material, including cytophotometry, physiological and molecular investigation, before we can consider sticky connections as a reflection of the high physiological activity of this tissue in development. At this point current knowledge allows hypotheses interpreting the sticky connections as "recognition" of identical, homologous parts of repetitive sequences between non-homologous chromosomes.

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Megagametophyte Salt-soluble Proteins as Genetic Markers in *Pinus pinaster* AIT.

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Summary

Salt-soluble proteins from haploid megagametophytes of *Pinus pinaster* seeds were analyzed by sodium dodecyl sulphate – polyacrylamide gel electrophoresis (SDS-PAGE). Seven polymorphic proteins were observed and their inheritances are reported. The genes encoding 6 of these proteins were found to be clustered into 2 linkage groups, each consisting of 3 loci. Variation at these proteins was estimated in seeds from nine locations within the natural area of distribution of *P. pinaster*. Our results demonstrate a close relationship between Tamjout (Morocco) and Ronda (Southern Spain) populations, as well as the uniqueness of the Corsican population within the Mediterranean group.

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Key words: Pinus pinaster, seed proteins, genetic markers, provenance differentiation, SDS-PAGE.

FDC: 165.3; 174.7 *Pinus pinaster.*

Introduction

The natural distribution area of *Pinus pinaster* AIT. is circumscribed to the Western Mediterranean basin (MIROV, 1967) with large populations found in France, Spain, Portugal and Italy. In addition to naturally occurring populations, *P. pinaster* covers vast areas in these countries as a result of important reforestation programs (BARADAT and MARPEAU, 1988; GIL et al., 1990). Selecting suitable material for these programs relies increasingly on the availability of useful genetic markers. The variability of *P. pinaster* seed proteins, as well as their inheritance and linkage relationships between their loci, have been investigated by 2-dimensional electrophoresis (BAHRMAN and DAMERVAL, 1989; GERBER et al., 1993). More recently, these seed proteins have been used as biochemical markers to compare populations from seven geographical locations (BAHRMAN et al., 1994). Two-dimensional electrophoresis allows a large number of markers to be analyzed simultaneously, but it is time-consuming and expensive when many samples are to be examined. This paper describes a simple method to identify potential markers among the seed proteins of *Pinus*, as well as to analyze their variability. A study was made of the inheritance of 7 polypeptide bands corresponding to megagametophyte salt-soluble proteins from *P. pinaster*, fractionated by onedimensional SDS-PAGE. Even though the number of markers that can be analyzed by this procedure is limited, as compared to more complex methods, it has proven useful to differentiate provenances of various *P. pinaster* populations.

Materials and Methods

Plant material

Nine naturally established populations of *Pinus pinaster* were chosen for this study (*Fig. 1*). For each geographical location, 58 to 144 megagametophytes from at least 30 trees were analyzed (no more than 2 megagametophytes per tree). Mature seeds were provided by Drs. J. A. PARDOS and L. GIL. (Dept. of Forestry, Universidad Politécnica de Madrid). Seed coats and embryonic axes were removed before protein extraction.

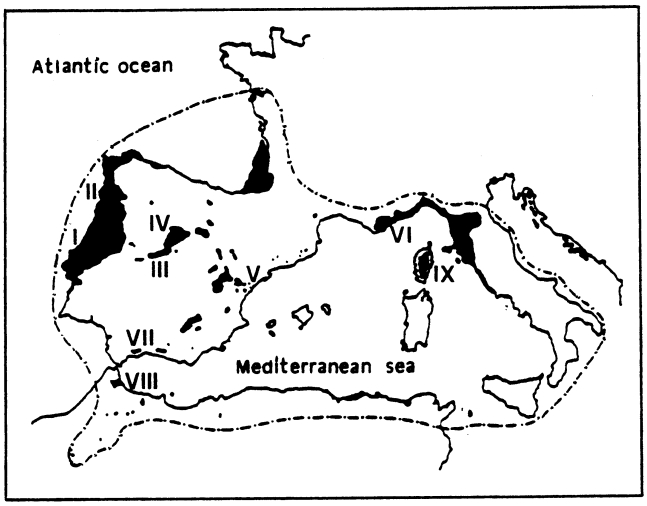

Figure 1. – Natural distribution and locations of the 9 geographical origins of *P. pinaster* considered in this work. Origin code: I-Leiria (Portugal), II-Puenteareas (Spain), III-Arenas de San Pedro (Spain), IV-Coca (Spain), V-Chóvar (Spain), VI-L'Esterel (France), VII-Ronda (Spain), VIII-Tamjout (Morocco), and IX-Corsica (France).

