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The Bud Enzymes of Beech (Fagus sylvatica L.) Genetic Distinction and Analysis of Polymorphism in Several French Populations

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Summary

This paper describes the methods used to study enzymatic genetic markers in Beech (*Fagus sylvatica* L.), and indicates the reasons which led us to work particularly on buds.

Starch gel electrophoresis was used to study the genetics of 3 loci, two coding for peroxidases (Px1 and Px2) and one coding for a glutamate-oxaloacetate transaminase (GOT_1), in Beech buds. The peroxidases are monomeric enzymes in both cases, the first locus is composed of 2 alleles $Px_1^{1.00}$ and $Px_2^{1.05}$ (with existence of silent alleles in certain cases) and the second of 3 alleles $Px_2^{1.13}$, $Px_2^{0.26}$ and $Px_2^{0.40}$. The glutamate-oxaloacetate transaminases are dimeric enzymes specified by one locus composed of two alleles: $GOT_1^{1.00}$ and $GOT_1^{1.05}$.

Using 11 Southern and 2 Northern populations, polymorphism is examined simply for the peroxidases (2 loci). The variation of allelic frequencies show clearly the influence of climate; in the first locus the moisture regime seems to be involved, and in the second the temperature regime.

Key words: Beech, genetic determinism, peroxydases, glutamate-oxaloacetate-transaminases, polymorphism.

Zusammenfassung

Diese Arbeit beschreibt die Methoden, die zur Untersuchung enzymatischer genetischer Marker bei Buche (*Fagus sylvatica* L.) verwendet wurden und zeigt auf, warum wir insbesondere mit Knospen gearbeitet haben. Für die Untersuchung der Genetik von Loci, von denen 2 für Peroxidasen (Px1 und Px2) und einer für Glutamat-oxalacetat Transaminase (GOT_1) codieren, wurde Stärkegelelektrophorese bei Buchenknospen angewendet. Die Peroxidasen sind in beiden Fällen monomere Enzyme, der erste Locus besteht aus den 2 Allelen $Px_1^{1.00}$ und $Px_2^{1.05}$ (wobei die Anwesenheit von Nullallelen nicht auszuschließen ist), der zweite Locus aus den 3 Allelen $Px_2^{0.13}$, $Px_2^{0.26}$ und $Px_2^{0.40}$. Die Glutamat-oxalacetat Transaminasen sind dimere Enzyme, gekennzeichnet durch einen Locus mit 2 Allelen: $GOT_1^{1.00}$ und $GOT_1^{1.05}$.

In 11 südlichen und 2 nördlichen Populationen wurden lediglich die Polymorphismen für die Peroxidasen (2 Loci) untersucht. Die Variation der Allelfrequenzen zeigte deutlichen Klimaeinfluß; beim ersten Locus schienen die Feuchtigkeitsverhältnisse, beim zweiten die Temperatur von Einfluß zu sein.

Introduction

Beech is widely distributed over much of Northern Europe. At its southern limit, in the mediterranean region it can be found in various habitats with differing climates. In SE France, while the majority of Beechwoods occur at some altitude, in a fairly humid climate, some isolated islands of fully developed Beech can be found at low altitude, under a drier climate (THIEBAUT, 1978 and in prep.).

The diversity of environments, and fragmented distribution of Beech at its southern limit could have favoured genetic differentiation within the species. This hypothesis, upon which our work is based, is substantiated by the many publications on the morphological and phenological variations of Beech in northern and central Europe. Cultural experiments have shown a genetic basis for some of these variations (CZECZOTTOVA, 1933; HØLM, 1937; KRAHL-URBAN, 1952; DIMITRIU-TATARANI, 1959; ARNSWALDT, 1959; DAJOZ, 1961; SMAGLJUK, 1964; GØHRN, 1972; ABASHIDZE, 1973 and 1974; GARELKOVA, 1977; ISTRATH, 1977; TYSHKEVITCH, 1977 a, b, c, d; TEISSIER DU CROS, 1977, 1980).

These morphological and phenological variations, often of a quantitative nature, and under polygenic control, are not easy to use as markers, Meanwhile, biochemical characters, such as presence or absence of allozymes, are usually monogenic in control, and much easier to use. Electrophoresis allows study of enzymatic variability, and thus the genetic structure of natural and artificial populations of forest trees. In effect the allelic and genetic frequencies observed can be used to characterise genetic variations. For these reasons, these techniques have a great potential in forestry research (RUDIN *et al.*, 1974; HAYASHI *et al.*, 1975; BERGMANN, 1978; BONNET-MASIMBERT and BIKAY-BIKAY, 1978; LUNDKVIST, 1979).

In fact, biochemical studies on beech are very few. PAGANELLI *et al.* (1973) examined variation of deshydrogenases in winter buds; ZIN-SUH-KIM (1979) studied the genetic determination of leucine-amino peptidases (LAP) and acid-phosphatases in the young leaves. Thus, it interested us, to try to investigate, in a more systematic manner a range of enzymes of various functions: peroxidases, glutamate-oxaloacetate-transaminases (GOT), leucine-aminopeptida-

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Table 1. — Mating design and numbers of 5 progenies resulting from controlled pollinations cultivated at Horsholm Arboretum (Denmark)

Identification of progenies	female parent x male parent	Number of individuals				% of individuals analysed comnared to the initial number
		Spring 1961 (planting out in the Arboretum)	Survivors in 1977	Survivors in 1979	Spring 1980 number of individuals analysed	
4270	882 x 1623	78	63	39	37	47 %
4272	882 x *F.orientalis*	54	27	21	20	37 %
4273	882 x 885	78	62	44	38	48 %
4274	882 x 881	78	64	46	44	56 %
4276	882 x 1622	54	40	29	26	48 %
		342	256	179	165	

ses (LAP), esterases and acid phosphatases, in several organs: buds, leaves and nuts. The present work describes the methods used to detect enzymatic loci, and explains the reasons which led us to work particularly on buds. It also clearly shows the genetic determinism of the peroxydases (2 loci) and the glutamate-oxaloacetate-transaminases GOT (1 locus) present in the buds. Finally it permits us to compare the polymorphism for peroxydases of several French populations.

