuřák 1988	7	29 [#]	5		43.1 ^(a)		Great allelic variation between two regions (Slovakia)
Mejnartowicz 1980	5	>25 ⁺	5	4.7	41.6 ^(e)		Great intrapop., moderate interpop. differentiation (Poland)
Schröder 1989	43	10–50 ⁺	4	2.2			Distinct differentiation among regions (Germany)
<i>Larix decidua</i> Mill.							
Lewandowski and Mejnartowicz 1992	11	100 ⁺	18	1.9	16.3 ^(e)	2.6	Relatively little differentiation among pop. (Poland)
<i>Picea abies</i> (L.) Karst.							
Bergmann 1974	9	200 ⁺	4	2.7		4.0	Great differentiation only between pop. in Central Europe and Scandinavia
Bergmann 1975	15	200 ⁺	6	2.6			Great differentiation between northern, central and southern European pop.
Bergmann and Gregorius 1979	21	200 ⁺	7	2.6	41.1 ^(e)		Differences in intrapop. variat. between marginal and central pop. (Europe)

Table 2. (Continued)

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A_L	H (%)	G_{ST} (%)	Main conclusions about intra- and/or interpopulational genetic variation
Bergmann 1983	38	200 ⁺	3				Distinct differentiation between pop. based on private alleles (Central Europe and Scandinavia)
Giannini et al. 1991	9	150 ⁺	21	1.8	16.5 ^(e)	4.2	Minor polymorphism; small interpop. variation (north. Italy)
Konnert and Franke 1990	39	12–45 [*]	11	2.2			Interpop. variation between indigenous and artificial pop. (South. Germany)
Lagercrantz and Ryman 1990	70	28–51 [*]	22	1.6	11.5 ^(a)	5.2	Rel. great intra- and rel. small interpop. variation; diversity differences between pop. (Northeast. and Central Europe)
Lundkvist and Rudin 1977	11	35–80 [*]	4	4.3	35.8 ^(e)	2.0	Small interpopul. variation among populations (Sweden)
Lundkvist 1979	4	49–64 [*]	11	3.8	36.0 ^(a)	3.0	Small interpopul. variation among populations (Sweden)
Muona et al. 1990	2	23 [*]	14	2.7	20.0 ^(e)	12.0	Rel. great intrapop. variation and clear differentiation between pop. (Finland, Slovakia)
Stutz 1990	19	40 [*]	6			2.5	Certain differentiation among pop.
Tigerstedt 1973	2	45 [*]	4	2.5	43.0 ^(a)		Rel. great intrapop. variation in marginal and central pop. (Finland)
Tigerstedt 1979	10	18–107 [*]	6			5.0	No differences in intrapop. variation among pop.; higher homozygosity at the species margin
<i>Pinus cembra</i> L.							
Krutovskii and Politov 1991 ²⁾	1	16 [*]	19	1.5	12.8 ^(a) 10.9 ^(e)		Very small intrapop. variation (Siberia)

Table 2. (Continued)

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A _L	H (%)	G _{ST} (%)	Main conclusions about intra- and/or interpopulational genetic variation
Szmidt 1982	11	22.5*	8	1.9	26.0 ^(e)	32.0 ³⁾	Very large interpop. variation among European pop.
<i>Pinus halepensis</i> Mill.							
Loukas et al. 1983	3	16–83*	10	2.1	17.1 ^(e)	1.3	Great intrapop. variation and very small interpop. variation
Schiller et al. 1986	19	75 ⁺	30	1.2	4.0 ^(e)		Small intrapop. variation; greater differentiation between two races
<i>Pinus leucodermis</i> Ait.							
Morgante and Vendramin 1990	5 2	23* 145 ⁺	23 23	1.6 1.4	12.4 ^(e) 11.0 ^(e)	4.0	Little intra- and interpop. variation (Italy (5), Greece (2))
<i>Pinus nigra</i> Arnold							
Bonnet-Masimbert and Bikay-Bikay 1978	40	125 ⁺	4	2.4		9.8	Differentiation among the five subspec. in mediterranean area
Fineschi 1984	11	64 ⁺	2	2.5			Great differentiation among geographical groups of pop. (Italy)
Nikolić and Tucić 1983	28	14–72+*	4	3.0	27.2 ^(e)	13.5	Great intra- and rel. small interpop. variation; differentiation between subspecies
<i>Pinus pumila</i> (Pall.) Regel							
Krutovskii and Politov 1991 ²⁾	3	56*	17	2.3	24.7 ^(a) 24.8 ^(e)		Rel. large intra- and interpop. variation (Siberia)
<i>Pinus sibirica</i> Du Tour							
Krutovskii et al. 1989	9	37*	14	1.6	16.3 ^(a)	1.6	Little interpop. variation (Eastern Siberia)

Table 2. (Continued)

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A_L	H (%)	G_{ST} (%)	Main conclusions about intra- and/or interpopulational genetic variation
<i>Pinus sylvestris</i> L.							
Gullberg et al. 1982	3	45*	9	2.9	29.7 ^(a) 30.3 ^(e)	1.0	Moderate genetic variation among adjacent pop.
Gullberg et al. 1985	9	60*	11	2.9		2.0	Great intra- and little interpop. variation (Sweden)
Krzakowa 1982 ⁴⁾	8	32*	6				Differentiation between north. and south. pop. (Poland)
Mejnartowicz 1979	19	30*	3	3.9	38.6 ^(a)	16.0 ³⁾	Very large intra- and interpop. variation (Poland)
Mejnartowicz and Bergmann 1985	9	17.5*	9	2.6	33.5 ^(e)		Great intra- and little interpop. variation (Poland)
Mejnartowicz and Palowski (1989)	6	25*	8	3.3	30.7 ^(a) 37.5 ^(e)	7.6	Great intra- and rel. little interpop. variation (Poland)
Müller-Starck 1987, Müller-Starck and Gregorius 1986	9	120*	10	3.1	26.8 ^(a)	2.0	Great intra- and little interpop. variation (Bavaria)
Muona and Szmidi 1985	3	133*	14	3.0	25–30 ^(e)	0.6	Little interpop. variation (Northern Sweden)
Prus-Głowacki (pers. comm.)	17	30*	8	2.8	35.9 ^(a)		Great intra- and interpop. variation (European habitat)
Rudin et al. 1974	3	207*	3	4.3		3.0 ³⁾	Great intra- and little interpop. variation (Sweden)

