Thus, in the present study, provenances from the north showed comparatively better growth than the southern provenances. It is interesting to mention here that southern provenances showed better seed germination and seedling growth (up to 1 year) in the nursery (KUMAR, 1993). In another study (KUMAR and TOKY, 1993) we reported that 3-year old trees of these 12 provenances also differed significantly in leaf chemical composition. Thus, the variation observed in the present study are mainly genetical in nature as all the plants were growing in a similar environment. The large variations in *A. lebbek* may be due to its cross pollination behaviour and also due to its natural occurrence in highly varied agro-climatic conditions.

We did not come across any other provenance study on *A. lebbek* for comparison. However, some studies conducted on *Eucalyptus* (TOKY and BISHT, 1991), *Acacia nilotica* (KRISHAN, 1992) and *Populus deltoides* and *P. X. euramericana* (TOKY *et al.,* 1995a and b) growing in arid and semi-arid environmental conditions in India also reported wide variations in plant growth of different provenances. In the present study the provenances from north-western particularly that of Jammu, were superior in growth than rest of the provenances. Thus, selection of superior seed source is possible for future breeding programme.

Acknowledgements

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Allozyme Variation among European Beech (*Fagus sylvatica* L.) Stands in Piedmont, North-Western Italy

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Summary

The genetic diversity and the genetic differentiation of 11 native populations of European beech from Piedmont (north-western Italy) were studied by means of the allozyme variation at 10 *loci.* Data obtained also contributed to the identification of the most valuable stands for the production of high quality seed.

Horizontal electrophoresis on starch gel was employed to separate the variants of 7 enzyme systems: Got, G3pdh, Idh, Mdh, Mnr, 6Pgdh and Pgi.

The expected heterozygosity ranged from 0.177 to 0.278 with an average of 0.232; the mean number of alleles per *locus* was 2.12 and 68.18% of *loci* were polymorphic.

Only 4.3% of the total genetic diversity was due to differentiation among populations and the mean value of NEI's genetic distance was 0.013. The sharing of one gene pool among the studied beechwoods suggests a lack of barriers to gene flow.

It was possible to score a significant correlation between the frequency of the allele 6Pgdh-B1 and the altitude where the samples were collected, while the north exposure was related to a higher mean heterozygosity.

Although no correlation between genotype and geographical distance could be found, the stands from the same province showed a certain degree of similarity. On the basis of the genetic distances, the very old stand of Palanfrè was clearly distinguishable from the others. Moreover, it displayed the highest level of expected heterozygosity.

Key words: allozyme variation, *Fagus sylvatica,* genetic diversity, population differentiation.

FDC: 165.3; 165.5; 176.1 *Fagus sylvatica;* (450).

Introduction

European beech (*Fagus sylvatica* L.) grows in Europe under very different ecological conditions, particularly in the southern part, close to the Mediterranean sea (COMPS *et al.,* 1990). This environmental diversity, together with natural selection and genetic isolation, accounts for the genetic

differentiation of beechwoods. Genetic isolation is mainly due to phenological differences (COMPS *et al.,* 1987).

Although beech is an anemophilous species with an outcrossing rate varying between 0.90 and 1.00 (MERZEAU *et al.,* 1989), gene flow is expected to be limited due to the high density within the stands, which favours the mating between closely spaced individuals (CUGUEN *et al.,* 1988).

Historical factors also play an important role in the present genetic structure of beechwoods. After the last glacial period, beech spread from the Balkans and from several less important sources in south-western Europe. The beech reached the present areas of diffusion at different times: about 5000 BC in southern and 2000 years later in central Europe (VERNET, 1981). Since then a relatively low number of generations have passed, considering one beech generation lasting from 60 to 100 years (COMPS *et al.,* 1990). Due to the higher number of sources as well as generations, and the more heterogeneous climatic conditions, genetic differentiation among and within stands is higher in the southern part of the species diffusion area (COMPS *et al.,* 1990).

