

Survey of genetic variation in European tree populations

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Abstract

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The paper reviews the present state of knowledge of genetic variation in the main native European forest trees species. Isozyme tests have already shown that as a group these forest trees are extremely variable both in terms of number of alleles per locus and the level of heterozygosity in populations. The maintenance of high levels of intrapopulation genetic variation in many of these trees is interpreted as a necessary strategy to survive in the heterogeneous environmental conditions that these long-lived plants face. Suggestions are offered how to preserve such vital genetic variation in forest tree populations in face of increasing environmental stresses.

Introduction

Compared to environmental conditions of crops and other economically important plant species, forest environments are extremely heterogeneous in time and in space.

Most forest tree populations can be considered as wild populations which are exposed to highly variable constellations of stress factors. Due to limited efficiency, provisions for plant protection and amelioration of forest sites are rather the exception than the rule. Changes in environmental stress conditions cannot be predicted in long-lived tree populations.

Such environmental heterogeneity severely challenges the ability of forest tree populations to adapt genetically and thus to survive. The adaptive potential of forest tree populations is determined by the realized amount and pattern of genetic variation. Consequently, genetic variation (e.g. heterozygosities, genetic multiplicity, diversity, differentiation) is considered as a parameter of stability of complex forest ecosystems.

The objective of this contribution is to review the present state of knowledge on genetic variation within predominant native European forest tree species and to infer briefly on short comings and research needs.

Materials and methods

The majority of genetic studies on intra- and interpopulational genetic variation employ enzyme gene markers. Molecular genetic markers (RFLP, VNTR, RAPD) imply extremely high information potential but are not yet utilized for large scale routine monitoring of multilocus genotypes of individual trees. Other markers like terpenes (only conifers), polyphenols or immunoproteins show limitations in the scoring of multilocus genotypes due to ambiguities in the verification of its genetic control and/or mode of inheritance (for details see Müller-Starck & al. 1992).

Intrapopulational variation is characterized by means of the average number of alleles per locus and the observed and expected heterozygosities (H_a , H_e ; see Table 1). The most frequently employed measure for interpopulational variation is G_{ST} (Nei 1973). In order to summarize information for each species, results from different studies were weighted because the respective sample sizes and number of studied loci varied tremendously. The number of studied gene loci was weighted by the number of individuals, the remaining parameters by the number of individuals and of gene loci.

Results and discussion

Table 1 refers to forest tree species which are commonly considered to be ecologically and/or economically important. Populations of these species are managed predominantly as natural populations. Data are selected from Müller-Starck (1991, 1992). For *Quercus* species, recent results (Zanetto & al. 1994) were supplemented. The compiled results reveal substantial variation among species with respect to intra- and interpopulational genetic variation. Within species, observed patterns of genetic variation can deviate substantially among studies. In Table 1, an attempt is made to briefly summarize characteristic trends with respect to genetic variation.

Table 1. Compilation of data on genetic variation in European tree species. Results refer to adult trees unless asterisks indicate embryos or juvenile plants. Observed or expected heterozygosities (H) are indexed by (a) or (e). The number of populations is given in brackets if data refer to a subset.

Total number of pop.	Total individ.	Weighted arithmetic means			Comments
		gene loci	alleles per locus	H (%)	
Coniferous tree species:					
<i>Abies alba</i> Mill.					
104	2856	6.6	2.1 ⁽⁹⁷⁾	49.0 ^(a:11) 41.6 ^(e:5)	Maximum individual variability (heterozygosities) but relatively low proportion of polymorphic loci.

Total number of pop.	Total individ.	Weighted arithmetic means			G_{ST} (%)	Comments
		gene loci	alleles per locus	H (%)		
<i>Larix decidua</i> Mill.						
12	1020	17.6	1.9	16.3 ^(e)	2.6 ⁽¹¹⁾	Studies only in a small part of the geographic range; relatively low intra- and interpopulational variation.
<i>Picea abies</i> (L.) Karst.						
211	16795	10.5	2.1	12.8 ^(a,95) 29.3 ^(e,43)	4.7 ⁽¹³⁴⁾	Heterogeneity of results (large geographic range); low heterozygosities (H_a); relatively small differentiation (for comparison see <i>Pinus sylvestris</i>)
<i>Pinus cembra</i> (L.) (incl. var. <i>sibirica</i> Loud.)						
12	264	8.7	1.8	12.8 24.0 ^(e)	32.0	Extraordinarily great inter-populational genetic variation in geographically distant habitats.
<i>Pinus nigra</i> Arnold						
79	7132	3.8	2.5	27.2 ^(e,28)	10.8 ⁽⁶⁸⁾	Great intra- and remarkably large inter-populational variation (subdivided (disjunct) geographic range).
<i>Pinus sylvestris</i> L.						
74	2963	6.5	3.4 ⁽⁶⁶⁾	34.8 ^(a,45) 33.7 ^(e,18)	3.5 ⁽⁴⁰⁾	Large geographic range; much greater intrapopulational variation than <i>Picea abies</i> but smaller variation among populations (probably not so many different glacial refuges).
12*	1479	11.1	3.1	26.8 ^(a,9) 27.7 ^(e,3)	1.5	

