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Provenance Variation of *Pinus radiata* Grown in Greece

By D. I. MATZIRIS[1])

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Summary

Analyses of a *Pinus radiata* experimental plantings, including 18 provenances from the 1978 International Collection (4 from Ano Nuevo, 6 from Monterey, 3 from Cambria and 1 each from Cedros and Guadalupe islands, plus 3 controls), grown at 2 locations in Greece, gave the following results:

There are significant differences between provenances in total tree height, diameter at breast height, bark thickness, stem straightness, crown form, number of whorls, number of branches per whorl, branch diameter and resistance to frost.

The fastest growing populations were Ano Nuevo and Monterey while Cedros island was the slowest and is completely unadapted to Greek conditions.

There is a highly significant correlation between frost resistance and latitude of the provenances and populations (r= 0.80**). An exception is the Guadalupe island population, which although it originates from a low latitude was the most frost resistant in both locations.

The natural populations of radiata pine are suffering from inbreeding depression, however, heterosis is released in interpopulation hybrids. The "Guadalupe ex Camberra" provenance (control) which is a hybrid between Guadalupe and Monterey at the age of 12 years had a mean height at Raches 12.19 m, while the original Guadalupe island population was only 9.83 m. The Guadalupe ex Camberra was also the best at Granitsa planting with mean height at the age of 9 years of 6.56 m, followed by Talaganda seed orchard (control) at 6.27 m.

The differences between provenances within populations were insignificant for all characteristics studied, indicating that selection within the best populations (Ano Nuevo and Monterey) can be practiced without a concern at the provenance level.

Key words: Pinus radiata, Monterey pine, population, provenance, variation, correlation.

FDC: 165.52; 232.12; 174.7 *Pinus radiata;* (495).

Introduction

Pinus radiata D. DON also called radiata, Monterey or insignis pine is a well known and widely grown species. Its natural

[1]) National Agricultural Research Foundation, Forest Research Institute, Terma Alkmanos, Athens 11528, Greece

range is restricted to 3 small isolated populations on the California coast, Ano Nuevo, Monterey and Cambria and 2 small island populations of Guadalupe and Cedros of the coast of Mexico. The natural habitat has been described in details by many investigators (SCOTT, 1960; FORDE, 1964a and b; LIBBY et al., 1968; GRIFFIN and CRITCHFIELD, 1972). The species grows in a variety of soil types, mainly acidic. Acceptable soil types vary widely, ranging from infertile sandy and clay loam at Monterey, skeletal soils on Cedros island to basaltic loam on Guadalupe (SCOTT, 1960; LIBBY et al., 1968; BURDON and BANNISTER, 1973). The growth is restricted on clay and shallow soils and in poorly drained sites. The climate of the natural species range is of the Mediterranean type, with a total rainfall per year ranging from 250 mm at Cedros island to 1000 mm at Ano Nuevo, with a dry but cool, moist, foggy summer (SCOTT, 1960; LIBBY et al., 1968).

On the deepest well-drained soils the height increment increases almost linearly with the rainfall, whereas on the shallowest soils the increment is restricted because of poor aeration in the soil (JACKSON and GIFFORD, 1974; MATZIRIS, 1979a).

Despite the limited natural range (1.5 degree latitude in mainland California and 7000 ha total area), considerable variation between populations in silvicultural characteristics have been observed in many parts of the world (BANNISTER, 1959; FIELDING, 1961; ECCHER, 1969; BURDON and BANNISTER, 1973; MATZIRIS, 1979a; SHELBOURNE, 1983; FALKENHAGEN, 1991). Significant differences between provenances and populations have been also found in wood properties (BURDON and HARIS, 1973), frost resistance (BURDON and BANNISTER, 1973; MENZIES, 1976; HOOD and LIBBY, 1980; ALAZARD and DESTREMAU, 1981), suspectibility to *Dothistroma pini* (BURDON and BANNISTER, 1973; WILCOX, 1982; ADES and SIMPSON, 1991), aphid infections (FALKENHAGEN, 1991), tree form (BURDON and BANNISTER, 1973; MATZIRIS, 1979a) and morphological and anatomical needle characteristics (FORDE, 1964a and b). Family x site interactions in economically important characteristics have been recently studied in New Zealand (JOHNSON and BURDON, 1990) and in Australia (JOHNSON, 1992).