+ Seed lot (macrogametophyte)

1) Populations in common

* Seed lot (embryo)

2) See also Krutovskii et al. 1990

* Adult trees

3) Loc. cit. Gullberg et al. 1985

4) See also Krzakowa and Szweykowski (1979)

A_L stands for "average number of alleles per locus", H for "average heterozygosity per population" (index (a) indicates "actual", index (e) "expected" heterozygosity), G_{ST} for "proportion of total diversity among populations", and pop. for "population(s)" (see text for further explanation).

Table 3. Survey of genetic variation in European angiosperm tree species based on isoenzymes.

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A_L	H (%)	G_{ST} (%)	Main conclusion about intra- and/or interpopulational genetic variation
<i>Castanea sativa</i> Mill.							
Fineschi et al. 1990	13	101*	8	2.1			Differentiation between north. and south. pop. (Italy)
Pigliucci et al. 1990	18	16*	15	1.7	24.0 ^(a)	10.0	Little intrapop. variation; clinal variation suggested (Italy)
Villani et al. 1991a	15	25*	13	1.6	21.0 ^(e)	8.7	Rel. great interpop. variation; no geographical trends (Italy)
Villani et al. 1991b	13	29*	16	2.3	27.2 ^(a)	16.7	Clear differentiation between eastern and west. pop. (Turkey)
<i>Fagus sylvatica</i> L.							
Barrière et al. 1984 ²⁾	210 ¹⁾	50*	3	2.3			Differentiation among geographical groups of pop. (Europe)
Comps et al. 1987	104 ¹⁾	50*	4	2.2			Differentiation through the Atlantic range
Comps et al. 1990	140 ¹⁾	50*	6	2.3	28.9 ^(a)	5.4	Differentiation between continental and Mediterr. regions
Comps et al. 1991	35 ¹⁾	50*	6	2.2		3.6–5.2	Differentiation between low- and highland pop. (Croatia)
Felber and Thiebaut 1984	41 ¹⁾	50*	2	2.5			Differentiation among geographical groups of pop. (Central Europe)
Kim 1980, 1985	2	596*	1	4.0	31.2 ^(a)		Great intra- and interpop. variation (Germany, Rumania)
Merzeau et al. 1989	2	12.5 ^{#3)}	4 (2)	2.3			Great intrapop. variation in pollen (South. France)
Müller-Starck 1985, 1989	6	96*	16	2.6	25.1 ^(a)		Great intrapop. variation (Germany)

Table 3. (Continued)

Species and reference	No. of pop.	Indiv. per pop.	No. of loci	A _L	H (%)	G _{ST} (%)	Main conclusion about intra- and/or interpopulational genetic variation
Müller-Starck and Ziehe 1991	5	172*	13	2.7	22.2 ^(a)	1.6 4.5 ⁽⁴⁾	Great intra- and small interpop. variation (Germany)
Thiebaut et al. 1982	13 ¹⁾	50 [#]	2	2.5			Intrapop. variation greater under marginal environments (South. France)
<i>Ficus carica</i>							
Valizadeh 1977	4	90 [#]	2	2.7			Deficiency of heterozygotes, small variation (South. France)
<i>Quercus ilex</i> L.							
Lumaret et al. 1991	37	35 [#]	3	2.8		7.3	Differentiation among North African and South. European pop.
<i>Quercus petraea</i> Liebl.							
Zanetto and Kremer 1991	32	120*	15	3.2	27.5 ^(e)	1.7	Large intrapop. and small interpop. variation (West. Europe)
Müller-Starck and Ziehe 1991	5	155 ⁺	13	3.1	21.9 ^(a)	3.6 8.5 ⁽⁴⁾	Large intrapop. and moderate interpop. variation (Germany)
<i>Quercus robur</i> L.							
Müller-Starck and Ziehe 1991	5	166 ⁺	13	3.2	21.3 ^(a)	1.8 5.5 ⁽⁴⁾	Large intrapop. and small interpop. variation (Germany)

* Seeds

+ 2-year old plants

* Adult trees

1) Partially populations in common

2) See also Cuguen et al. 1985, 1988

3) Pollen contribution to seed lots from single trees

4) Subpop. differentiation δ (Gregorius and Roberds 1986)

A_L stands for "average number of alleles per locus", H for "average heterozygosity per population" (index (a) indicates "actual", index (e) "expected heterozygosity), G_{ST} for "proportion of total diversity among populations", and pop. for "population(s)" (see text for further explanation)

- (b) Species with large geographic ranges, but subdivided into different subspecies (races) such as *Pinus nigra*, *Pinus halepensis* or *Larix decidua*, reveal little interpopulational variation within subspecies, but great differentiation among subspecies (disjunct species).
- (c) Species with small and geographically disjunct ranges like *Abies alba* or *Pinus cembra* tend to show a great interpopulational differentiation and moderate intrapopulational genetic variation (endemic species).
- (d) Species with extremely small geographic ranges like *Pinus pumila* reveal relatively great interpopulational differentiation (relic species). Further studies may help to find out why this does not seem to hold for another species of this type, *P. leucodermis*.