In spite of its importance, genetic characterization of beech populations has been rarely carried out. To this end, since the morphological and phenological variations are of quantitative nature and usually under polygenic control, biochemical markers have proved to be very suitable in the study of genetic variation. The genetic characterization of beech populations employing isozyme markers started 15 years ago (KIM, 1980): since then only a few studies have been carried out (for a review see MÜLLER-STARCK *et al.,* 1992. See also GÖMÖRY *et al.,* 1992a and b; TUROK, 1993). Isozyme analysis has also been used to assess the mating system of beech (MERZEAU *et al.,* 1989), to prove the correlation between genetic diversity, heterozygosity and adaptability (MÜLLER-STARCK, 1985), to study viability selection during development (KIM, 1985), to correlate the allelic frequencies with geographical and/or climatic conditions of the population site (GÖMÖRY *et al.,* 1992a) and to distinguish among closely related species of beech (COMPS *et al.,* 1991; GÖMÖRY *et al.,* 1993).

In Piedmont (north-western Italy) beech is one of the most important broad-leaf tree, covering a surface larger than 60.000 ha (Regione Piemonte, 1981). It is found mainly in mountain areas, usually at altitudes ranging between 900 m and 1.500 m a.s.l.

In this study the genetic variability among different beech populations in Piedmont was assessed through isozyme analysis. This also contributed to the identification of the most valuable stands for the production of high quality seed. It is well-known that high levels of genetic diversity and heterozygosity of populations are associated respectively with survival capacity (HERTEL, 1992) and adaptability, regardless of the specific allozyme present in the individuals (WILLS, 1973).

Table 1. – The geographical location of the studied beechwoods.

Station (see Fig. 1)		Valley	Province	Altitude (m)	Exposure
1	Palanfrè	Vermenagna	Cuneo	1,450-1,600	North
2	S. Giacomo	Stura di Demonte	Cuneo	1,300-1,450	North
3	Cugn	Grana	Cuneo	1,100-1,250	South
4	Richiaglio	Lanzo (Viù)	Torino	1,000-1,200	North
5	Belfè	Lanzo (Ala)	Torino	1,100-1,200	North
6	Oropa	Oropa	Biella	1,150-1,300	East
7	Campiglia	Cervo	Biella	1,000-1,100	East
8	Fobello	Mastallone	Vercelli	1,000-1,100	West
9	Viganella	Antrona	Ossola	1,100-1,250	North
10	Altoggio	Isorno	Ossola	1,000-1,150	East
11	Finero	Vigezzo	Ossola	950-1,100	North

Materials and Methods

Plant Material and Sampling

Samples of 11 adult beech stands were collected, representing the topographic locations where the species grows in Piedmont (*Fig. 1* and *Table 1*). All of them possess the requisites for the inclusion in the official Italian List of Seed Stands, being native, free from disease, large enough to prevent inbreeding phenomenon, and isolated by other stands of low quality. Moreover, the trees within the chosen stands showed superior phenotypes.