In Greece the first introduction of the species dates back to 1913, when it was planted in the arboretum of Vetina (MICHOPOULOS, 1931). There are still a few trees growing from this first introduction. Since 1969 radiata pine has been used in small scale by the Forest Service and at that same time the first provenance trials were established (MATZIRIS, 1979a and b).

In 1978 an International expedition was made to collect seed from stands of the 3 natural mainland populations in California and the 2 islands, Cedros and Guadalupe (ELDRIDGE, 1979). Seed from this collection was provided by CSIRO of Australia to the Forest Research Institute of Athens and was used to establish the provenance tests reported in the present study. The purpose of this paper is to report the results of the prov-

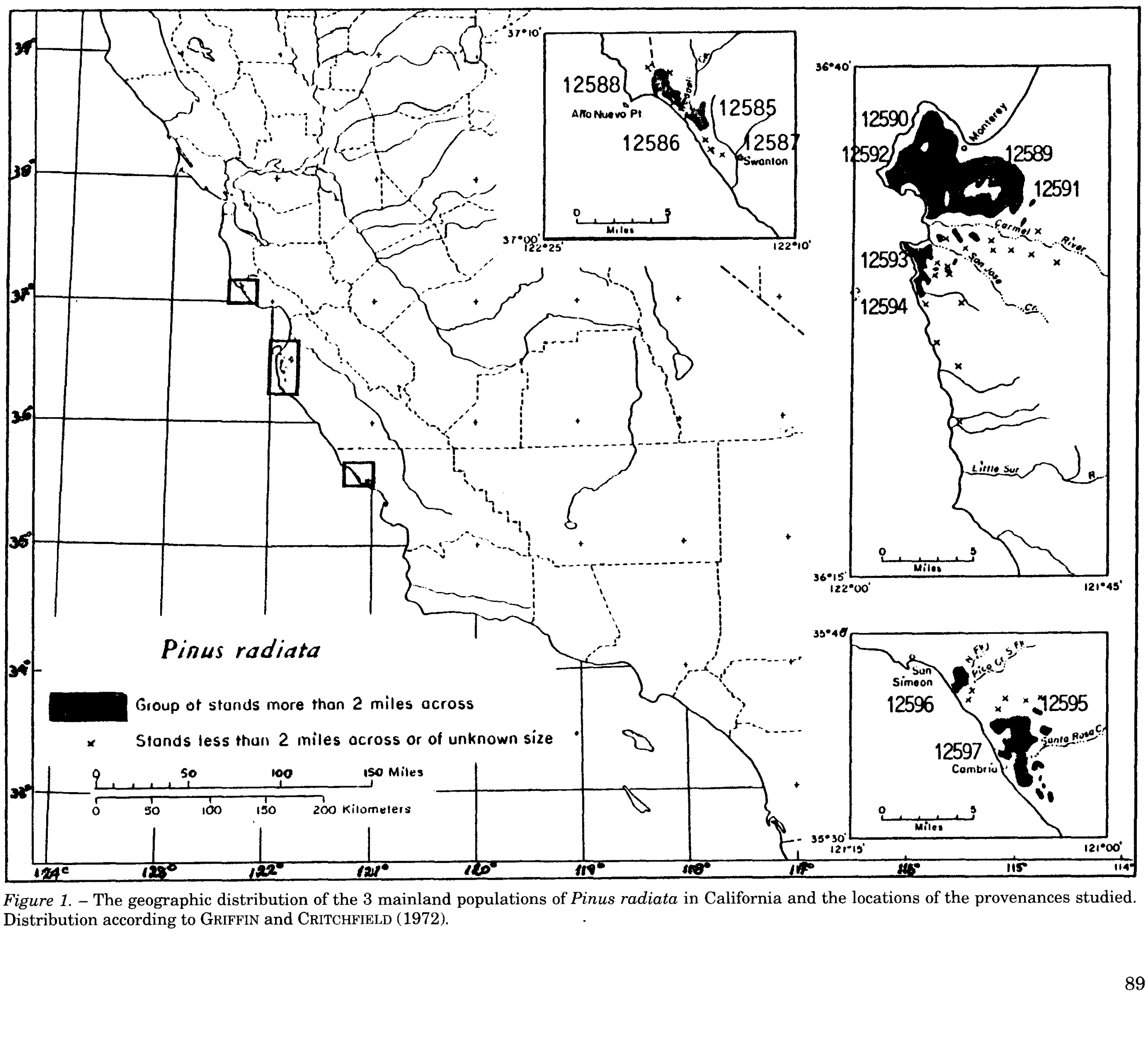

Figure 1. – The geographic distribution of the 3 mainland populations of *Pinus radiata* in California and the locations of the provenances studied. Distribution according to GRIFFIN and CRITCHFIELD (1972).