Protein extraction and electrophoresis

Megagametophytes were individually extracted with 1.2 ml of 0.05 M Tris-HCl, pH 8.2, 0.5 M NaCl at room temperature. After centrifugation at 9000 g for 8 min, proteins were precipitated with trichloracetic acid (12.5 % final concentration). Precipitates were washed with acetone (1 ml) and air-dried prior to electrophoresis. Sodium dodecyl sulphate-polyacrylamide gel electrophoresis (SDS-PAGE) was performed essentially as described by LAEMMLI (1970), using 15 % polyacrylamide in 0.53 M Tris-HCl, pH 8.8, for the separating gels. Gels were stained with Coomassie Brilliant Blue G as described by BLAKESLEY and BOEZI (1977). Since the observed electrophoretic patterns are not identical at different stages of seed development, those analyzed by us correspond to mature seeds and remain invariable since mid-september (Coca location; see *Fig. 1*).

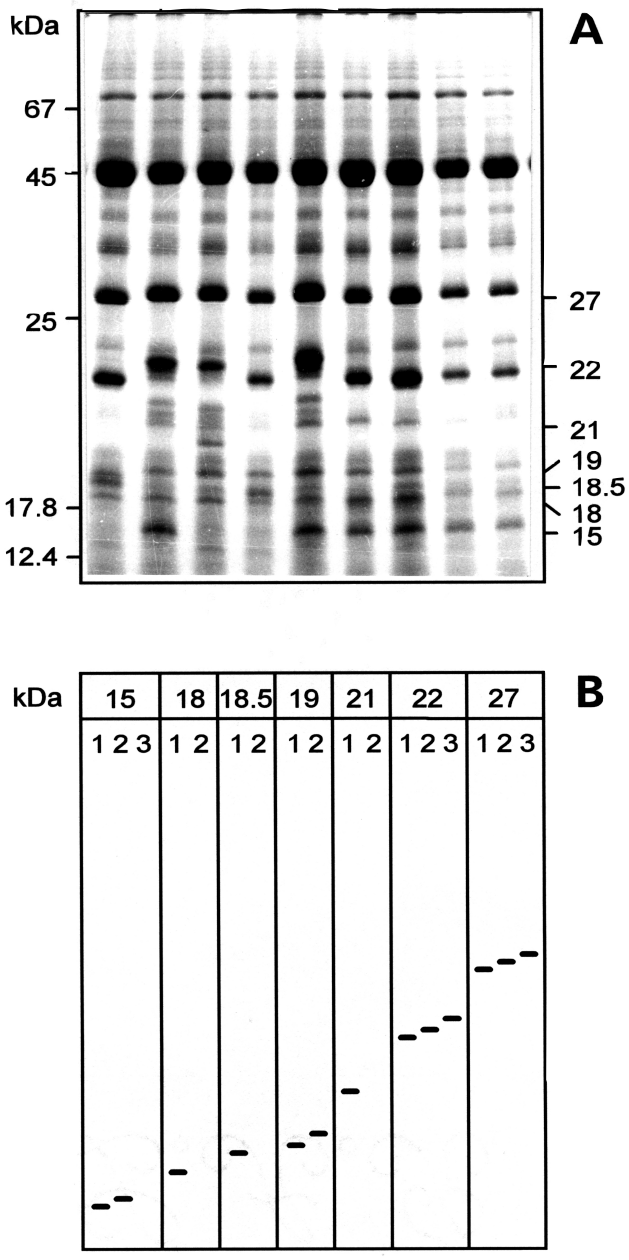

Figure 2. – (A) SDS-PAGE of salt-soluble proteins from megagametophytes of individual seeds of Coca Provenance. Polymorphic polypeptides considered in this study are indicated on the right of the figure by their Mrs. (B) Representative diagrams corresponding to alleles of the 7 polymorphic loci. Alleles 15 kDa (3), 18kDa (2), 18.5 kDa (2) and 21 kDa (2) are null alleles (see text).

Statistical analysis

Heterozygous mother trees were expected to segregate in a 1:1 ratio in haploid tissue (the megagametophyte). Chi-square analysis for 'goodness of fit' to the expected ratio was used in single-locus segregation tests. Linkage relationships were estimated from the segregation data of pairs of protein loci. Linkage analysis was performed as described by BAILEY (1961). Standard genetic distances (NEI, 1972) were calculated between all pairs of stands and these values were used for clustering populations by the unweighted pair-group method using arithmetic means (UPMGA) (SNEATH and SOKAL, 1973).