Heterogeneity of population types and environments

Various types of populations may be sampled, mostly indigenous ones, but within the same species introduced populations or mixtures of both may also be sampled. Populations may differ in amounts of genetic variation because some may have gone through historical bottlenecks in population sizes, others not. It cannot be excluded that different silvicultural management affect the genetic structures of the respective populations. It is self-evident that environmental conditions can differ substantially even within small areas. The great natural micro- and macro-habitat variation always will complicate standardization of genetic inventories.

Furthermore, intra-specific heterogeneity in genetic variation within populations can be a consequence of sampling at different census stages, biased sampling, or small sample sizes. Due to varying reproduction, effective neighborhood sizes, fertility and/or viability selection (e.g. against inbreds), sampling at the seed stage or subsequent stages may not be representative of the genetic structure in the parental population. Even within the same age class, sampling of only flowering trees will not necessarily represent the entire population. As can be seen from Tables 2 and 3, sample sizes varied considerably among the studies. This is true for the number of investigated populations per region, as well as the number of individuals per population.

Methodical pitfalls

(a) *Choice of enzyme systems*

Heterogeneity in isoenzyme data for the same tree species can result when the numbers and types of enzyme gene loci differ among studies. In the early days of isoenzyme surveys in tree species, enzyme systems such as

peroxidases, esterases, phosphatases and aminopeptidases were studied, which later turned out to be very polymorphic. Hence, the respective estimates of the variation measures were relatively high compared to later studies, in which many other — partly invariant — enzyme systems, such as aminotransferases, dehydrogenases and isomerases, were included.

(b) *Different interpretations of genetic control of isoenzymes*

Differences in diversity estimates among studies can also occur if the number of loci controlling an enzyme is interpreted differently by different investigators of the same tree species. For example, the GOT system in Scots pine is assumed to be encoded by two, three or five gene loci depending on the results of different research groups (see Szmidt 1980). Estimates of the genetic diversity are likely to be much greater if isoenzymes, actually under the control of multiple loci, are assumed to be controlled by a single locus. Therefore it is always necessary to identify the correct number of gene loci underlying enzyme polymorphisms prior to estimating genetic variability in populations. This includes a check on possible ontogenetic and/or environmental instabilities in the expression of enzyme systems on zymograms (e.g., Bergmann et al. 1989).

(c) *Inclusion of monomorphic gene loci*

Some investigators include monomorphic loci in their estimates of genetic variation while others do not. In one case, these estimates will be biased upwards, the other, downwards. The problem is that many investigators do not communicate whether or not monomorphic loci were excluded.

If the extent of intra- and interpopulational genetic variation should be compared in studies on geographical variation, it is not advisable to include monomorphic enzyme loci in samples of enzyme loci: patterns of variation will be the same, but the absolute magnitude of differences will be less when all loci are included. In particular, the “averaging effect” in the calculation of measures of genetic distance and F_{ST} or G_{ST} values would bias the extent of differentiation, if the proportion of monomorphic loci among the loci used in the study is relatively high.

Concluding remarks

In spite of the great variety of environmental conditions and forest stand characteristics in different studies, general tendencies are observed in

genetic patterns of geographic variation related to species distribution, i.e., continuous, disjunct, endemic, and relic.

Methodological problems are evident which concern the choice of population and of samples per population, the choice of enzyme systems and loci, the methods used to quantify genetic variation, and in several cases also the verification of the genetic control and inheritance of markers. Generally, it appears that the quantification of interpopulational genetic variation suffers from a lack of appropriate measures: The widely applied F_{ST} or G_{ST} values represent in reality fixation indices which therefore cannot be considered as the most favourable condition for the measurement of genetic differentiation among populations. Furthermore, the partition of a total genetic variation into an intra- and interpopulational additive component appears as a concept which needs to be extended or restated in order to improve the accuracy of measures of genetic variation among populations (for suggestions see Gregorius 1988).

Although there is an increase in forest genetics research in Europe, the majority of published results still refer to coniferous and not to angiosperm tree species. While there is increasing work on *Fagus sylvatica*, there are no studies on *Acer*, *Fraxinus*, *Tilia*, or *Ulmus* species. The choice of which forest tree species to study seems to depend primarily on their economic importance, and not on their ecological significance. Studies on ecologically important species are especially needed in Central Europe, where forest tree populations are severely threatened by air-pollution.

It appears that ecological genetic research in forestry has to be intensified in nearly all European countries. Moreover, present and future information on genetic variation in European tree species needs to be incorporated into strategies for the preservation of genetic resources so that adaptability of forest tree populations to changing environments can be maintained.

Acknowledgments

We are grateful to many colleagues who provided reprints and in some cases also unpublished data. At the same time we apologize that not all contributions could be cited in this review. We greatly appreciate the help of H. Glock, M. Günther, and A. Uteau in the preparation of the manuscript. Finally, we wish to thank unknown referees for very helpful comments and suggestions.