Table 1. – Characteristics of the *Pinus radiata* provenances used in the experimental plantings in Greece.

No.	Provenance I.D. Australia	Provenance I.D. Greek	Locality	Latitude	Longitude	Altitude m	Seed trees No	Geomorphology	Soil parent material
1	12586	370	01/1 Ano Nuevo coastal strip	37 06	122 17	20	70	Rocky coast	Pliocene marine sediments
2	12565	371	01/2 Ano Nuevo inland center	37 06	122 15	200	40	First ridge inland from sea	As above
3	12587	372	01/3 Ano Nuevo inland Swanton	37 04	122 14	130	40	Furthest inland	As above
4	12588	373	01/4 Ano Nuevo inland northern	37 08	122 18	140	29	Hillsides and marine terraces	As above
5	12590	374	02/1 Monterey coastal sand dunes	36 37	121 57	30	54	Sand dunes close to sea	White recent sand
6	12589	375	02/2 Monterey Monterey-Delmonde	36 35	121 52	45	38	Low sand dunes of NE slopes	Recent sand
7	12592	376	02/3 Monterey Huckleberry Hill	36 35	121 55	135	36	Central Monterey	Leached shallow podsol
8	12591	377	02/4 Monterey Jacks Peak Park	36 33	121 52	200	59	Ridges	As above
9	12593	378	02/5 Monterey Point Lobos Yankee Pt	36 30	121 57	50	22	Coastal rocky outcrops	Granodiorite, Paleocene
10	12594	379	02/6 Monterey Carmel Highlands	36 30	121 55	330	31	Sides of steep ridges	Granodiorite
11	12596	380	03/1 Cambria , Pico Creek	35 37	121 09	75	25	Gently sloping marine terraces	Cretaceous
12	12597	381	03/2 Cambria , Cambria Town	35 34	121 06	75	50	As above	Sandstones
13	12595	382	03/3 Cambria Scott Rock inland	35 35	121 04	120	25	Well drained slopes	Highly podsolised soils
14	12874	384	Guadalupe island	39 9	118 15	400	50		Sedimentary
15	12725	369	Cedros island	28 9	115 20	380	50		
16	12657	383	Guadalupe , ex Camberra						
17		261	Control : Euboia, Greece				›100		
18		260	Control : seed stand Borsi, Greece				›100		

enance tests concerning the variation in growth, branching, tree form, resistance to frost and a number of other important characteristics and find out the interrelationship that may exist among them.

Materials and Methods

In 1978 seed of radiata pine was collected from natural stands with the objective of conservation and provenance testing. The collections were made by an International team (Australian/New Zealand/United States) along the Californian coast and from the 2 Mexican islands of Guadalupe and Cedros (ELDRIDGE, 1979). The seed collected covers the full geographic range of the species which comprises 5 widely separated populations; Ano Nuevo, Monterey, Cambria, Cedros island and Guadalupe island. In the collection process 15 sub-populations, called provenances in the present study, were sampled as follows: 4 at Ano Nuevo, 6 at Monterey, 3 at Cambria and 1 from each island Cedros and Guadalupe. Within each of the first mentioned 13 provenances of the mainland, between 22 to 70 trees were sampled. The trees were chosen to have more than 40 or more closed cones and were more than 100 m from other collected trees. In Cedros and Guadalupe islands about 40 cones from each of the 50 randomly selected trees were collected (ELDRIDGE, 1979). More details for the locations of seed collection are given in *table 1* and *figure 1.* All provenances tested were collected in the natural stands, except the "Guadalupe ex Camberra" provenance the seed of which was collected in a small plantation in Camberra, established by Guadalupe seed. Since Camberra planting is surrounded with other plantations of Monterey origin, part of the seed collected is rather hybrid resulting from free pollinations between Guadalupe and Monterey populations (FALKENHAGEN, 1991). In the trails established, 2 controls originating from Greek plantings have been included; 1 from open pollinated seed of an old provenance test grown in Euboia island (MATZIRIS, 1979b) and 1 from a seed stand grown at Borsi Peloponnesos. The last planting has been raised from seed introduced from New Zealand, where radiata pine is grown as exotic.