Materials and Methods

1. *To list some isozymes and to study their expression*

To examine the enzyme systems in the buds leaves, six trees were chosen in the forest of Valbonne (NE of Nîmes, in the department of Gard, altitude 150 m). The trees were growing on calcareous sandstone, in small humid valleys, in isolated 100% Beech patches, under coppice with standards forest management. To study the stability of expression of the bands- twenty samples were made over the course of one annual cycle (autumn 1978 — autumn 1979): once every 3 weeks, but weekly during the period of bud opening and leaf growth.

We also sowed some seeds in order to collect material at different stages of cotyledon development and young leaves from the dormant nut to the stage of opening of the first pair of leaves.

2. *To study genetic determinism*

The trees studied were the descendants of both controlled crosses and free pollinations. In the latter case, for

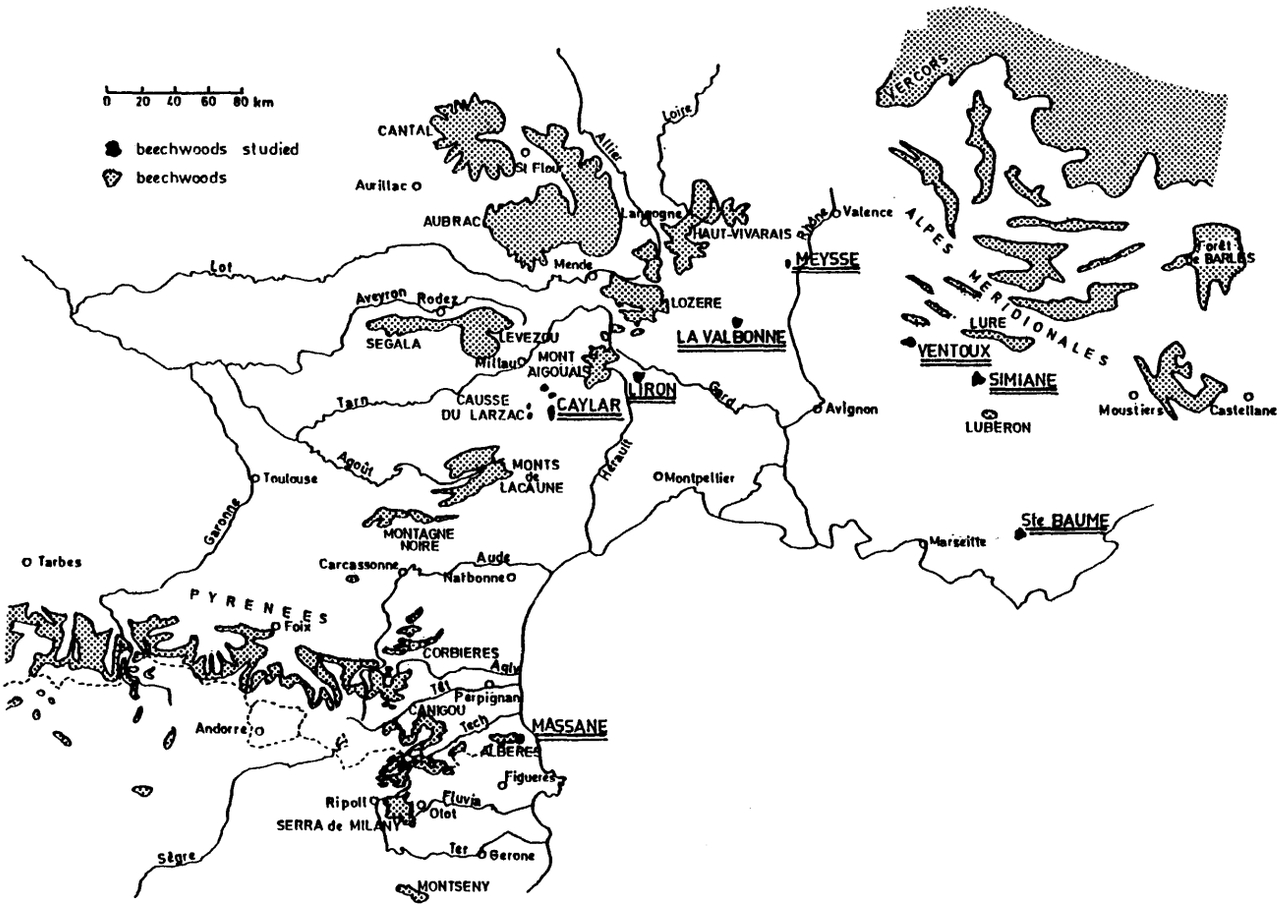


Fig. 1. — The beechwoods studied, in the SE of France.

some individuals, the female parent was known and analysed. The trees from controlled crosses came from five trees cultivated since 1961 at HØRSHOLM Arboretum in Denmark. They were all from the same female parent, each with a different male parent, one being of the related species *Fagus orientalis* LIPSKY, according to the plan of crosses given in *Table 1.* The mortality, or elimination of weak subjects, explain the discrepancies observed between the numbers of trees planted out in 1961 and the numbers still present in 1977 and 1978.

Some of the free pollinated material came from a single female parent (n°28), from the forest of Lyons, in France (Haute-Normandie). Twenty-five offsprings from this tree were cultivated between 1977 and 1979 at the Station d'Améliorations des Arbres Forestiers (I.N.R.A.) near Orléans in France.

The other free pollinated trees were collected at random in places of homogeneous ecology in 11 southern populations in SE France, at the rate of 50 trees from each population.

3. *For the study of polymorphism in the French populations*

The 11 southern populations were sampled between the Eastern Pyrénées and the Alps *(Fig. 1* and *Table 2),* and were growing on both basic and acid soils. The stations were spaced according to topography, in lowlands (Valbonne and Meysse), in the hills and foothills (Massane, Simiane and Sainte-Baume) and in the mountains (Le Caylar, Liron and Ventoux). Thus, these beechstands grow in a variety of climates from lowland mediterranean through sub-mediterranean to upland and subalpine.