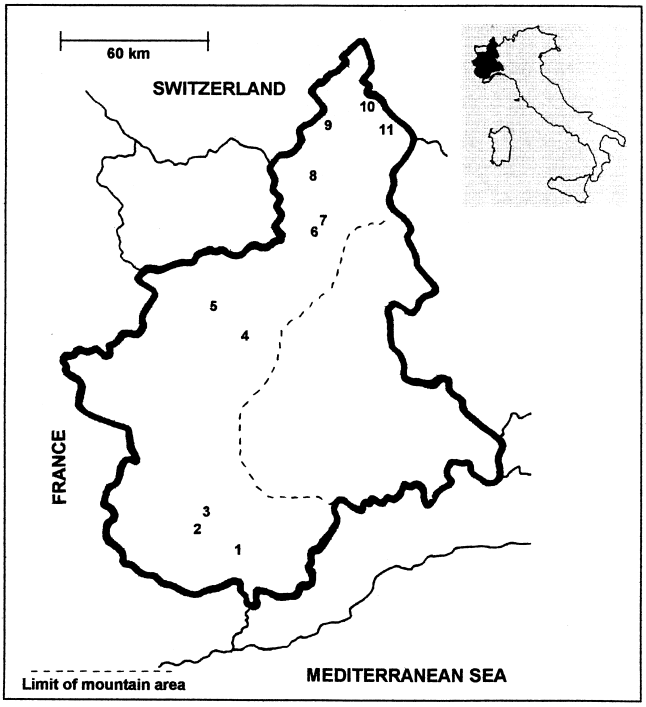

Fig. 1. – The beechwoods studied, in the North-western of Italy.

In each stand, plant material (winter buds) was collected from at least 80 non-adjacent plants, chosen at random over a 10 ha to 12 ha area.

Electrophoretic Procedure

Horizontal electrophoresis on starch gel was employed to separate the variants of 7 enzyme systems. The gel was made of 11% hydrolysed potato starch (Sigma S4501). Two different buffer systems were used depending on the enzyme system (*Table 2*). Approximately 100 mg of tissue from fresh and descaled winter buds was ground in 100 µl of extraction buffer containing tris 0.1 M, EDTA di-sodium salt 3 mM, dithiothreitol 5 mM, supplemented with 50 mg/ml polyvinylpyrrolidone and 0.5% mercaptoethanol, and titrated at pH 7.3 with HCl 1N. The gels were run at 5 (tris-borate) or 18 (tris-citrate) V/cm for 30 minutes before removing the wicks and then overnight.

Staining was done according to WENDEL and WEEDEN (1989), with the exception for Mnr (CONKLE *et al.,* 1982). In staining for Idh and Pgi 5 mg of NADP were used instead of NAD.

Capital letters following the enzyme acronyms were used to label the enzymes: the most anodal zone was designated with the first letter. Within a single zone of activity the different alleles were designated with numbers, assigning the lowest number to the band migrating fastest.

Table 2. – Enzyme systems used in study.

Enzyme	Abbreviation	EC code	Buffer system[a]	No. of *loci*
Glutamate oxaloacetate transaminase	Got	2.6.1.1	TB	1
Glyceraldehyde 3-phosphate dehydrogenase	G3pdh	1.2.1.9	TC	1
Isocitric dehydrogenase	Idh	1.1.1.42	TC	1
Malate dehydrogenase	Mdh	1.1.1.37	TB/TC	2
Menadione reductase	Mnr	1.6.99.2	TC	1
6-Phosphogluconate dehydrogenase	6Pgdh	1.1.1.44	TC	3
Phosphoglucose isomerase	Pgi	5.3.1.9	TB	1

[a]) TB = tris borate: electrode buffer, boric acid 0.3 M titrated at pH 8.2 with NaOH; gel buffer, tris 0.076 M titrated at pH 8.7 with HCl.
TC = tris citrate: electrode buffer, tris 0.135 M titrated at pH 7.0 with citric acid; gel buffer, diluted electrode buffer (4:1).

Statistical analysis

The following measures of gene diversity were used: the expected proportion of heterozygotes, H_e (NEI, 1975), the average number of alleles per *locus* and the percentage of polymorphic *loci* (by convention, *loci* were considered polymorphic if the frequency of the most common allele did not exceed 0.95). The genetic differentiation among populations were estimated by partitioning the total gene diversity, H_T, in gene diversity within populations, H_S, and among populations, D_{ST} (NEI, 1973). The relative degree of genetic differentiation, G_{ST}, was calculated as D_{ST}/H_T.

The genetic distances were calculated according to NEI (1972) and were used to construct a dendrogram of populations by the unweighted pair-group method using arithmetic means (SNEATH and SOKAL, 1973).