Table 2. – Characteristics of the locations of the experimental plantings.

Characteristic	Location of the experimental plantings[1]	
	Raches	Granitsa
Latitude	37 ° 43 '	39° 07'
Longitude	24° 54'	25° 35'
Elevation (m)	605	650
Year of establishment	Oct. 1980	Nov. 1983
Provenances	18	17
Design	RCB	RCB
Replications	7	10
Plot size	10 tree - row plot	10 tree - row plot
Spacing	3X3 m	3X3 m
Natural vegetation	*Arbutus spp, Erica spp*	*Arbutus spp, Erica spp*
Soil parent materials	Tertiary siliceous deposits	Flysch
Rainfall/year, mm	1100	1440
Summer rainfall, mm	68.5	114
Abs. max. temperature	42	39
Abs. min. temperature	-6	-6

[1]) The experimental planting at Vresthena had been destroyed by a fire in summer 1988 and is not included in the analyses.

In fall of 1980 2 experimental plantings were established in southern Greece, in Raches Arkadias and Vresthena Lakonias (*Table 2*), using 1-year-old seedlings raised in paper pots filled with peat moss. In both plantings a randomized complete block design was used including 18 provenances in 7 replications. The experimental unit (plot) was comprised of 10 tree-row plot. The spacing applied was 3 m x 3 meters.

In November 1983 an additional planting was established in centralwest Greece at Granitsa Evritanias (*Table 2*) including all provenances previously used, except the Cedros and Guadalupe island populations. In this trial a new seed lot from Talaganda seed orchard of Australia was included. Seedlings production and experimental design was the same as previously, with the exception that 10 replications instead 7 were used.

The characteristics of the plantings are presented in *table 2.* The experimental planting at Vresthena has been destroyed by fire and is not included in the analysis.

Measurements

At Raches the following characteristics were measured. Total tree height (HT) at the ages 1, 2, 3, 4, 5, 9 and 12 years. Diameter at breast height (DBH) at ages 9, 10 and 12 years. At the age of 8 years (October, 1988) several additional characteristics were measured. Bark thickness at breast height (BTH) was estimated as the average of 2 diametrically opposite measurements. Stem straightness (STR) and crown form (CF) were evaluated according to a 5 class scale (1 very good, 5 very poor).

The number of whorls (WN) were counted along the stem; the number of foxtailed trees were also counted. A tree was characterized as foxtailed if the leader was unbranched over a length greater than one year's usually height growth. The total number of branches of the fifth whorl from the ground were counted and their diameter at a distance 5 cm from the main stem were measured. The diameter of the thicker branch (DTB), as well as, the mean branch diameter (MBD) of the whorl were calculated and assessed. Frost resistance (FR) was evaluated in Spring 1988 when an unusual late frost damaged the trees. The evaluation of injuries was made by assigning numerical values (scores) to trees as follows:

1 = no injury;
2 = slight injuries to few needles;
3 = injuries to needles of the greater part of the crown;
4 = injuries to needles and terminal shoots of the main stem and branches;
5 = injuries to all newly expanded shoots.

At the Granitsa location the characteristics measured were: Total tree height at 6 and 9 years and breast height diameter at age 9 years. Frost damages were evaluated in 1988 by assigning numerical values (1 to 5) as in the Raches planting.

Statistical Evaluation

Simple analyses of variance were performed for all characteristics measured or assessed. The analyses were based on plot means. Nested analyses of variance were also carried out in order to test the provenance within population effects. For the nested analyses only the 13 provenances of the 3 mainland populations were used. Orthogonal contrasts were calculated to break down the population degrees of freedom and make single comparisons between populations (SNEDECOR and COCHRAN, 1967, 10.1).

The data of Raches were also analysed by discriminal procedures (WILKINSON, 1986). Each provenance was classified into one of the populations by calculating its discrimination function or Mechalanobis distance from every population mean or centroid and classified it to the population whose centroid was nearest or equivalent to the population with the highest posterior probability of membership (JAMES and MCCULLOCH, 1990).

Product moment and SPEARMAN's rank correlations among all combinations of the characteristics were calculated following appropriate procedures (SNEDECOR and COCHRAN, 1967, page 193). It is worth mentioning here, that SPEARMAN's rank correlation is the best known procedure for studying the degree of relationship between 2 variables when there is subnormality in both pairs of variables.