In these diverse situations, beechstands show varying aspects of physionomy and associated flora. At lowland medium altitude beechstands form outposts from the main distribution. It is really a case of small isolated beechstands among oakstands *(Quercus pubescens* WILLD.) on basic soils, or among chestnutstands *(Castanea sativa* MILLER) on acid soils. Because of their floristic composition, their phytosociology relates mostly to the oak range, being *Quercion pubescenti-sessiliflora* (Braun-Blanquet, 1931) or *Quercion robori-sessiliflorae* (Malcuit, 1929, Braun-Blanquet, 1931). Higher up, beechstands cover large areas, a case usually of the characteristic beechstand association, *Fagion* (Luquet, 1926; Tyxen and Diemont, 1936).

Table 2. — The ecological conditions in southern Beechwoods

Stations (see fig. 1)	Position	Altitude (m)	Geology	local climate	Serie of vegetation (1)	pH (2)	Type of beechwood (3)
LA MASSANE	Foothills, Roussilon/ Pyrénées-Or.	450/500	Primary metamorphic schists	mediterranean climate	*Quercus lanuginosa* Lmk. *Quercus ilex* L.	5	*Quercion*
LE CAYLAR	Mountains, Causses du Larzac	900/ 1 000	Dolomitic limestone	mountain climate under both mediterranean and temperate influences	*Quercus lanuginosa* Lmk.	6 à 7	*Fagion*
LIRON S	Mountains, Cévennes	900	Primary metamorphic schists	mountane to submediterranean climate	*Quercus ilex* L. *Castanea sativa* Miller *(Quercus ilex* L.*)*	5	*Quercion*
LIRON N	Mountains, Cévennes	900	Primary metamorphic schists	mountane to submediterranean climate	*Fagus sylvatica* L. *Castanea sativa* Miller	5	*Fagion*
VALBONNE	Hills, Languedoc	150	Calcareous sandstone	mediterranean climate	*Quercus lanuginosa* Lmk. *Quercus ilex* L.	7 à 8	*Quercion*
MEYSSE	Rhône Valley	200	Hard limestone	mediterranean climate	*Quercus ilex* L. *Quercus lanuginosa* Lmk.	7 à 8	*Quercion*
VENTOUX Ht	Mountains, Alpes méridionales	1 600	Hard limestone	mountane to sub-alpin climate	*Fagus sylvatica* L. *Pinus uncinata* Ram.	7 à 8	*Fagion*
VENTOUX Bas	Mountains, Alpes méridionales	900/ 1 000	Hard limestone	mountane to submediterranean climate	*Quercus lanuginosa* Lmk. *Fagus sylvatica* L.	7 à 8	*Quercion*
SIMIANE S	Foothills, Monts du Vaucluse	800/900	Hard limestone	submediterranean climate	*Quercus lanuginosa* Lmk. *Quercus ilex* L.	7 à 8	*Quercion*
SIMIANE N	Foothills, Monts du Vaucluse	800/900	Hard limestone	submediterraneen climate	*Quercus lanuginosa* Lmk. *Fagus sylvatica* L.	7 à 8	*Fagion*
S^te BAUME	Hills, Provence	680/750	Hard limestone	submediterranean to mediterranean climate	*Quercus lanuginosa* Lmk. *(Quercus ilex* L.*)*	7 à 8	*Quercion*
LYONS	Normandie	150/200	Clay with flints	oceanic climate	*Fagus sylvatica* L. *Quercus pedonculata* Ehrh.	-	*Fagion*
AUBERIVE	Haute-Marne	400	limestone	oceanic/continental transitional climate	*Fagus sylvatica* L. *Quercus sessiliflora* Salisb.	-	*Fagion*

(1) according to "Cartes de la végétation de la France au 1/200 000e" Service de la Carte de la végétation de la France, C.N.R.S. Toulouse sheets n° 78, Perpignan; n° 68, Carcassone; n° 65, Rodez; n° 66, Avignon; n° 67, Gap; n° 74, Marseille.

(2) pH measured with Hellige equipment, Boden-indikator, Litton.

(3) for more information concerning phyto-ecological and phytosociological characterisations of these populations, see THIEBAUT (1978).

To widen our field, two northern French populations were also analysed, originating from the forest of Lyons in Normandy and the forest of Auberive in Haute-Marne. These were respectively located on acid soil in an atlantic climate in the first case, and on basic soil and in a transitional climate between atlantic and continental in the second.

4. *Extraction technique*

All our extractions used fresh material, the buds being descaled. The extraction consisted of crushing 300 mg of plant material in a mortar with some silversand, 10 mg of isoluble polyvinyepyrolidone (Polyclar) and 0.3 ml Tris-HCl buffer (pH 7.6), containing 0.1 M tris, 1% polyethylene glycol 20 000 and 4 mM sodium thioglycolate (modified after Valizadeh, 1977). After centrifugation at 40 000 g for 20 minutes, the supernatant was poured off and stored at -80^0 C.

5. *Electrophoresis*

The quantity of extract absorbed by (between 1 and 3) rectangles of Watman n°3 paper (size 3 × 10 mm) was subjected to starch gel electrophoresis (hydrolised according to Moretti's technique, 1957). The best results were obtained as follows; for peroxydases with a 12% starch gel, following the buffering system of Kristjanson (1963); for GOT and LAP respectively with a gel of 14% and 12.5% in a buffering system of tris-borate (pH 8.7), containing 0.10 M tris, 0.04 M orthoboric acid and 50 mg EDTA; for the esterases and acid phosphatases with a 12.5% gel in the buffering system of Poulik (1957), containing 5 mM/1 EDTA. The migration was first effected with a current of 60 mA (180 v) for the gel buffered as Kristjanson; at 70 mA (180 v) for the tris-borate gel at the start; then under a constant potential of 250 v until the front, marked with bromophenol blue, had covered a distance of 10 cm for peroxydases, esterases and acid phosphatases and 13 cm for GOT and LAP.