Total number of pop.	Total individ.	Weighted arithmetic means			G_{ST} (%)	Comments
		gene loci	alleles per locus	H (%)		
Deciduous tree species:						
<i>Castanea sativa</i> Mill.						
46	1040	14.6	1.9	25.9 ^(a;31)	12.2	Relatively little intrapopulation variation as compared to other deciduous species; large interpopulation variation only in case of geographically distant habitats.
13*	1313	8.0	2.1	21.0 ^(e;15)		
<i>Fagus sylvatica</i> L.						
293	12801	5.6	2.3	28.2 ^(a;146)	5.4 ⁽¹⁴⁰⁾	Very large intrapopulation varia- tion but relatively small genetic differentiation among populations (little more than in <i>Picea abies</i>).
7*	2095	6.6	3.1	23.1 ^(a)		
<i>Quercus petraea</i> Liebl.						
37*	4615	14.7	3.2	21.9 ^(a;5)	2.0	Very large intrapopulation varia- tion but smaller genetic differentiation among populations than other species with large continuous geo graphic ranges (e.g. <i>Fagus sylvatica</i>).
7	840	13.0	3.7	27.5 ^(e;32)		
<i>Quercus robur</i> L.						
5*	830	13.0	3.2	21.3 ^(a)	1.8	Very similar trends to those observed in populations of <i>Quercus petraea</i> .
7	840	13.0	3.5	25.2 ^(e)		

The following classification is suggested:

— Species with large geographical 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).

— Species with large geographic ranges, but subdivided into different subspecies (races) such as *Pinus nigra*, reveal little interpopulational variation within subspecies, but great differentiation among subspecies (disjunct species).

— Species with small and geographically disjunct ranges like *Abies alba* tend to show moderate interpopulational differentiation and considerable intrapopulational genetic variation (endemic species).

In order to compare genetically forest trees with other species, results of studies are summarized in Table 2 which all refer to enzyme gene markers. As can be seen there, observed heterozygosities indicate high levels of individual genetic variation in forest trees as compared to other species with inclusion of agricultural crops. At the population level, a corresponding surplus does not seem to be evident.

For better illustration, the potential of forming genetically different multilocus genotypes was compared between forest tree species and monocots. For tree populations, results from recent studies in high elevated stands of Norway spruce (*Picea abies* (L.) Karst.) in Switzerland were utilized: Based on 17 polymorphic gene loci, the average number of alleles per locus was 2.5 (13 indigenous populations with 100 studied individuals per population).

Under such conditions, a maximum number of 76 527 504 000 genetically different 17 locus types can be formed hypothetically. The corresponding number of monocotyledonous individuals would be 472 392 (1.72 alleles per locus).

Table 2. Observed heterozygosity (H_a) and number of alleles per locus for European forest tree species in contrast to monocotyledonous/dicotyledonous species. (¹ Müller-Starck 1991, ² Mitton 1983, ³ Hamrick & Godt 1990).

	Number of species	Average heterozygosity (H_a)	Average number of alleles per locus
Coniferous tree species	10	25.1 % ¹	2.2 ¹
Deciduous tree species	6	23.0 % ¹	2.7 ¹
Monocotyledonous species	28 ² , 80 ³	16.5 % ²	1.7 ³
Dicotyledonous species*	74 ² , 338 ³	11.3 % ²	1.4 ³

* Excluding tree species.

The maintenance of such high levels of intrapopulational genetic variation in forest tree populations is interpreted as a necessary strategy to survive in heterogeneous environmental conditions.

Conclusions

Forest tree populations cover a wide range of environmental conditions. Genetic inventories are therefore confronted with a large number of variable population and site characteristics. Under such conditions, individual studies are not necessarily representative. The entirety of results suggests the above given trends which have to be confirmed by further studies.

Generally, information on genetic variation in European tree populations is still very small and refers to some major tree species but not to numerous other species which are part of significant forest ecosystems (e.g. genera *Acer*, *Alnus*, *Fraxinus*, *Tilia*, *Ulmus*). Generally, inventories on genetic variation and its dynamics in tree populations need to be intensified in order to quantify genetic resources of species which are significant elements in European forest ecosystems.

A severe problem of many forest ecosystems is the threat by increasing environmental stress as a consequence of edaphic, biotic and also climatic changes. Forest practices which reduce the natural genetic variability can magnify the negative impacts of stress conditions. In order to maintain the adaptability of forest tree populations to changing environments, and thus maintain their multiple environmental, social and economic functions, the following provisions are suggested:

- (a) Elaboration of concepts to avoid genetic destabilization following losses of genetic variation and occurrence of inbreeding.
- (b) Increase of genetic variation in genetically impoverished populations and reproductive material respectively (based on results of genetic inventories).
- (c) Quantification of genetic resources and long term conservation of genetic variability with main emphasis on *in situ* conservation by means of reservation forests.

The challenging research tasks in complex forest ecosystems, which are increasingly threatened by environmental stress, require close cooperation between European working groups and need further political support.

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