References

- Arbez, M., Bernard-Dagan, C. and Fillon, C. 1974. Variabilité intraspécifique des monoterpènes de *Pinus nigra*. Bilan des premiers résultats. Ann. Sci. For. 31(1): 57–70.
- Baradat, Ph., Bernard-Dagan, C., Fillon, C. and Marpeau, A. 1972. Les terpènes du Pin maritime: aspects biologiques et génétiques. 2. Hérité de la teneur en monoterpènes. Ann. Sci. For. 29(3): 507–334.
- Baradat, Ph., Bernard-Dagan, C. and Pauly, G. 1974. Les terpènes du Pin maritime: aspects biologiques et génétiques. 3. Hérité de la teneur en myrcène. Ann. Sci. For. 32(1): 29–54.
- Baradat, Ph., Bernard-Dagan, C. and Marpeau, A. 1979. Variation of terpenes within and between populations of Maritime pine, pp. 151–168. In: Rudin, D. (Ed) Proceedings of the IUFRO Conference on Biochemical Genetics of Forest Trees, Umeå, Sweden, 1978.
- Baradat, Ph. and Yazdani, R. 1988. Stability of genotypic expression for monoterpene synthesis in clones of Scots pine growing in different sites. Scand. J. Forest Res. 3: 25–36.
- Baradat, Ph. and Marpeau, A. 1991 a. Reconstitution of differentiation of Maritime pine on the basis of terpenic data. (submitted to Ann. Sci. For.)
- Baradat, Ph. and Marpeau, A. 1991 b. Genetic structure of natural stands of Maritime pine on the basis of terpenic data. (submitted to Ann. Sci. For.)
- Baradat, Ph., Lambardi, M. and Michelozzi, M. 1989. Terpene composition for four Italian provenances of Aleppo pine. J. Genet. Breeding 43: 195–200.
- Baradat, Ph., Barhman, N. and Petit, R. 1991. Comparison of relationships between geographical races of Maritime pine based on three kinds of gene markers: terpenes, isozymes and total proteins. (submitted to Theor. Appl. Genetics).
- Barrière, G., Comps, B., Cuguen, J., N'Tsiba, F. and Thiebaut, B. 1984. The genetical ecological variability of beech (*Fagus sylvatica* L.) in Europe — an allozymatic study: genetic isolations of beechwoods, pp. 24–50. In: Proceedings of the First Symposium on Improvement and Silviculture of Beech, Grosshansdorf 1984, IUFRO Project Group P1 10–00.
- Bergmann, F. 1974. Genetischer Abstand zwischen Populationen. II. Die Bestimmung des genetischen Abstands zwischen europäischen Fichtenpopulationen (*Picea abies*) auf der Basis von Isoenzym-Genhäufigkeiten. Silvae Genetica 23: 28–32.
- Bergmann, F. 1975. Herkunfts-Identifizierung von Forstsaatgut auf der Basis von Isoenzym-Genhäufigkeiten. All. Forst- u. Jagdzeitung 146(10): 191–195.
- Bergmann, F. 1983. Ein besonderer Fall geographischer Variation an zwei Enzym-Genloci der Fichte (*Picea abies*), pp. 8–24. In: Verhandlungen 3. Arbeitstagung: FORUM Genetik-Wald-Forstwirtschaft. Universität Göttingen.
- Bergmann, F. and Gregorius, H.-R. 1979. Comparison of the genetic diversities of various populations of Norway spruce (*Picea abies*), pp. 99–107. In: Rudin, D. (Ed) Proceedings of the IUFRO Conference on Biochemical Genetics of Forest Trees. Umeå, Sweden, 1978.
- Bergmann, F. and Kownatzki, D. 1988. The genetic variation pattern of silver fir (*Abies alba*) in Europe monitored from enzyme gene loci, pp. 21–26. In: Paule, L. and Korpel, Š. (Eds) 5. IUFRO-Tannensymposium. VŠLD, Zvolen, ČFSR.
- Bergmann, F., Gregorius, H.-R. and Scholz, F. 1989. Isoenzymes, indicators of environmental impacts on plants or environmentally stable gene markers? pp. 17–25. In: Scholz, F., Gregorius, H.-R. and Rudin, D. (Eds) Genetic Effects of Air Pollutants in Forest Tree Populations. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Bergmann, F., Gregorius, H.-R. and Larsen, J. B. 1990. Levels of genetic variation in