The gel, which was 10 mm thick was then cut horizontally into 2 mm slices. The slice situated at the bottom of the mould was considered the first. The second strip of the „Kristjanson" gel was developed for the peroxydases following the technique of Yen and Sadanaga (1977). The second slice of the „tris borate" gel at 14% was developed for the GOT using the method of Selander *et al.* (1971). The third "tris-borate" slice at 12.5% was kept for the LAP. For these, the slice was incubated at 37° C for 15 minutes in a tris-maleate buffer made up of 0.2 M tris, 0.15 M maleic anhydride and 5 mM Mg Cl_2; it was adjusted to pH 5.2 with Na OH containing 15 mg/l HCl leucyl-naphtylamide. Coloration was effected with 30 mg of Fast Garnet GBC (Sigma), which is very rapid. Finally, in the „Poulik" gel, the second slice was developed for esterases following the method of De Stordeur (1975) and the third for acid phosphatases following Lumaret (1981).

Results and Discussion

Availability of fresh material collected at a precise phenological stage does not pose the same problems in each the organs studied. In practice the buds and the leaves cannot be conserved for long and must be gathered directly before the extraction, while the dormant nuts are easily kept in a cool, dry place without significant modifications (Bonnet-Masimbert and Muller, 1973a and b, 1976).

1. *Enzymatic expression in various organs in time*

Following the calendar provided by *Table 3* we can see that, the buds represent an interesting material in that they are present on the trees for a large part of the year, from July (when they have reached a large enough size) till April or May when they burst. In the buds of Valbonne trees the peroxydases, GOT and LAP are visible in stable electrophoretic bands for the entire period, although with variations of intensity. Paganelli *et al.* (1973) have already established that the dehydrogenases are stable in Beech buds in winter. In each enzymatic system studied the observed bands (which were not necessarily the same between individuals) were so few in type that it is easy to advance hypotheses on their genetic determination. These hypotheses have been verified using material of known genetic composition from the Arboretum of Hørsholm in Denmark.

On the contrary, the leaves are less interesting because they are present only for a short period and pass through diverse phenological stages, such that zymogram variations observed are likely to be due to physiological changes at least as much as genetic ones. All the systems examined showed activity, except peroxydases, but the activity diminished in August.

Finally, the nuts were a good material for study of esterases, which were very active and stable. However, the high number of bands rendered the interpretation of the

Table 3. — Periods of stability of the expression of enzymes, studied in buds and leaves over an annual cycle at Valbonne.

MONTH	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J
PHENOLOGICAL STAGES :																		
of BUD	dormancy			bud opening	formation and growth							dormancy				bud opening	formation and growth	
of LEAF				leaf growth	active assimilation				senescence	leaf fall						leaf growth	active assimilation	
ACTIVE AND STABLE ENZYME SYSTEMS STUDIED :																		
in BUD	Peroxydases GOT LAP								Peroxydases GOT LAP									
in LEAF				GOT LAP acid phosphatases esterases														

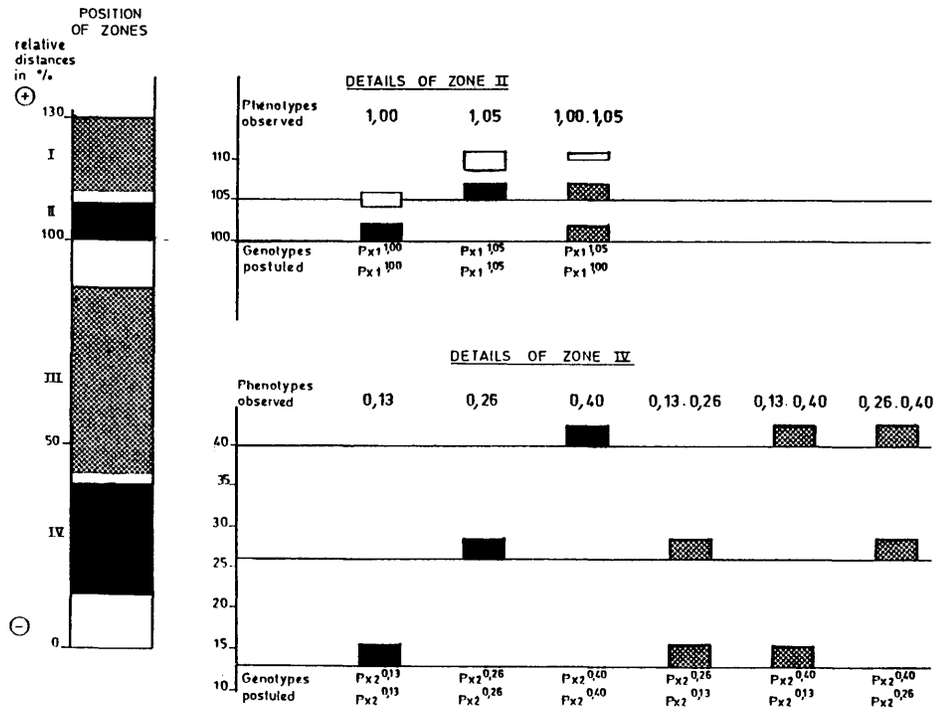


Fig. 2. — Schematic representations of zymograms for peroxydases

genetic determinism very difficult, and also, we did not have known material to verify our hypotheses. The Beech reaches sexual maturity when it is about 40 years old, and the cultivated plots at Hørsholm are only 20 years old.

Our first analyses were thus carried out on the buds, both because they are easy to work with and because the same extracts can be used to study three systems: peroxydases, GOT and LAP. An inventory of the isozymes of Beech is at present being pursued.

2. *Genetic determinism*

In the buds we have been also to establish the presence of LAP, the genetic determinism of which has been studied by ZIN-SUH-KIM (1979) in young leaves. These LAP can thus serve us as genetic markers. For our part, we have studied the inheritance of the other two active systems met in the buds: peroxydases and GOT.

a. *Study of peroxydases*

— Description of zymograms: With peroxydases we see 4 active zones *(Fig. 2)*. The bands of the first zone only appear in the floral buds. Their appearance depends essentially on a physiological state associated with the presence of male inflorescences. This first system always consists of 4 bands, 3 intense ones near the top and a rather faint one below. In the other systems which we encountered, only zones II and IV are sufficiently stable and clear for us to examine their genetic determination.