Results and Discussion

Segregation of polymorphic loci and linkage analysis

SDS-PAGE analysis of salt-soluble proteins from individual megagametophytes (*Fig. 2*) revealed the existence of variation in many electrophoretic bands, and allowed us to identify 7 proteins controlled by polymorphic loci. *Figure 2A* shows the electrophoretic mobilities of these polymorphic proteins, identified by their mean apparent Mrs. *Figure 2B* shows the electrophoretic variants observed for each locus.

The absence of an electrophoretic band was considered as a genetic variant by itself only when the presence/absence segregation did not significantly deviate from a 1:1 ratio. The analysis of gametophytes of trees putatively heterozygous for each of these polypeptides indicated an allelic behaviour in all cases (*Table 1*). Data corresponding to the 22 and 27 kDa polypeptides are not included here, as they are components of a 7 S globulin-like protein whose genetic analysis has been reported previously (ALLONA et al., 1994)

Table 1. – Observed segregation of allelic variants of salt-soluble proteins from megagametophytes of heterozygous mother trees and goodness-of-fit to the 1:1 expected ratio.

Protein	Electrophoretic variants				Deviation from expected to 1:1 ratio	
	1	*2*	*3*	*n*	χ^2 (1)	P
15kDa	-	54	37	91	3,18	0,074
15kDa	29	28	-	57	0,02	0,887
18kDa	24	20	-	44	0,36	0,548
18,5kDa	40	56	-	96	2,67	0,102
19kDa	63	55	-	118	0,54	0,046
21kDa	46	51	-	97	0,26	0,061

Availability of mother trees heterozygous at 2 loci allowed each polymorphic locus to be considered in at least 1 pair (*Table 2*). Seeds from these trees were used to determine the existence of linkage groups. Two-locus segregation was homogeneous for all pairs in which more than 1 mother tree was analyzed. Therefore, only combined data are given in *Table 2*. Strong evidence for linkage between loci corresponding to 15 kDa, 18 kDa and 18.5 kDa polypeptides, as well as 21 kDa, 22 kDa and 27 kDa polypeptides was found. The results obtained for pairs 15 kDa to 21 kDa, and 15 kDa to 22 kDa suggest that the above 2 groups may also be linked.

Provenance differentiation

The possible usefulness of these polypeptides as genetic markers was tested in a provenance differentiation study. The allelic frequencies of 5 polymorphic loci, corresponding to 15 kDa, 18.5 kDa, 19 kDa, 22 kDa and 27 kDa polypeptides, were calculated in 9 populations from the natural area of distribution of *P. pinaster* (*Fig. 1*). Polypeptides of 18 kDA and 21 kDa were not considered since it was not possible to unequivocally identify their alleles in all populations. *Table 3* shows the genetic distance values (NEI, 1972) estimated from allelic frequencies. These values are typical of the divergence level observed between different populations of the same species in a variety of conifers (GIANNINI et al., 1991; YEH and EL-KASSABY, 1980). Three major considerations can be inferred from the dendrogram obtained when the UPGMA method is applied to NEI's genetic distance (*Fig. 3*): (1) The Atlantic populations of *P. pinaster* (I, II, III and IV) and some of the Mediterranean ones (V and VI) appear to be clustered. Two subgroups are found within this cluster that correspond to those pairs of populations closest geographically to one another (Leiria-Puenteareas and Arenas de San Pedro-Coca). (2) The Moroccan and Ronda (Southern Spain) populations appear closely related as well. This is in agreement with previous results of BARADAT and

Table 2. – Two locus segregation data and chi-square tests for linkage analysis.

Combination	Observed numbers by allelic combinations					Deviation from expected to independent segregation	
						χ^2 (1)	P
15kDa-18kDa	*2-1*	*2-2*	*3-1*	*3-2*	*n*		
	0	19	23	0	42	42,00	0.000
15kDa-18.5kDa	*2-1*	*2-2*	*3-1*	*3-2*	*n*		
	0	35	13	0	48	48,00	0.000
15kDa-19kDa	*1-1*	*1-2*	*2-1*	*2-2*	*n*		
	16	13	11	17	57	1,42	0,233
15kDa-21kDa	*2-1*	*2-2*	*3-1*	*3-2*	*n*		
	9	10	17	6	42	3,43	0,064
15kDa-22kDa	*1-1*	*1-3*	*2-1*	*2-3*	*n*		
	5	11	12	5	33	5,12	0,024
15kDa-22kDa	*2-1*	*2-3*	*3-1*	*3-3*	*n*		
	10	9	6	18	43	3,93	0,047
19kDa-22kDa	*1-1*	*1-2*	*2-1*	*2-2*	*n*		
	14	12	8	14	48	1,33	0,249
19kDa-22kDa	*1-1*	*1-3*	*2-1*	*2-3*	*n*		
	19	22	19	24	84	0,05	0,823
21kDa-22kDa	*1-1*	*1-3*	*2-1*	*2-3*	*n*		
	0	46	49	1	96	92,04	0,000
22kDa-27kDa	*1-1*	*1-3*	*3-1*	*3-3*	*n*		
	85	0	0	97	182	182,00	0,000
22kDa-27kDa	*1-1*	*1-2*	*2-1*	*2-2*	*n*		
	22	0	0	26	48	48,00	0,000
22kDa-27kDa	*2-1*	*2-2*	*3-1*	*3-3*	*n*		
	0	14	34	0	48	48,00	0,000