Results

Two *loci* out of the 10 found for 7 enzyme systems were monomorphic in all the populations (Got-A and G3pdh-A). Allele frequencies and expected heterozygosity for the 8 polymorphic *loci* are reported in *table 3*. At *locus* Mdh-B, the allele B-2 was the most frequent, while B-1 was the less frequent in 5 stands and B-3 in the remaining 6. At *locus* 6Pgdh-B, the allele B-2 was the most frequent, with the exception of the stand 1 (Palanfrè). At *locus* 6Pgdh-C the allele C-1 was the most frequent and C-3 the less frequent, with the exception of the stand 8 (Fobello), where the allele C-2 was the less frequent.

On the whole, it was possible to find the following rare alleles: Idh-A3 (frequency of 0.020 on average and absent in 4 stands), Mnr-A1 (0.010 and 4), Pgi-B1 (0.017 and 7) and Pgi-B3 (0.011 and 3).

The values of genetic diversity are reported in *table 4*. The mean expected heterozygosity per population ranged from 0.177 (Oropa) to 0.278 (Palanfrè) with an average of 0.232. The mean number of alleles per *locus* was on average 2.12: Cugn and Altoggio had the lowest values (2.00) and Oropa the highest (2.30). The percentage of polymorphic *loci* ranged from 60 (Richiaglio, Viganella and Altoggio) to 80 (Fobello) with an average of 68.18.

Table 3. – Allele frequencies and expected heterozygosity, H_e, in 11 beechwoods from Piedmont, north-western Italy.

		Population										
Locus	Allele	1	2	3	4	5	6	7	8	9	10	11
IDH	A-1	.393	.347	.343	.263	.202	.145	.113	.250	.320	.189	.223
	A-2	.583	.647	.657	.635	.737	.849	.887	.750	.669	.805	.777
	A-3	.024	.005	.000	.103	.061	.006	.000	.000	.011	.006	.000
	H_e	**.505**	**.460**	**.451**	**.518**	**.412**	**.258**	**.200**	**.375**	**.450**	**.316**	**.347**
MDH	B-1	.181	.160	.028	.063	.051	.054	.182	.105	.076	.056	.107
	B-2	.663	.756	.907	.833	.864	.878	.716	.895	.854	.883	.839
	B-3	.156	.083	.065	.104	.086	.068	.102	.000	.070	.062	.054
	H_e	**.504**	**.395**	**.172**	**.291**	**.244**	**.221**	**.444**	**.188**	**.259**	**.214**	**.281**
	C-1	.373	.208	.192	.361	.299	.082	.162	.186	.342	.311	.298
	C-2	.627	.792	.808	.639	.701	.918	.838	.814	.658	.689	.702
	H_e	**.468**	**.330**	**.311**	**.461**	**.419**	**.151**	**.272**	**.302**	**.450**	**.428**	**.418**
MNR	A-1	.010	.005	.019	.000	.000	.018	.020	.029	.006	.000	.000
	A-2	.894	.926	.916	.859	.874	.898	.929	.839	.921	.890	.926
	A-3	.096	.068	.065	.141	.126	.084	.051	.132	.073	.110	.074
	H_e	**.191**	**.137**	**.157**	**.242**	**.221**	**.187**	**.133**	**.278**	**.146**	**.195**	**.137**
6PGDH	A-1	.938	.895	.942	.960	.894	.911	.931	.925	.966	.957	.968
	A-2	.063	.105	.058	.040	.106	.089	.069	.075	.034	.043	.032
	H_e	**.117**	**.188**	**.109**	**.077**	**.190**	**.163**	**.128**	**.138**	**.065**	**.082**	**.061**
	B-1	.510	.468	.320	.244	.173	.130	.250	.101	.335	.329	.328
	B-2	.490	.532	.680	.756	.827	.870	.750	.899	.665	.671	.672
	H_e	**.500**	**.498**	**.435**	**.369**	**.287**	**.226**	**.375**	**.182**	**.446**	**.442**	**.441**
	C-1	.701	.543	.477	.372	.577	.630	.575	.756	.528	.659	.511
	C-2	.279	.378	.375	.321	.240	.241	.306	.113	.472	.274	.430
	C-3	.020	.080	.148	.308	.184	.130	.119	.131	.000	.067	.059
	H_e	**.430**	**.557**	**.610**	**.664**	**.576**	**.529**	**.562**	**.399**	**.498**	**.487**	**.551**
PGI	B-1	.000	.000	.000	.018	.000	.006	.000	.105	.000	.000	.061
	B-2	.966	1.000	1.000	.973	.990	.982	.989	.872	.994	1.000	.927
	B-3	.034	.000	.000	.009	.010	.012	.011	.023	.006	.000	.012
	H_e	**.065**	**.000**	**.000**	**.053**	**.020**	**.035**	**.022**	**.228**	**.011**	**.000**	**.137**