Frost resistance was correlated with the latitude of the origin of the provenances. Stability of the frost resistance of the provenances was checked by correlation analysis.

Results and Discussion

Provenances averages for the Raches planting including mean heights, DBH, bark thickness, stem straightness, crown form, number of whorls, number of branches per whorl, diameter of the thicker branch, mean branch diameter, frost resistance, proportion of foxtailed trees and survivals are shown in *table 3.*

The mean heights and DBH for the Granitsa planting are listed in *table 4.* The analyses of variance for all characteristics are presented in *table 5* for the Raches and in *table 6* for the Granitsa,

Table 4. – Means of total tree height at the age of 6 (HT6) and 9 (HT9) years, DBH at the age of 9 (DBH9) years and frost resistance (FR) of *Pinus radiata* experimental planting grown at Granitsa.

Population and Provenance		HT6 m	HT9 m	DBH9 cm	FR score
ANO NUEVO	01/1	3.21	5.96	9.01	2.50
	01/2	3.07	5.96	8.24	2.67
	01/3	2.82	5.49	7.95	2.67
	01/4	3.34	5.86	8.88	2.67
	$\bar{X}$	3.11	5.82	8.52	2.63
MONTEREY	02/1	2.76	5.21	7.53	3.67
	02/2	3.07	5.99	8.43	2.30
	02/3	3.07	5.85	8.51	3.00
	02/4	3.03	5.89	8.36	4.00
	02/5	2.99	5.81	8.33	3.67
	02/6	2.93	5.66	8.08	3.33
	$\bar{X}$	2.98	5.74	8.21	3.33
CAMBRIA	03/1	2.85	5.29	7.54	4.00
	03/2	2.91	5.53	7.97	4.00
	03/3	2.80	5.58	8.40	4.33
	$\bar{X}$	2.85	5.47	7.97	4.11
GUADALUPE EX CAMBERRA		3.48	6.56	9.13	1.57
EUBOIA (local control)		2.92	5.76	8.16	2.67
BORSI (local control)		3.01	5.83	8.29	2.67
TALAGANDA S.O. (ACT)		3.34	6.27	9.68	4.00

Table 3. – Mean values of the characteristics[1]) studied at the *Raches* experimental planting.