— Genetic determinism of bands of zones II and IV: In *zone II*, all the phenotypes showed (principle) bands matched by some clear (secondary) bands. Genetic studies showed that these principal and secondary bands corresponded to the same gene. They could either be two different molecular forms or an artefact. We shall only consider the principle bands.

Table 4. — Peroxydase of zone II, study of 5 progenies from controlled fertilizations, cultivated in Denmark

Progenies	Parents		Descendants						
	Phenotypes observed	Genotypes postulated	Phenotypes observed	Genotypes postulated	Number expected	Number observed	n	χ^2	p**
4276	♀ 1,00 . 1,05 ♂ 1,05	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,05}\ Px_1^{1,05}$	1,00 . 1,05 1,05	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,05}\ Px_1^{1,05}$	13 13	10 16	26	1,38	0,29
4274	♀ 1,00 . 1,05 ♂ 1,00 . 1,05	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,00}\ Px_1^{1,05}$	1,00 1,00 . 1,05 1,05	$Px_1^{1,00}\ Px_1^{1,00}$ $Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,05}\ Px_1^{1,05}$	10,75 21,50 10,75	10 18 15	43	2,30	0,48
4273	♀ 1,00 . 1,05 ♂ 1,00	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,00}\ Px_1^{1,00}$	1,00 1,00 . 1,05	$Px_1^{1,00}\ Px_1^{1,00}$ $Px_1^{1,00}\ Px_1^{1,05}$	18 18	21 15	36	1,0	0,19
4272	♀ 1,00 . 1,05 ♂ *1,00 . 1,05**	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,00}\ Px_1^{1,05}$	1,00 1,00 . 1,05 1,05	$Px_1^{1,00}\ Px_1^{1,00}$ $Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,05}\ Px_1^{1,05}$	5 10 5	6 9 5	20	0,30	0,039
4270	♀ 1,00 . 1,05 ♂ *1,00 . 1,05**	$Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,00}\ Px_1^{1,05}$	1,00 1,00 . 1,05 1,05	$Px_1^{1,00}\ Px_1^{1,00}$ $Px_1^{1,00}\ Px_1^{1,05}$ $Px_1^{1,05}\ Px_1^{1,05}$	9,25 18,50 9,25	11 16 10	37	0,72	0,13

Table 5. — Study of the progeny obtained by free pollinations from a known female parent cultivated near Orléans (France)

mother n° 28		Progeny		
Phenotype observed	Genotype postulated	Phenotypes observed	Genotypes postuled	Number of individuals
1,05	$Px_1^{1,05}\ Px_1^{nil}$	1,00	$Px^{1,00}\ Px_1^{nil}$	12
		1,00.1,05	$Px^{1,00}\ Px_1^{1,05}$	11
		1,05	$Px_1^{1,05}\ Px_1^{1,05}$ or $Px_1^{1,05}\ Px_1^{nil}$	2

The grouped results of our analyses in natural populations reveals the existence of 3 phenotypes; two phenotypes with one band [1.00*], [1.05*] and one with two bands [1.00; 1.05]. We have thus made the hypothesis that this is a case of one polymorplic locus with two codominant alleles, which specify monomeric enzymes.

The results of study of the Danish progenies are given in *Table 4*. Although two male parents were unavailable, in each case the nature and number of the phenotypes of their descendants seemed to confirm the existence of a single locus: Px_1, with two alleles $Px_1^{1.00}$ and $Px_1^{1.05}$.

* We have arbitrarily given the index 1.00 to the most frequent band, then by consideration of the relative migration distance of the two bands, the index 1.05 was given to the second.

Meanwhile, the possible presence of a silent allele cannot be excluded in certain populations, as shown by the free bred descendants of female parent n°28 *(Table 5)*.

In *zone IV*, the study of the group of individuals from natural populations revealed six phenotypes: three with one band each [0.13], [0.26] and [0.40], and three with two bands [0.13; 0.26], [0.13; 0.40] and [0.26; 0.40] which are shown in *Figure* 2. Thus we have hypothesed that they act from a single polymorphic locus with three codominant alleles, specifying monomeric enzymes.

The results from the 5 danish populations are shown in *Table 6*. In the line 4273, the X^2 obtained is rather elevated; the quality of the sample analysed could be responsible for the high value. Indeed, without considering the numbers of crosses aborted from the controlled crosses, the disappearance of a rather large number of individuals since their planting in 1961 *(Table 1)* could explain, in itself, the divergences between the total strength observed and those expected; especially if a selective mortality has occured over the last 20 years. Nevertheless, even with the number of phenotypes observed in the line 4273, the grouped phenotypes of the thirteen populations (northern and southern) seem to indicate that the most likely hypothesis is that they are controlled by a single locus, Px_2, with three codominant alleles $Px_2^{0.13}$, $Px_2^{0.26}$ and $Px_2^{0.40}$.

Table 6. — Peroxydase of zone IV — study of the 5 progenies from controlled fertilizations cultivated in Denmark

Progenies	Parents		Descendants						
	Phenotypes observed	Genotypes postulated	Phenotypes observed	Genotypes postulated	Number expected	Number observed	n	X^2	p**
4276 + 4274 + 4272 + 4270	♀ 0,26 ♂ 0,26 *	$Px_2^{0,26}\ Px_2^{0,26}$ $Px_2^{0,26}\ Px_2^{0,26}$	0,26	$Px_2^{0,26}\ Px_2^{0,26}$	127	127	127	-	
4273	♀ 0,26 ♂ 0,13 . 0,26	$Px_2^{0,26}\ Px_2^{0,26}$ $Px_2^{0,13}\ Px_2^{0,26}$	0,13 . 0,26	$Px_2^{0,13}\ Px_2^{0,26}$	19	13	38	3,79	0,71
			0,26	$Px_2^{0,26}\ Px_2^{0,26}$	19	25			

*) phenotype is observed for the male parent of lines 4276 and 4274 and is supposed for lines 4272 and 4270.
**) probability of observation by chance differences equal or superior to those observed according to the hypothese chosen.

Table 7. — Locus Px_1, distribution of phenotypes and alleles for 13 populations, allelic diversity and deviation to the panmictic genotypic.