Table 4. – Values of genetic diversity among the studied beechwoods.

Stand	Mean expected heterozygosity	Mean number of alleles per *locus*	Percentage of polymorphic *loci*[a]
1. Palanfrè	.278	2.20	70.00
2. S. Giacomo	.257	2.10	70.00
3. Cugn	.224	2.00	70.00
4. Richiaglio	.268	2.20	60.00
5. Belfè	.237	2.10	70.00
6. Oropa	.177	2.30	70.00
7. Campiglia	.214	2.10	70.00
8. Fobello	.209	2.10	80.00
9. Viganella	.233	2.10	60.00
10. Altoggio	.216	2.00	60.00
11. Finero	.237	2.10	70.00
Average	**.232**	**2.12**	**68.18**

[a]) 0.95 criterion

The values of genetic differentiation are reported in *table 5*. Since the gene diversity within populations was very similar to the total gene diversity, the relative degree of genetic differentiation was as low as 0.043.

Table 5. – Values of genetic differentiation at the polymorphic *loci*. H_T is the total gene diversity, H_S the gene diversity within populations, D_{ST} the gene diversity among populations and G_{ST} the degree of genetic differentiation.

Locus	H_T	H_S	D_{ST}	G_{ST}
Idh-A	.407	.390	.017	.042
Mdh-B	.302	.292	.010	.033
Mdh-C	.381	.365	.016	.042
Mnr-A	.187	.184	.003	.016
6Pgdh-A	.122	.120	.002	.016
6Pgdh-B	.412	.382	.030	.073
6Pgdh-C	.559	.533	.026	.047
Pgi-B	.055	.052	.003	.055
Average	**.303**	**.290**	**.013**	**.043**

The matrix of measurements of genetic distances and genetic similarities, calculated according to NEI (1978), is reported in *table 6*. The average of the NEI's genetic distances was 0.013, showing a very low level of differentiation among the studied beechwoods. The maximum distance, 0.041, was observed between Palanfrè (No. 1) and Oropa (No. 6), while the minimum, 0.001, occurred between Viganella (No. 9) and Finero (No. 11). The correlation between genetic distance and geographical distance was 0.206, which is not significant ($p = 0.130$).

The dendrogram constructed with the UPGMA method is reported in *figure 2*.

Discussion and Conclusions

The genetic control of the studied isoenzymes proved to agree with the findings of MÜLLER-STARCK and STARKE (1993). Only, it was not possible to find the second region of activity of

Table 6. – Genetic distance (above the diagonal) and genetic similarity (below the diagonal) among the 11 beechwoods, calculated according to NEI (1978).

Stand	1	2	3	4	5	6	7	8	9	10	11
1. Palanfrè	-----	.006	.019	.025	.026	.041	.026	.038	.011	.014	.015
2. S. Giacomo	.994	-----	.004	.016	.017	.023	.012	.029	.006	.009	.006
3. Cugn	.981	.996	-----	.005	.007	.012	.010	.018	.004	.006	.003
4. Richiaglio	.975	.984	.995	-----	.004	.019	.015	.021	.009	.010	.007
5. Belfè	.974	.983	.993	.996	-----	.006	.007	.006	.010	.004	.007
6. Oropa	.959	.977	.988	.981	.994	-----	.004	.005	.021	.011	.014
7. Campiglia	.974	.988	.990	.985	.993	.996	-----	.013	.014	.006	.006
8. Fobello	.962	.971	.982	.979	.994	.995	.987	-----	.025	.012	.018
9. Viganella	.989	.994	.996	.991	.990	.979	.986	.975	-----	.005	.001
10. Altoggio	.986	.991	.994	.990	.996	.989	.994	.988	.995	-----	.002
11. Finero	.985	.994	.997	.993	.993	.986	.994	.982	.999	.998	-----