No	Provenance[2] I.D.	HT1 m	HT2 m	HT3 m	HT4 m	HT5 m	HT9 m	DBH9 cm	DBH10 cm	HT12 m	DBH12 cm	BTH mm	STR score	CF score	WN no	BN no	DTB mm	MBD mm	FR score	Foxtails (%)	Surv. (%)
1	O1/1	0.46	0.68	0.99	1.47	2.23	6.70	9.51	11.01	10.96	13.24	3.86	2.70	2.45	10.26	7.10	22.0	15.83	2.02	4.4	97.1
2	O1/2	0.52	0.73	1.03	1.56	2.37	7.34	10.60	12.21	12.13	14.87	3.81	2.26	2.37	10.72	7.20	24.16	17.40	2.02	3.1	91.4
3	O1/3	0.51	0.77	1.06	1.57	2.38	6.94	10.09	11.91	11.34	14.43	3.78	2.20	2.25	10.24	7.61	23.10	16.40	1.89	4.7	91.4
4	O1/4	0.51	0.73	1.00	1.53	2.28	6.82	10.20	11.58	11.12	14.37	3.67	2.51	2.31	10.18	7.09	22.94	16.93	1.82	6.4	88.6
	$\bar{X}$	0.50	0.73	1.02	1.53	2.31	6.95	10.10	11.68	11.39	14.23	3.78	2.42	2.34	10.35	7.25	23.05	16.64	1.94	4.65	92.1
5	O2/1	0.55	0.81	1.10	1.68	2.53	6.82	10.43	12.10	10.80	14.57	4.20	2.54	2.92	10.20	7.59	23.51	16.31	2.65	1.5	92.8
6	O2/2	0.55	0.80	1.34	1.72	2.49	6.93	10.59	12.33	11.51	14.74	4.31	2.37	2.85	10.07	7.29	25.01	17.42	2.56	5.8	98.6
7	O2/3	0.54	0.77	1.07	1.64	2.49	6.93	10.06	11.83	11.61	14.04	4.19	2.17	2.90	9.67	7.66	24.39	17.26	2.80	1.6	91.4
8	O2/4	0.52	0.76	1.04	1.59	2.38	6.86	10.14	11.81	11.13	13.96	4.24	2.08	2.37	10.95	7.59	22.64	16.40	3.00	0.0	84.3
9	O2/5	0.55	0.85	1.18	1.75	2.60	7.19	10.84	12.63	11.53	15.16	4.22	2.31	2.66	10.25	7.53	25.69	17.59	2.45	7.9	90.0
10	O2/6	0.52	0.71	0.99	1.48	2.34	6.70	9.60	11.20	10.98	13.61	3.97	2.74	2.77	9.34	7.78	22.16	16.07	2.20	0.0	91.4
	$\bar{X}$	0.54	0.78	1.12	1.64	2.47	6.90	10.28	11.98	11.25	14.35	4.19	2.37	2.74	10.08	7.57	23.90	16.84	2.61	2.8	91.4
11	O3/1	0.50	0.78	1.08	1.56	2.33	6.64	9.71	11.20	11.27	13.24	4.13	2.63	2.81	9.73	7.16	23.38	16.24	2.57	3.1	91.4
12	O3/2	0.48	0.72	0.99	1.46	2.16	6.38	9.56	11.03	10.87	13.37	4.16	2.20	2.45	9.49	6.85	22.25	15.95	2.25	5	85.7
13	O3/3	0.49	0.73	1.01	1.50	2.24	6.78	9.61	11.11	11.07	13.33	4.15	1.96	2.48	9.90	7.03	21.44	15.19	2.34	3.3	85.7
	$\bar{X}$	0.49	0.74	1.03	1.51	2.24	6.60	9.63	11.11	11.07	13.31	4.15	2.26	2.58	9.71	7.01	22.36	15.79	2.39	3.8	87.6
14	Guadalupe	0.38	0.62	0.85	1.27	1.94	5.80	7.07	8.30	9.83	10.53	2.77	1.98	1.95	8.71	6.28	17.00	12.80	1.83	0.0	91.4
15	Cedros	0.31	0.46	0.61	0.90	1.47	4.66	5.39	6.50	8.22	8.53	2.70	2.67	2.64	7.46	4.52	14.08	11.47	1.47	2.4	58.6
16	Guadalupe ex Camberra	0.51	0.76	1.09	1.65	2.61	7.43	10.46	12.04	12.19	14.87	3.47	1.96	2.22	12.27	6.91	21.62	16.09	1.95	0.0	88.6
17	Euboia (Greek)	0.54	0.77	1.12	1.69	2.55	7.71	11.00	12.61	12.25	15.24	3.75	2.20	2.31	10.75	7.13	22.92	17.07	1.83	6.2	91.4
18	Borsi (Greek)	0.50	0.75	1.06	1.62	2.46	7.29	10.56	12.27	12.17	15.01	4.16	2.44	2.50	11.03	7.11	23.47	16.93	2.06	4.7	91.4

[1]) HTi DBHi total tree height and DBH at the age i years respectively;
BTH bark thickness, STR stem straightness, CF crown form, WN number of whorls,
BN number of branches per whorl, DTB diameter of the thicker branch in the whorl,
MBD mean branch diameter in the whorl, FR frost resistance.

[2]) O1/i, O2/i, O3/i, Provenance i of Ano Nuevo (O1), Monterey (O2) and Cambria (O3) population.

Table 5. – Analyses of variance of 18 characteristics of the *Pinus radiata* provenance experimental planting grown at Raches.

	MEAN SQUARES[1]		
Characteristic[2]	Replications	Provenances	Error
HT1	0.014	0.027**	0.005
HT2	0.009	0.051**	0.007
HT3	0.055	0.110**	0.020
HT4	0.099	0.268**	0.042
HT5	0.288	0.522**	0.085
HT9	0.694	3.192**	0.377
DBH9	3.150	13.469**	1.024
DBH10	4.138	16.837**	1.370
HT12	4.149	6.353**	0.761
DBH12	5.081	20.373**	1.815
BTH	0.299	1.565**	9.405
STR	1.943	0.463**	0.139
CF	1.901	0.507**	0.158
WN	1.185	7.153**	1.377
BN	4.445	3.777**	0.859
DTB	20.599	53.210**	6.846
MBD	14.979	17.605**	3.758
FR	0.742	1.492**	0.113

[1]) Degrees of freedom for all characteristics: Replications 6, Provenances 17, Error 102.