- European silver fir (*Abies alba*) — Are they related to the species decline? *Genetica* 82: 1—10.
- Bernard-Dagan, C., and Baradat, Ph. 1977. Utilisation des terpènes comme outil en génétique forestière. Proceeding of EEC-Symposium on Forest Tree Biochemistry, Brux. 25—27, January 1977: 109—132.
- Bernard-Dagan, C., Fillon, C., Marpeau, A. and Pauly, G. 1982. Les terpènes du Pin maritime: aspects biologiques et génétiques. 2. Hérité de la teneur en monoterpènes. *Ann. Sci. For.* 29: 307—334.
- Bernard-Dagan, C., Pauly, G., Marpeau, A., Gleizes, M., Carde, J. P. and Baradat, Ph. 1982. Control and compartmentation of terpene biosynthesis in leaves of *Pinus pinaster*. *Physiologie Vegetale* 20(4): 775—795.
- Birks, J. S. and Kanowski, J. S. 1988. Interpretation of the composition of coniferous resin. *Silvae Genetica* 37(1): 29—39.
- Bonnet-Masimbert, M. and Bikay-Bikay, V. 1978. Variabilité intraspécifique des isozymes de la glutamate-oxaloacetate-transaminase chez *Pinus nigra* Arnold. Intérêt pour la taxonomie des sous especès. *Silvae Genetica* 27: 71—79.
- Comps, B., Barrière, G., Merzeau, D. and Letouzey J. 1987. La variabilité alloenzymatique des hêtraies dans les sous-domaines médio- et eu-atlantiques d'Europe. *Canad. Journ. For. Res.* 17(7): 1043—1049.
- Comps, B., Thiebaut, B., Paule, L., Merzeau, D. and Letouzey, J. 1990. Allozyme variability in beechwoods (*Fagus sylvatica* L.) over central Europe: spatial differentiation among and within populations. *Heredity* 65: 407—417.
- Comps, B., Thiebaut, B., Sugar, I., Trinajstic, I. and Plazibat, M. 1991. Genetic variability of the croatian beech stands (*Fagus sylvatica* L.): Spatial differentiation with environment. *Ann. des Sci. For.* 48:15—28.
- Cori, O. M. 1983. Enzymic aspects of the biosynthesis of monoterpenes in plants. *Phytochemistry* 22: 331—341.
- Cuguen, J., Thiebaut, B., N'Tsiba, F. and Barrière, G. 1985. Enzymatic variability of beech stands (*Fagus sylvatica* L.) on three scales in Europe: evolutionary mechanisms, pp. 17—39. In: Jacquart, P., Heim, G. and Antonovics, J. (Eds) *Genetic Differentiation and Dispersal in Plants*. NATO ASI Series, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Cuguen, J., Merzeau, D. and Thiebaut, B. 1988. Genetic structure of the european beech stands (*Fagus sylvatica* L.): F-statistics and importance of mating system characteristics in their evolution. *Heredity* 60: 91—100.
- Dupouey, J. L., Fougere, V. and Kremer, A. 1990. Variabilité génétique des chênes sessile et pédonculé estimée à l'aide de marqueur morphologique moléculaire. *Revue Forestière Française* 42: 198—204.
- Esteban, I., Bergmann, F., Gregorius H.-R. and Huhtinen, O. 1976. Composition and Genetics of monoterpenes from cortical oleoresin of Norway spruce and their significance for clone identification. *Silvae Genetica* 25(2): 59—66.
- Fady, B. 1991. Genetic variability of the Greek fir. (submitted to *Ann. Sci. For.*)
- Felber, F. and Thiebaut, B. 1984. Etude préliminaire sur le polymorphisme enzymatique du hêtre, *Fagus sylvatica* L.: variabilité génétique de deux systèmes de peroxydases en relation avec les conditions écologiques. *Acta Oecologica. Oecol. Plant.* 5: 133—150.
- Fineschi, S. 1984. Determination of the origin of an isolated group of trees of *Pinus nigra* through enzyme gene markers. *Silvae Genetica* 33(4—5): 169—172.
- Fineschi, S. and Grossoni, P. 1981. Contenuto in monoterpene di oleoresine xilematiche in provenienze diverse di Pino laricio. *Italia forestale montana* 36(1): 232—259.
- Fineschi, S., Malvolti, E., Morgante, M., Vendramin, G. and Paciucci, M. 1990. Erhaltung von Genressourcen bei der Kastanie (*Castanea sativa* Mill.), pp. 155—164. In: Hattemer,

- H. H. (Ed) Erhaltung forstlicher Genressourcen. Schriften aus der Forstl. Fak. d. Univ. Göttingen und der Nds. Forstl. Vers. Anst. 98, J.D. Sauerländer's Verlag, Frankfurt a.M.
- Forrest, G. I. 1979. Monoterpenic variation in lodgepole pine and Scots pine, pp. 136–150. In: Rudin, D. (Ed) Proceedings of the IUFRO Conference on Biochemical Genetics of Forest Trees. Umeå. Sweden 1978.
- Forrest, G. I. 1990. Genotypic variation among native Scots pine populations in Scotland based on monoterpene analysis. *Forestry* 53: 101–128.
- Gansel, C. E. and Squillace, A. E. 1976. Geographic variation in cortical oleoresin of Slash pine. *Silvae Genetica* 25(5–6): 150–154.
- Gerber, S., Arbez, A., Baradat, Ph. and Marpeau, A. 1991. Geographical variation and terpenic composition of *Pinus nigra*. (submitted to *Silvae Genetica*)
- Giannini, R., Vendramin, G. and Morgante, M. 1991. Allozyme variation in Italian populations of *Picea abies* (L.) Karst. *Silvae Genetica* 40(3–4): 160–166.
- Gillet, E. 1990. Probleme der genetischen Analyse von Restriktionsfragment-Längen-Polymorphismen (RFLP), pp. 272–277. In: Marker und Genidentifizierung – Methoden und Ergebnisse. Tagungsberichte Arbeitsgemeinschaft Pflanzenzüchtung 8/9. März 1990, Hannover, Vorträge für Pflanzenzüchtung, H. 18.
- Gregorius, H.-R. 1978. The concept of genetic diversity and its formal relationship to heterozygosity and genetic distance. *Math. Biosci.* 41: 253–271.
- Gregorius, H.-R. 1987. The relationship between the concepts of genetic diversity and differentiation. *Theor. Appl. Genet.* 74: 397–401.
- Gregorius, H.-R. 1988. The meaning of genetic variation within and between subpopulations. *Theor. Appl. Genet.* 76: 947–951.
- Gregorius, H.-R. and Roberds, J. H. 1986. Measurement of genetical differentiation among subpopulations. *Theor. Appl. Genet.* 71: 826–834.
- Gregorius, H.-R., Krauhausen, J. and Müller-Starck, G. 1986. Spatial and temporal genetic differentiation among the seed in a stand of *Fagus sylvatica* L. *Heredity* 57: 255–262.
- Gullberg, U., Yazdani, R. and Rudin, D. 1982. Genetic differentiation between adjacent populations of *Pinus sylvestris*. *Silva Fennica* 16(2): 205–214.
- Gullberg, U., Yazdani, R., Rudin, D. and Ryman, N. 1985. Allozyme Variation in Scots pine (*Pinus sylvestris* L.) in Sweden. *Silvae Genetica* 34(6): 193–201.
- Idrissi-Hassani, M. and Lebreton, P. 1992. Les Flavonoïdes du Pin maritime: une approche chimiotaxinomique. *Forêt méditerranéenne* 13(1): 3–8.
- Kim, Z. S. 1980. Veränderungen der genetischen Struktur von Buchenpopulationen durch Viabilitätsselektion im Keimlingsstadium, pp. 1–88. Göttingen Res. Notes in Forest Genetics 3.
- Kim, Z. S. 1985. Viability selection at an allozyme locus during development in European beech (*Fagus sylvatica* L.) *Silvae Genetica* 34(4–5): 181–186.
- Konnert, M. and Franke, F. 1990. Nachkommenschaftsprüfung und Generhaltung von Fichtenbeständen im Schwarzwald, pp. 165–177. In: Hattemer, H. H. (Ed) Erhaltung forstlicher Genressourcen. Schriften aus der Forstl. Fak. d. Univ. Göttingen und der Nds. Forstl. Vers. Anst. J. D. Sauerländer's Verlag, Frankfurt a.M.
- Kormuťák, A. 1988. Isozyme polymorphism in Slovak populations of silver fir (*Abies alba* Mill.), pp. 27–39. In: Paule, L. and Korpel', Š. (Eds) 5. IUFRO-Tannensymposium. VŠLD, Zvolen, ČFSR.
- Kormuťák, A., Benčáň, F., Rudin, D. and Seyedyazdani, R. 1982. Isoenzyme variation in the four Slovakian populations of *Abies alba* Mill. *Biológia (Bratislava)* 37: 433–440.
- Krutovskii, K. V., Politov, D. V., Altukhov, Y. P., Milutin, L. I., Kuznetsova, G. V., Iroshnikov, Vorobyev, V. N. and Vorobyeva, N. A. 1989. Genetic variability in Siberian stone pine, *Pinus sibirica* in Tour. IV. Genetic diversity and amount of genetic differentiation between natural populations. *Genetika* 25(11): 2009–2032.