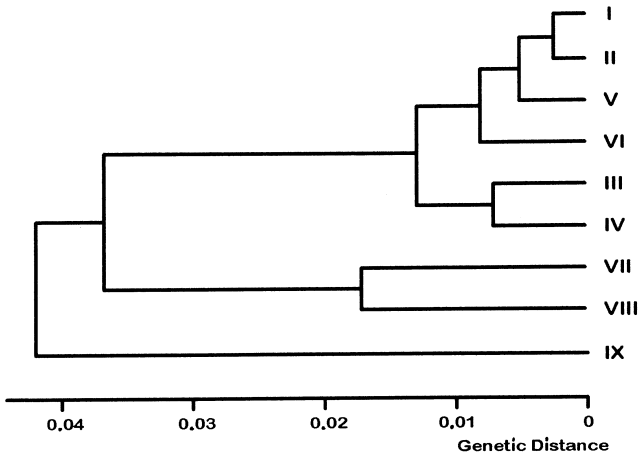

Figure 3. – UPGMA dendogram using NEI's genetic distance matrix.

Table 3. – Matrix of genetic distance among individual populations calculated following NEI (1972).

	I	II	III	IV	V	VI	VII	VIII	IX
I	0.000								
II	0.005	0.000							
III	0.022	0.023	0.000						
IV	0.037	0.039	0.014	0.000					
V	0.012	0.008	0.015	0.034	0.000				
VI	0.015	0.021	0.016	0.018	0.012	0.000			
VII	0.098	0.116	0.083	0.047	0.096	0.055	0.000		
VIII	0.055	0.069	0.090	0.060	0.068	0.043	0.034	0.000	
IX	0.115	0.102	0.058	0.035	0.085	0.063	0.084	0.126	0.000

MARPEAU (1988) using terpene polymorphism to differentiate provenances of *P. pinaster*. These authors suggested that the Ronda population has remained isolated from other maritime pines of Southern Spain since the formation of the Straits of Gibraltar, thus becoming a relict that has survived to different episodes of glaciation. (3) Genetically the Corsican population is the most distant from all others. It has been suggested that this population originated recently through human intervention, being the Liguria region of Italy and the East of Spain its most likely origins (BAHRMAN et al., 1994). Our results are compatible with this hypothesis and suggest that the Corsican population arose from a few founders, remaining ever since genetically isolated. The uniqueness of this population within the Mediterranean group has also been reported by BARADAT and MARPEAU (1988), and it was already mentioned in the classic work of DUFF (1928).

The results presented here indicated that fractionation of the megagametophyte proteins of *P. pinaster* by 1-dimensional SDS-PAGE can provide useful genetic markers complementary to those identified by more complex methods. The simplicity of this fractionation procedure may allow its use in laboratories unfamiliar with biochemical methods.

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Variation in Growth and Form of *Alnus acuminata* KUNTH. Grown in Costa Rica

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Summary

Results of a provenance/progeny test of *Alnus acuminata* in Costa Rica are presented. The treatments consisted of 45 open-pollinated families of one Guatemalan and 4 Costa Rican provenances. At 34 months, the Guatemalan provenance was significantly inferior in height and diameter growth rate, basal forking, stem lean and stem straightness. In addition, it was heavily attacked by the bark beetle *Scolytodes alni,* whilst the Costa Rican provenances were not attacked. There was little evidence for genetic differentiation between the Costa Rican provenances. There was no evidence of provenance related variation in the traits basal sweep and branch angle, nor in growth traits before age 34 months (except height increment between months 22 and 34). The family analysis, from which the Guatemalan families were omitted, revealed significant additive genetic variation in all the form and growth traits examined, except stem lean and non-basal forking. Estimates of heritability and additive genetic coefficient of variation for growth, stem straightness and branching traits were within the ranges typically found in forest trees. In spite of the presence of some adverse genetic correlations between height growth and form traits, in general the estimated values of the genetic parameters confirmed the potential for genetic improvement of *Alnus acuminata* in Costa Rica.

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