**) statistically significant at 0.01 probability level.

[2]) HTi, DBHi total tree height and DBH at the age i years respectively: BTH bark thickness, STR stem straightness, CF crown form, WN number of whorls, BN number of branches per whorl, DTB diameter of the thicker branch in the whorl, MBD mean branch diameter in the whorl, FR frost resistance.

Table 6. – Analyses of variance for total tree height at the age of 6 (HT6), 9 (HT9), and DBH 9 (DBH9) years for the Granitsa experimental planting.

Source of variation	D. F.	Mean Squares[1]		
		HT6	HT9	DBH9
Replications	9	8.125**	28.371**	58.536**
Provenances	16	0.366*	1.088*	3.043*
Prov. x replications	144	0.136	0.433	1.204

[1]) HT6, HT9, DBH9, Total tree height and DBH at the ages 6 and 9 years respectively.

*), **), statistically significant at 0.05 and 0.01 probability level respectively.

Differences Among Provenances

Growth Characteristics

At Raches the provenance means for total tree height at the age of 12 years varied from 8.22 m (provenance from Cedros island) to 12.25 (local Greek control from Euboia island). The 2 local growing controls outperformed all the provenances of the natural populations (*table 3*) which was not unexpected. Similar results have been reported in Italy (ECCHER, 1969), New Zealand (BURDON and BANNISTER, 1973; BURDON, 1983), Australia (GRIFFIN, 1977) and recently in South Africa (FALKENHAGEN, 1991). In all these cases provenances grown and selected under local conditions were the best in growth. There are, however, many other reasons for the better performance of the Greek provenances (controls).

(i) The Greek populations of radiata pine were introduced from New Zealand, where they were cultivated for 2 generations under the conditions of the host country (BURDON and BANNISTER, 1973). This population was originated from Ano Nuevo, which is considered as the fastest growing among the natural populations of radiata pine. Therefore, 2 generations in New Zealand, followed by 1 generation in Greece were enough to modify to some degree the genetic structure of the original population.

(ii) There are indications that in the natural population inbreeding has taken place (BURDON and BANNISTER, 1973). Natural stands may be derived from a small number of trees escaping fires (LIBBY et al., 1968) and therefore all neighbouring trees may be closely related. A linear decline in growth rate with an increasing inbreeding coefficient has been shown to occur in radiata pine (BURDON and MATHESON, 1983). It was found that at 12 months there was a mean 5.4% decrease in height growth for each 0.1 increase in the inbreeding coefficient. Collecting seed from widely separated trees and raising artificial stands is expected to reduce the inbreeding coefficient and favor good tree growth.

(iii). The seed of Euboia island (control) was a mixture of natural hybrids resulting from crosses between different provenances, since the seed was collected within an old provenance tests (MATZIRIS, 1979a). Therefore greater heterosis is expected in the progeny as the result of crosses between unrelated trees of different provenances and populations. The heterosis effect is more obvious in the Guadalupe ex Camberra provenance. The seed of this lot has been collected in a small trial in Camberra (Australia), established from Guadalupe seed and therefore is considered to be a hybrid resulting from open pollination with the surrounding plantations, which are largerly of Monterey origin (FALKENHAGEN, 1991). The mean height of this control at the age of 12 years was 12.19 m and ranked second (after the local Greek of Euboia island), while the original Guadalupe provenance had a mean height 9.83, little slightly more than the slowest growing provenance of Cedros island (8.53). Cedros provenance was the worst not only for growth but also for survival.

At the age of 8 years the percentage of surviving trees of the Cedros island population was 58.6, while the overall mean of the planting was found 88.95% (*Table 3*). The inferiority of this provenance under Greek conditions was evident even in the nursery stage. After 1 year growth in the field the mean height was 0.31 m and its growth was the lowest in all following years (*Table 3*). Surprising enough, a few trees of this provenance are fast growing and may have some use in breeding programmes by providing genes for dry sites. Promising results from inter-provenance crossing including Monterey x Cedros have been obtained in Australia and New Zealand (ANONYMOUS, 1983). The Cedros island population was found to be the slowest in growth in provenance trials grown in Australia (BURDON and BANNISTER, 1973), as well as in South Africa (FALKENHAGEN, 1991).