- Krutovskii, K. V., Politov, D. V. and Altukhov, Y. P. 1990. Genetic differentiation by isozyme loci between Eurasian cedar pines. *Genetika* 26(4): 694–707.
- Krutovskii, K. V. and Politov, D. V. 1991. Study of intra- and interspecific genetic differentiation of Eurasian cedar pines (*Pinus cembra*) using isozyme loci and multi-dimensional analysis. In: *Molecular Mechanisms of Genetic Processes*, Nauka Publishers, Moscow. (in press)
- Krzakowa, M. and Szweykowski, J. 1979. Variation of 6-PGD in the populations of Polish Scots pine (*Pinus sylvestris*), pp. 86–98. In: Rudin, D. (Ed) *Proceedings of the Conference on Biochemical Genetics of Forest Trees*. Umeå, Sweden 1978.
- Krzakowa, M. 1982. Genetic differentiation of Scots pine populations. 1. Genotypes. *Silva Fennica* 16(2): 200–205.
- Lagercrantz, U. and Ryman, N. 1990. Genetic structure of Norway spruce (*Picea abies*): Concordance of morphological and allozymic variation. *Evolution* 44: 38–53.
- Lebreton, P., Laracine-Pittet, C., Bayet, C. and Lauranson, J. 1990. Variabilité des polyphénoliques et systématique du Pin sylvestre. *Ann. Sci. For.* 47: 117–130.
- Lewandowski, A. and Mejnartowicz, L. 1992. Levels and patterns of allozyme variation in some European larch (*Larix decidua* Mill.) populations. *Hereditas* (in press).
- Li, P. and Adams, W. T. 1989. Range — wide patterns of allozyme variation in Douglas-fir. *Can. J. For. Res.* 19: 149–161.
- Loukas, M., Vergini, Y. and Krimbas, C. B. 1983. Isozyme variations and heterozygosity in *Pinus halepensis* L. *Biochemical Genetics* 21(5–6): 497–509.
- Lumaret, R., Yacine, A., Berrod, A., Romane, F. and T. X. Li. 1991. Mating system and genetic diversity in holm oak (*Quercus ilex* L., *Fagaceae*), pp. 149–153. In: *Biochemical markers in the population genetics of forest trees*. Fineschi, S., Malvolti, M. E., Cannata, F. and Hattemer, H. H. (Eds) SPB Academic Publishing by, The Hague, The Netherlands.
- Lundkvist, K. 1979. Allozyme frequency distributions in four Swedish populations of Norway spruce (*Picea abies* K.). *Hereditas* 90: 127–143.
- Lundkvist, K. and Rudin, D. 1977. Genetic variation in eleven populations of *Picea abies* as determined by isozyme analysis. *Hereditas* 85: 67–74.
- Marpeau, A. and Baradat, Ph. 1975. Les terpènes du Pin maritime: aspects biologiques et génétiques. 4. Hérité de la teneur en deux sesquiterpènes: le longifolène le caryophyllène. *Ann. Sci. For.* 32 (4): 185–204.
- Marpeau, A., Baradat, Ph. and Bernard-Dagan, C. 1983. Les terpènes du Pin maritime: aspects biologiques et génétiques. 5. Hérité de la teneur en limonène. *Ann. Sci. For.* 40(2): 197–216.
- Mejnartowicz, L. 1979. Genetic variation in some isoenzyme loci in Scots pine (*Pinus sylvestris* L.) populations. *Arboretum Kornickie* 24: 91–104.
- Mejnartowicz, L. 1980. Polymorphism at the LAP and GOT loci in *Abies alba* Mill. populations. *Bulletin de l'Académie Polonaise des Sciences. Série des Sciences Biologiques*. C1. V., 27(12): 1063–1070.
- Mejnartowicz, L. and Bergmann, F. 1985. Genetic differentiation among Scots pine populations from the lowlands and the mountains in Poland, pp. 253–266. In: Gregorius, H.-R. (Ed) *Population Genetics in Forestry. Lecture Notes in Biomathematics*, 60. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Mejnartowicz, L. and Palowski, B. 1989. Studies of Scots pine populations in polluted and clean areas, pp. 115–125. In: Scholz, F., Gregorius, H.-R. and Rudin, D. (Eds) *Genetic Effects of Air Pollutants in Forest Tree Populations*. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Merzeau, D., Di Giusto, F., Comps, B., Thiebaut, B., Letousey, J. and Cuguen, J. 1989.