Populations and number of trees analysed		PHENOTYPES, number of individuals observed $[Px_1^{1,00}]$	$[Px_1^{1,05}]$	$[Px_1^{1,05}_{1,00}]$	ALLELES, relative frequencies observed in % (q) $Px_1^{1,00}$	$Px_1^{1,05}$	confidence limits $2\sqrt{\frac{q\ (1-q)}{n}}$	Allelic diversity	Deviation of the population from the panmictic genotypic structure X_2	Phyto-sociological conditions
MASSANE	48	12	8	28	54,0	46,0	± 14,0	0,497	2,020	*Quercion*
VENTOUX haut	48	14	8	26	56,3	43,7	± 14,3	0,494	0,527	*Fagion*
VENTOUX bas	53	19	4	30	64,0	36,0	± 13,2	0,471	2,33	*Quercion*
MEYSSE	48	23	7	18	66,6	33,4	± 13,6	0,462	0,265	*Quercion*
LIRON sud	57	25	5	27	67,0	33,0	± 12,4	0,456	0,405	*Quercion*
Ste-BAUME	64	33	10	21	67,0	33,0	± 11,7	0,456	0,749	*Quercion*
SIMIANE sud	46	22	2	22	72,0	28,0	± 13,2	0,424	1,040	*Quercion*
LIRON nord	49	29	6	14	73,0	27,0	± 12,7	0,418	3,629	*Fagion*
SIMIANE nord	45	27	4	14	75,5	24,5	± 12,8	0,397	0,669	*Fagion*
CAYLAR	51	35	4	12	80,0	20,0	± 11,2	0,356	2,090	*Fagion*
AUBERIVE	49	38	7	4	82,0	18,0	± 10,9	0,340	13,060*	*Fagion*
VALBONNE	54	37	1	16	83,4	16,6	± 10,1	0,323	0,658	*Quercion*
LYONS	48	38	1	9	89,0	11,0	± 9,0	0,250	0,601	*Fagion*

*) significant diviation at the 5% level.

Studies upon other species of plants show that peroxydases are usually monomers (Asim Esen and Soost, 1976; Yen and Sadanaga, 1977) but occasionnaly dimers (Chiang Pai, Toru Endo and Hiro-Tchi Oka, 1973).

b. *Study of glutamate-oxaloacetate-transaminases (GOT)*

— Description of zymograms and genetic control: In GOT we observed 3 actives zones *(Figure 3)*, but only the bands of zone I were studied.

The individuals from the natural populations tell into 3 phenotypes, two with one band [1.000] or [1.050] and one with 3 bands [1.000; 1.025; 1.050]. The most likely explanation is that here we have dimeric enzymes specified by one gene showing two corresponding allelic forms. The two homodimers corresponding with the indices 1.000 and 1.050 and the heterodimer at 1.025.

It is impossible to confirm this hypothesis by studying the 5 danish lines. This is because the four known parents present the same phenotype [1.000] and are homozygotes: $GOT_1^{1.000}$; $GOT_1^{1.000}$. Meanwhile we have been able to verify that the descendants are all the same phenotype as their parents, that is [1.000].

We then have a single locus: GOT_1 with two codominant alleles, $GOT_1^{1.000}$ and $GOT_1^{1.050}$. These enzymes are already described as dimers in other species (Gottlieb, 1973; Hart and Market, 1975; Roose and Gottlieb, 1976; Lumaret and Valdeyron, 1978).

By examining Beech buds for polymorphism, we can now list eleven different alleles distributed between four loci: locus LAP (4 alleles coding for monomers), the locus Px_1 (2 alleles coding for monomers), the locus Px_2 (3 alleles coding for monomers) and the locus GOT_1 (2 alleles coding for dimers). Unfortunately the controlled crosses analysed does not offer the possibility to test the genetic links between these different loci.

3. *Polymorphism of Beech*

Only the peroxidases (zones I and IV) were systematically analysed in 11 southern and 2 northern populations. *Tables* 7 and 8 show the results obtained respectively for the locus Px_1 and for the locus Px_2. They countain the phenotypic frequencies observed in each population and the allelic frequencies as they can be deduced from the phenotypic frequencies.

From these allelic frequencies observed in each population, an index of diversity has been calculated following the formula (Shannon, 1948):

$$H = \frac{1}{n} \sum_{i=1}^{n} P_i \log_2 \frac{1}{P_i}$$

where P_i is the frequency or the probability of the allele i and n the number of alleles at a single locus. This index