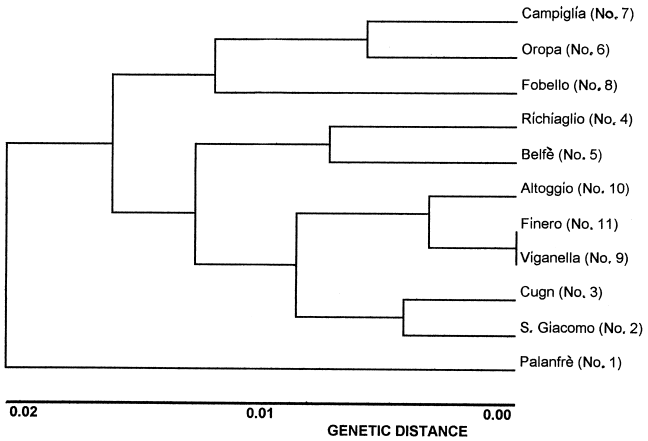

Fig. 2. – Dendogram of genetic distances between the 11 beechwoods obtained with UPGMA method.

Got. G3pdh-A and Mnr-A are tentative *loci* designations, pending identification of polymorphism and segregation analysis.

Acid phosphatase (E.C. 3.1.3.2.), Leucine aminopeptidase (3.4.11.1.) and Phosphoglucomutase (5.4.2.2, with 2 distinct regions of activity) also proved to be polymorphic, but their resolution was not consistent enough and therefore they were not included in the study. This possibly caused an underestimation of some given values of genetic diversity. On the other hand, Mdh and Pgi exhibited also an area of activity more anodal than that reported in the study, probably invariant but not sufficiently clear to be interpreted.

The obtained data for each population was seen to agree with HARDY-WEINBERG expectations, indicating the effectiveness of the outcrossing mating system. Only in a few cases the within population fixation index, F_{is}, was significantly higher than zero, indicating a slight heterozygote deficiency, probably due to inbreeding or to mating between closely located trees.

The mean expected heterozygosity (0.232) was similar to the ones found for broad-leaf species and lower than those related to coniferous species, which can reveal corresponding values greater than 30% (MÜLLER-STARCK and ZIEHE, 1991). It was not possible to find any correlation among the values of mean expected heterozygosity (H_e), mean number of alleles per *locus* (N) and percentage of polymorphic *loci* (P): none of the SPEARMAN's rank correlation coefficients was significant ($p > 0.50$). The higher observed value ($r_s = 0.273$) was found between H_e and N. The stand no. 6 (Oropa) showed the lowest value of H_e but the highest for N. This is possibly a consequence of the presence of rare alleles, which contribute to a small extent to H_e, while are relevant both for N and P. Moreover, N and P are genetic parameters which strongly depend on the sample size. GREGORIUS (1978) suggested that the best measure of genetic diversity is the effective number of alleles per *locus*, n_e, which is the harmonic mean of the values for individual *loci* (CROW and KIMURA, 1970). However, in our study, n_e values were not significantly different and ranged from 1.67 (stands no. 3 and 10) to 1.94 (stand no. 6). It appears that there is not a genetic univocal criterion for the choice of the stands most suitable for the production of high quality seeds and different aspects other than the genetic ones can play an important role.