- Genetic control of isozyme systems and heterogeneity of pollen contribution in beech (*Fagus sylvatica* L.). *Silvae Genetica* 38(5–6): 195–201.
- Moreau, M. and Pastuszka P. 1991. Contribution a l'étude de la structure génétique d'un peuplement de sapin pectiné de Basse Vosges. (submitted to *Ann. des Sci. For.*)
- Morgante, M. and Vendramin, G. 1990. Analyse von Genressourcen von *Pinus leucodermis* Ant., einer Art mit kleinem Verbreitungsgebiet, pp. 87–98. In: Hattemer, H. H. (Ed) Erhaltung forstlicher Genressourcen. Schriften aus der Forstl. Fak. d. Univ. Göttingen und der Nds. Forstl. Vers. Anst. J.D. Sauerländer's Verlag, Frankfurt a.M.
- Müller-Starck, G. 1985. Genetic differences between "tolerant" and "sensitive" beeches (*Fagus sylvatica* L.) in an environmentally stressed adult forest stand. *Silvae Genetica* 34(6): 241–247.
- Müller-Starck, G. 1987. Genetic differentiation among seed samples provenances of *Pinus sylvestris* L. *Silvae Genetica* 36(5–6): 232–238.
- Müller-Starck, G. 1989. Genetic implications of environmental stress in adult forest stands of *Fagus sylvatica* L., pp. 127–142. In: Scholz, F, Gregorius, H.-R. and Rudin, D. (Eds) Genetic Effects of Air Pollutants in Forest Tree Populations. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo.
- Müller-Starck, G. and Gregorius, H.-R. 1986. Monitoring genetic variation in forest tree populations. Proc. 18th IUFRO World Congress, Ljubljana, Yugoslavia, 1986, Div. 2, Vol. II., 589–599.
- Müller-Starck, G. and Ziehe, M. 1991. Genetic variation in populations of *Fagus sylvatica*, *Quercus robur*, and *Q. petraea* in Germany, pp. 125–140. In: Müller-Starck, G. and Ziehe, M. (Eds) Genetic variation in European Populations of Forest Trees. Sauerländer's Verlag, Frankfurt a.M.
- Muona, O. and Szmidi, A. E. 1985. A multilocus study of natural populations of *Pinus sylvestris*, pp. 226–240. In: Gregorius, H.-R. (Ed) Population Genetics in Forestry. Lecture Notes in Biomathematics, 60. Springer-Verlag, Berlin. Heidelberg, New York, Tokyo.
- Muona, O., Paule, L., Szmidi A. E. and Kärkkäinen, V. 1990. Mating system analysis in a central and northern European population of *Picea abies*. *Scand. J. For. Res.* 5: 97–102.
- Nei, M. 1973. Analysis of gene diversity in subdivided populations. *Proc. Nat. Acad. Sci. USA* 70(12): 3321–3323.
- Nikolić, D. and Tucić, N. 1983. Isoenzyme variation within and among populations of european Black pine (*Pinus nigra* Arnold) *Silvae Genetica* 32(3–4): 80–89.
- Paule L., Yazdani, R. and Gömöry, D. 1987. Monoterpene composition of silver fir foliar oleoresin, pp. 50–66. In: Paule, L. and Korpel', Š. (Eds) 5. IUFRO-Tannensymposium. VŠLD, Zvolen, ČFSR.
- Pigliucci, M., F. Benedettelli, S. and Villani, 1990. Spatial patterns of genetic variability in Italian chestnut (*Castanea sativa* Mill.). *Can. Journ. Botany.* 68: 1962–1968.
- Prus-Glowacki, W. and Rudin, D. 1981. Short Note: Studies on antigenic proteins of *Pinus sylvestris* from six Swedish provenances — A pilot study. *Silvae Genetica* 30(6): 200–203.
- Prus-Glowacki, W. 1982. Immunochemical methods in analysis of forest tree proteins. *Silva Fennica*, Vol. 16(2): 219–226.
- Prus-Glowacki, W., Szweykowski, J. J. and Nowak, R. 1985. Serotaxonomical investigation of the European pine species. *Silvae Genetica* 34(4–5): 162–170.
- Rudin, D., Erikson, E., Ekberg, I. and Rasmuson, M. 1974. Studies of allele frequency and inbreeding in Scots pine populations by the aid of the isozyme technique. *Silvae Genetica* 23(1–3): 10–13.