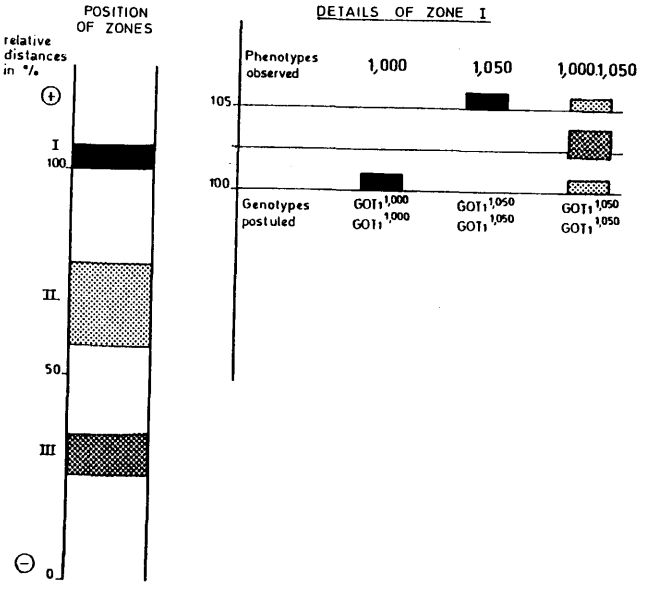
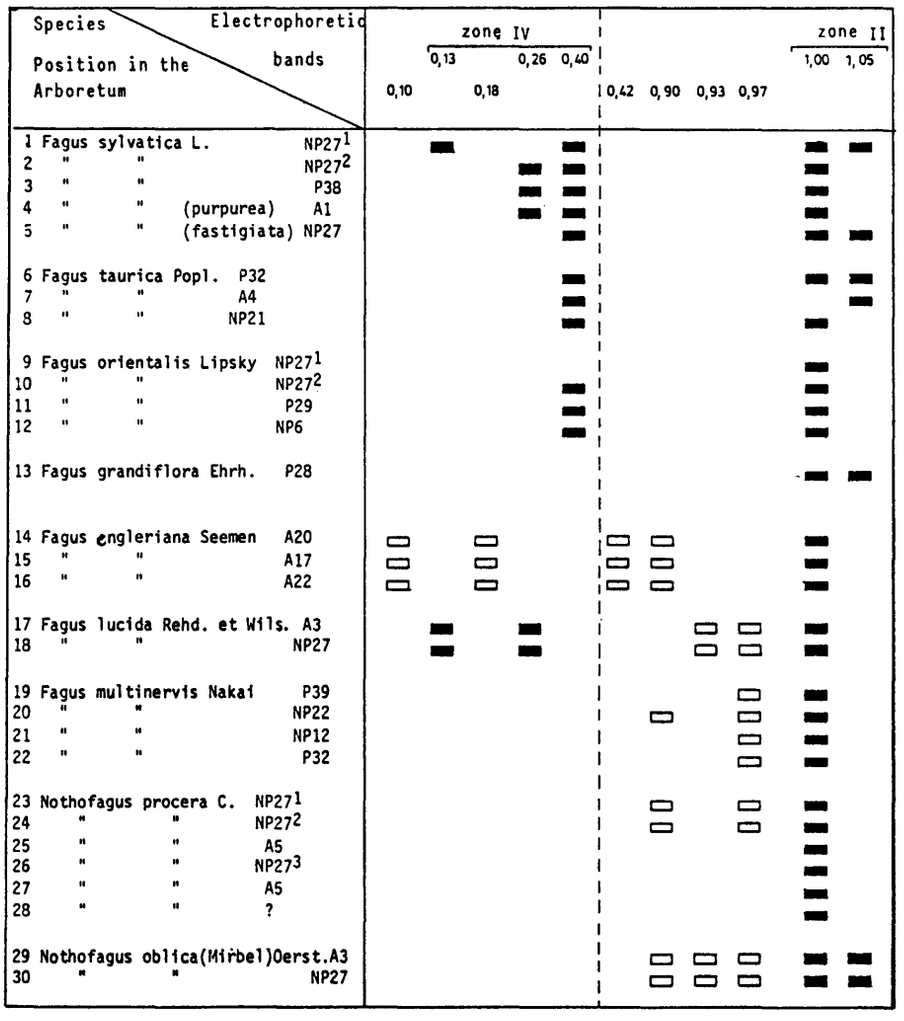


Fig. 3. — Schematic representations of zymograms for Glutamate-Oxaloacetate-Transaminases (GOT).

Table 8. — Locus Px_2, distribution of phenotypes and alleles for 13 populations, allelic diversity and deviation to the panmictic genotypic.

Populations and number of trees analysed		PHENOTYPES, number of individuals observed						ALLELES, relative frequencies observed in % (q), confidence limits $2\sqrt{\frac{q(1-q)}{n}}$				Deviation of the population from the panmictic genotypic structure X_2	Ecological conditions
		$Px_2^{0,13}$	$Px_2^{0,26}$	$Px_2^{0,40}$	$Px_2^{0,26}_{0,13}$	$Px_2^{0,40}_{0,13}$	$Px_2^{0,40}_{0,26}$	$Px_2^{0,13}$	$Px_2^{0,26}$	$Px_2^{0,40}$	Allelic diversity		
VENTOUX haut	48	0	18	3	2	12	13	14,7 ± 10	53,1 ± 14	32,2 ± 13	0,469	0,268	mountain
LIRON sud	57	1	21	5	11	6	13	16,6 ± 10	57,9 ± 13	25,5 ± 12	0,462	0,634	mountain
LIRON nord	53	0	23	5	7	8	10	14,2 ± 10	59,4 ± 14	26,4 ± 12	0,461	1,700	mountain
CAYLAR	56	1	13	8	8	1	25	9,8 ± 8	52,6 ± 13	37,7 ± 13	0,449	0,411	mountain
VENTOUX bas	53	2	17	5	3	2	24	8,6 ± 8	57,5 ± 14	33,9 ± 13	0,430	0,121	mountain
VALBONNE	54	1	29	3	9	3	9	12,9 ± 9	70,5 ± 13	16,6 ± 10	0,390	0,817	hills
Ste-BAUME	65	0	37	2	7	1	18	8,0 ± 7	72,0 ± 11	20,0 ± 10	0,365	0,213	hills
LYONS	50	2	31	1	6	0	10	10,0 ± 9	78,0 ± 12	12,0 ± 9	0,326	0,479	plain
MASSANE	48	0	29	0	7	1	11	8,3 ± 8	79,2 ± 12	12,5 ± 10	0,313	0,734	foothills
MEYSSE	48	0	28	0	12	0	8	12,5 ± 10	79,0 ± 12	8,5 ± 8	0,313	0,850	Rhône valley
SIMIANE nord	49	0	32	0	9	0	8	9,2 ± 8	82,6 ± 11	8,2 ± 8	0,283	0,219	foothills
SIMIANE sud	46	2	33	0	3	0	8	7,6 ± 8	83,7 ± 11	8,7 ± 8	0,275	0,173	foothills
AUBERIVE	49	1	36	0	6	1	5	9,2 ± 8	84,7 ± 11	6,1 ± 7	0,255	1,500	hills

Table 9. — Peroxydases among 30 trees from 9 distinct species cultivated at Arboretum des Barres (France)



▬ bands for which the genetic control is known : allozymes

▭ bands for which the genetic control is unknown : isozymes

has already been employed in a genetic sense by Lewontin (1972). One can *a priori* consider that it translates quite well to the evolutive and adaptive possibilities of a population since it increases, on the one hand, with the number of alleles, and on the other with their equilibrity. Then the distribution of genetypes in each population was tested by comparison to a situation of random-mating crossings (panmictic population). For this the number of homozygotes and heterozygotes obtained on the one hand and expected on the other hand (were calculated in counting the allelic frequencies observed), were compared with X^2. The geographic position or the phytosociological conditions of the beechwoods studied has been noted.