The major part of genetic diversity was localized within populations, since only the 4.3% of the total genetic diversity was found at the interpopulational level. This value is slightly lower that those found in other studies on European beech (COMPS et al., 1990 and 1991; MÜLLER-STARCK and ZIEHE, 1991; TUROK, 1993), where, indeed, the investigated areas were much larger than ours. From our data it appears that there are important gene flows from one population to another and, therefore, the studied beechwoods share the same gene pool. The lack of differentiation among populations indicates also a common migration path during the post-glacial period. The observed good fit to HARDY-WEINBERG expectations seems to confirm the lack of differentiation: in fact, the "isolation by distance" hypothesis has been proposed as the most important cause of heterozygote deficit in beech (COMPS et al., 1990). A small differentiation among populations is typical of species like European beech and conifers, characterized by large and high-density stands, wide pollen diffusion, high outcrossing rate. Furthermore, it must be kept in mind that the actual range of the beech is a consequence of its migration after the last glaciation, and since then there have been only few generations. It seems likely that there has not been sufficient time for a significant selection and genetic drift among the populations.

Among the studied *loci,* 6Pgdh-B showed the highest relative degree of genetic differentiation (0.073): on the contrary Mnr-A and 6Pgdh-A displayed the lowest value (0.016).

From an ecological point of view, it was possible to find a significant correlation between the frequency of the allele 6Pgdh-B1 and the altitude where the plant material was collected ($r = 0.675$, $p = 0.023$), showing a possible adaptative role of the allele. Variations of allelic frequencies related to environmental conditions were already observed for other *loci* (THIEBAUT *et al.,* 1982; COMPS *et al.,* 1990 and 1991; GÖMÖRY *et al.,* 1992a). No significant correlation was found between allelic frequencies and stand exposure although the exposure to the north (stands No. 1, 2, 4, 5, 9 and 11) seems to be linked with a higher mean heterozygosity, but not with a higher number of alleles per *locus* nor to a higher percentage of polymorphic *loci.* The north exposure accounts for a higher humidity degree and lower summer temperatures, which are the best conditions for the beech in north-western Italy. It is likely that, in less favourable growing conditions, a higher level of selection has led to a lower level of heterozygosity, although the lack of notable population differentiation did not allow the elimination of specific alleles.

We could not find any significant pattern related to geographic distance, although a tendency was quite clear. The dendrogram showed that populations from the same province are the first ones which group themselves, but the clustering of the Provinces do not follow any geographical criterion, being, for instance, Cuneo (stands no. 2 and 3) and Ossola (stands no. 9, 10 and 11) provinces strictly related, although located in the southern and in the northern part of Piedmont respectively. Stand no. 1 (Palanfrè) showed peculiar characteristics, and proved to be clearly separated from all the other stands. The beechwood of Palanfrè is located at the highest altitude, thus growing in the most severe climatic conditions. Moreover, it is

very old (some trees are older than 200 years) and has always been safeguarded because of its protection of the village beneath against avalanches. It also showed the highest value of heterozygosity, conferming the adaptative role of the latter.

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General and Specific Combining Ability from Disconnected Partial Diallels of Coastal Douglas-fir

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Summary

General and specific combining ability (GCA and SCA, respectively) were examined in 36, 6-parent disconnected partial diallels across 4 different experimental series in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* DOUGL.) to examine the ratios of the 2 genetic variances, the distribution of GCA and SCA effects, and estimates of genetic gain from GCA and SCA for 3 growth traits. Height at age-7 and height and volume at age-12 were measured on approximately 150 trees per full-sib family in each diallel, across 11 different test sites within each series. The average percentage ratio of SCA variance to GCA variance was 36%, across all series and the 3 growth traits, with a range of 19% to 65%. GCA and SCA variances did not appreciably change for height growth from age 7 to age 12. Diallel set effects were generally negligible. From theoretical considerations assumed for the diallel model, clear separations of additive and dominance effects (*vis-a-vis* the assumptions of selecting on GCA and SCA variances) are likely not possible: the effects are subject to degrees of dominance, epistasis and linkage in the population. However, these genetic details did not manifest themselves in any