- Rudloff E. von. 1973. Geographical variation in the terpene composition of the leaf oil of Douglas-fir. *Pure Appl. Chem.* 34: 401–410.
- Schiller, G., Conkle, M. T. and Grunwald, C. 1986. Local differentiation among mediterranean populations of Aleppo pine in their isoenzymes. *Silvae Genetica* 35(1): 11–19.
- Schiller, G. and Grunwald, C. 1987. Resin monoterpenes in range-wide provenance trials of *Pinus halepensis* in Israel. *Silvae Genetica*. 36(3–4): 109–114.
- Schiller, G. 1990. Variation in resin composition of the Italian cypress (*Cupressus sempervirens*) grown in Israel. *Silvae Genetica* 39(3–4): 89–95.
- Schröder, S. 1989. Die Weißtanne in Süddeutschland: Genetische Variation, Kline, Korrelationen. *Allg. Forst- und Jagdztg.*, 160: 100–104.
- Squillace A. E. 1976. Analysis of monoterpenes of conifers by gas liquid chromatography, pp. 129–157. In: Miksche, J. P. (Ed) *Modern methods in Forest Genetics*. Springer-Verlag, Heidelberg, Berlin, New York, Tokyo.
- Stutz, H. P. 1990. Eigenschaften und Ursachen der genetischen Differenzierung der Fichte im Wallis (Schweiz), pp. 99–114. In: Hattemer, H. H. (Ed) *Erhaltung forstlicher Genressourcen*. Schriften aus der Forstl. Fak. d. Univ. Göttingen und der Nds. forstl. Vers. Anst. J. D. Sauerländer's Verlag, Frankfurt a.M.
- Szmidt, A. 1982. Genetic variation in isolated populations of stone pine (*Pinus cembra*). *Silva Fennica* 16(2): 196–200.
- Szmidt, A. E., El-Kassaby, Y.-A., Sigurgeirsson, A., Alden, T., Lindgren, D. and Hällgren, J.-E. 1988. Classifying seedlots of *Picea sitchensis* and *P. glauca* in zones of introgression using restriction analysis of chloroplast DNA. *Theor. Appl. Genetics* 76: 841–845.
- Szmidt, A. E. 1990. Phylogenetic and applied studies on chloroplast genome in forest conifers. Biochemical markers in the population genetics of forest trees, pp. 185–196. In: Fineschi, S., Malvolti, M. E., Cannata, F. and Hattemer, H. H. (Eds) *Biochemical markers in the population genetics of forest trees*. SPB Academic Publishing bv, The Hague, The Netherlands.
- Thiebaut, B., Lumaret, R. and Vernet, Ph. 1982. The bud enzymes of beech (*Fagus sylvatica* L.). Genetic distinction and analysis of polymorphism in several french populations. *Silvae Genetica* 31(2–3): 51–60.
- Thielges, B. A. 1972. Intraspecific variation in foliage polyphenole of *Pinus* (subsection *sylvestris*). *Silvae Genetica* 21(3–4): 114–119.
- Tigerstedt, P. M. A. 1973. Studies on isozyme variation in marginal and central populations of *Picea abies*. *Hereditas* 75: 47–60.
- Tigerstedt, P. M. A. 1979. Genetic adaptation of plants in the subarctic environment. *Holarctic Ecology* 2: 264–268.
- Tigerstedt P. M. A., Hiltunen, R., Chung, M. S. and Moren, E. 1979. Inheritance and genetic variation of monoterpenes in *Pinus sylvestris*, pp. 29–39. In: Rudin, E. (Ed) *Proceedings of the IUFRO Conference on Biochemical Genetics of Forest Trees*, Umeå, Sweden 1978.
- Valizadeh, M. 1977. Esterase and acid phosphatase polymorphism in the fig tree (*Ficus carica* L.) *Biochemical Genetics* 15: 1037–1048.
- Villani, F., Benedettelli, S., Paciucci, M., Cherubini, M. and Pigliucci, M. 1991a. Genetic variation and differentiation between natural populations of chestnut (*Castanea sativa* Mill.) from Italy, pp. 91–103. In: Fineschi, S., Malvolti, M. E., Cannata, F. and Hattemer, H. H. (Eds) *Biochemical markers in the population genetics of forest trees*. SPB Academic Publishing bv, The Hague, The Netherlands.
- Villani, F., Pugliucci, M., Benedettelli, S. and Cherubini, M. 1991b. Genetic vs. geographical and climatic differentiation of Turkish chestnut. (*Castanea sativa* Mill.) *Heredity* 66: 131–136.

- Wellendorf H. and Kaufmann, U. 1977. This layer chromatography of fluorescent phenolic compounds in needles: A review of current activities in *Picea*, pp. 203–226. In: Proceedings of EEC Symposium on Forest Tree Biochemistry, Bruxelles, Belgium.
- White, E. C. and Nilsson, J. E. 1984. Genetic variation in resin canal frequency and relationships to terpene production in foliage of *Pinus contorta*. *Silvae Genetica* 33(2–3): 79–84.
- Wright, S. 1943. Isolation of distance. *Genetics* 28: 114–138.
- Wright, S. 1951. The genetic structure of populations. *Ann. Eugenics* 15: 323–354.
- Wright, S. 1969. *Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies.* Univ. of Chicago Press, Chicago.
- Yazdani R. and Lebreton, P. 1991. Inheritance pattern of the flavonic compounds in Scots pine. *Silvae Genetica* 40(2): 57–59.
- Yazdani, R., Nilsson, J. E. and Ericsson, T. 1985. Geographical variation in the relative proportion and monoterpenes in cortical oleoresin of *Pinus sylvestris* in Sweden. *Silvae Genetica* 34(6): 201–208.
- Yazdani, R. and Nilsson, J. E. 1986. Cortical monoterpene variation in natural populations of *Pinus sylvestris* in Sweden, *Scand. J. For. Res.* 1: 85–93.
- Yazdani, R., Rudin, R., Aldén, T., Lindgren, L., Harbom, B. and Ljung, K. 1982. Inheritance pattern of five monoterpenes in Scots pine. *Hereditas* 97: 261–272.
- Zanetto, A. and Kremer A. 1991. Allozyme polymorphism of sessile oak populations in western Europe. (submitted to *Ann. Sci. For.*)
- Zavarin E. 1970. Qualitative and quantitative co-occurrence of terpenoids as a tool of elucidation to their biosynthesis. *Phytochemistry* 9: 1049–1963.