Moreover the analyse of peroxydases was carried out on 30 trees from 9 distinct species, cultivated at Arboretum des Barres (France)*, *Table 9.*

On distribution of alleles among the populations, three observations can be noticed.

+ Firstly, it appears that all the alleles are found in each population; they simply show frequency variations between populations. The fact that one finds the same alleles in diverse populations of the same species is not so surprising, when one knows that certain isozymes are common not only to the genus *Fagus* but also to the genus *Nothofagus Table 9.* Some variations stand out between individuals of a single species, but the locus Px_2 is expressed in all studied species. Some new bands, located near zone II, are characteristic of asiatic species and meanwhile the bands of zone IV are less distinctly expressed. On the whole with these analyses, however, we can established that the European and North American species show the same isozymes, and form a homogeneous group, while the asiatic species form a second distinct and more heterogeneous group in which *Fagus multinervis* Nakai seems closer to *Nothofagus* than the other *Fagus* species.

+ Secondly, the genotypic structure of the 13 populations does not reveal significant differences (at the 5% level) from panmixy, except in the population from Auberive for Px_2 locus, where one observes an excess of homozygotes.

+ Finally, thirdly, the variation from one population to another of the allele frequencies and those of the diversity index is not distributed randomly.

— the locus Px_1:

At this locus the allele $Px_1^{1.05}$ becomes more frequent in the southern populations; its high frequency seems characterized those fragments of beechstands which occur in the driest biotopes comparatively to the others. It is interesting to note the same trend of variation can be showed in the same direction on a smaller scale in a single site according to exposure, eventhough the differences are not statistically significant. Thus at Simiane and Liron, the allele $Px_1^{1.05}$ is much more frequent in the trees from the drier southern aspect, than in those facing north where the climate is cooler. On the contrary, however, the differences between the high and low parts of Ventoux mountain seem to demonstrate that the higher station was drier. This is not surprising, however as it was located in a sub-alpine region, on a gravel soil.

Such variations of allelic frequencies over short distances, related to environmental conditions were already observed in example, in *Thymus vulgaris* L. (Ph. Vernet *et al.*, 1977), in *Dactylis glomerata* L. (R. Lumaret *et al.*, in press) and in Ponderosa pine from Colorado (J. B. Mitton *et al.*, 1977). Moreover in consideration of the ecological conditions and the floristic composition of populations it seems that the least polymorphic populations correspond with the most typical Beech association (that is to say *Fagion)* situated within the main area of beech range (low diversity index, stations at the bottom of *Table 7)*, while the most polymorphic populations (high diversity index, stations of the top of *Table 7)* are hose fragments which occur toward the southern limit, the allele $Px_1^{1.05}$ becomes more frequent and diversity increases.

— the locus Px_2:

The differences between populations depend, above all, on the variation of frequency of the alleles $Px_2^{0.26}$ and $Px_2^{0.40}$; the allele $Px_2^{0.13}$ playing here a modest role. The allele $Px_2^{0.40}$ is rarer, the allele $Px_2^{0.26}$ more frequent and the allelic diversity high under cold climate, on mountains (stations at the top of *Table 8);* it is the contrary in zones of low elevation.

Conclusions

The loci demonstrated here are only a small proportion of the polymorphic loci of Beech. For the first loci studied from an ecological genetics point of view the variations of allelic frequencies show clearly the influence of climate on their distribution; aridity seems to be implicated for the first locus, and temperature for the second. Meanwhile, in spite of the diversity of geological substrata upon which the various populations were growing, we have not seen a single influence of ecology upon the allelic frequency. However, on this last point, further research of other enzyme loci could lead to the discovery of markers which are useful for systematic characterisation. Nevertheless, at the generic level, the asiatic group of species can be distinguish from european and american ones with peroxidases.

Even though our analyses were too few to allow generalisation, they show that the allelic diversity tends to increase in marginal situation where the beech is found in less favourable ecological conditions; under dry climates, at the southern limit, or under a cold climate, on mountains. Conversely tends to diminish towards the centre of beech distribution, where the species finds its most favourable conditions. The analysis of the genetic variability of the populations for the two enzymatic loci Px_1 and Px_2 considered together — and not separatly as here — is now in progress for higher number of populations.

From the results obtained concerning these few markers, it is reasonable to suppose that the knowledge of the enzymatic variability of Beech is also of considerable use to foresters, anxious to plant the material which is best adapted to a given area. This variability should be taken into account even if the relations between the biochemical characters and the morphological and phenological ones habitually used as criteria of selection, are not yet known.

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'Crop' and 'Isolation' Ideotypes: Evidence for Progeny Differences in Nursery-grown Picea sitchensis

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Summary

Ten open-pollinated progenies and two provenance standards (Masset and Hoquiam) of *Picea sitchensis* were grown in a nursery for 4 years in two experiments: (1) as widely-spaced trees (140 cm spacing) so that the trees never came into contact, and (2) in large pure progeny or provenance plots at 14 cm spacing so that there was intense inter-tree competition, which decreased 4-year heights by 26% and mean tree diameters by 60% compared with the widely-spaced trees.

The ten progenies had been evaluated earlier in forest trials at several sites relative to Masset provenance at about 2 m spacing. Many of the progenies that had been ranked as superior in height at age 4—6 after planting in those forest trials, also grew significantly taller and greater in diameter than the provenance standards in this study, but only in experiment (1) as widely-spaced trees. When grown in closed stands in experiment (2) none of the superior progenies were significantly greater than the provenance standards in mean height and diameter per tree, nor in basal area, total above-ground or stem dry weight per unit ground area (means 17.8 and 7.6 t/ha, respectively).

It is suggested that most tree progeny tests favour the selection of genotypes with the attributes of 'isolation' ideotypes, which grow rapidly as widely-spaced individuals, and 'competition' ideotypes which grow large in progeny mixture at their neighbours' expense. Selected genotypes may have few of the attributes of 'crop' ideotypes, which

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