At the Granitsa trial, the differences among provenances in heights and DBH were statistically significant (*Table 6*). In this trial Cedros and Guadalupe provenances have not been included. Instead, a new control from Talaganda (Australia) seed orchard was used. The pattern of differences between provenances at the ages of 6 and 9 years remained fairly constant, with Guadalupe ex Camberra (control) being the best followed by Talaganda seed orchard (*Table 4*).

Branching Characteristics

There are significant differences between provenances in the number of whorls produced. The number was greater in provenances from Ano Nuevo and decreased gradually in provenances from Monterey and Cambria. There is a clear indication that the fastest growing provenances form more whorls (*Table 3*). In the slowest growing provenance of Cedros island, the mean number of whorls was found 7.46, while in the fastest growing provenance of Guadalupe ex Camberra it was 12.27. It is known that the number of whorls produced in radiata pine is controlled by environmental as well as genetic factors. MATZIRIS (1979a) in provenance trials grown in Greece found that the number of whorls is greater on better sites, where growth is faster. Other investigators (FIELDING, 1966;

BANNISTER, 1966; RAYMOND and COTTERILL, 1990) have determined that this characteristic is partially under genetic control. Internode length, which is a function of height growth and the number of whorls produced per year has created conflicting strategies in selection for multinodal or uninodal trees (HARRIS and WILCOX, 1976; LIBBY, 1983). In New Zealand selections have been made at both extremes, but the preferred type for general utility is the multinodal tree.

The average diameter of the branches of a whorl varies considerable among provenances. Similar variation has been also observed and in the diameter of the thicker branch (*Table 3*).

Branchless Stems or Foxtails

The production of branchless stems or as it is also known as "Foxtails" is a phenomenon that is common to tropical or subtropical pines. The leader of trees of this category are unbranched over a length greater than the one year's usual growth (KOZLOWSKI, 1971). Considerable variation was evident in the proportion of foxtails among the provenances studied. Provenance mean values ranked from 0 (Guadalupe, Guadalupe ex Camberra and 03/6 Monterey) up to 7.9% (provenance 02/5 from Ano Nuevo). The overall mean of foxtail trees was 3.3% (*Table 3*). The phenomenon is related to climatic and edaphic factors and to genotype (BURDON, 1971). It is also believed that high soil fertility may be a predisposing factor for foxtail attitude.

Frost Resistance

The analysis of variance (*Table 5*) showed that the differences among provenances in frost resistance are statistically significant. A characteristic clinal variation across the latitudinal gradient is evident. The northern population of the Ano Nuevo was the more resistant, while the southern of Cambria was the most sensitive. Monterey provenances were intermediate. An exception of this trend was observed in the Guadalupe ex Camberra (control), where it was found to be the most tolerant. There are indications that Guadalupe island, although is located in lower latitude, may has colder climate than the northern coastal areas of central California, where the other natural populations of the species originate. The correlation coefficient between latitude and frost resistance was very strong (r= –0.80**) in the northern planting of Granitsa and weaker but still significant in the souther planting of Raches (r= –0.39*). It is worth mentioning here that in the evaluation of frost resistance, lower values (scores) were given to more resistant trees and therefore the negative correlations found indicate that frost resistance is increasing with latitude. The 2 local grown provenances (controls) which have been introduced into Greece are from the Ano Nuevo population and as expected, are among the most resistant (*Table 3*). The results found here are in agreement with those reported by ALLAZARD and DESTREMAU (1981) in 2-year-old provenance trials grown in France. Highly significant differences between the 3 mainland populations have been also found in a clonal test grown in California (HOOD and LIBBY, 1980). The correlation coefficient in frost resistance between the provenances grown in the 2 locations, Raches and Granitsa, was found 0.68**, indicating that a cold resistant provenance in 1 location remains fairly consistent. Frost damage to radiata pine can be a problem, especially at a young age and in the higher altitudes and northern districts of Greece. The tolerance of the species to low winter temperatures is found to be –10 °C (MENZIES, 1976), while slight drop bellow 0 at Spring (late frost) can be harmfull to trees.

Other Characteristics

Among the other characteristics studied, stem straightness and bark thickness deserve attention, because of their economic importance. The differences among provenances in stem straightness were highly significant (*Table 5*). The Guadalupe provenance was the best, while provenances from Ano Nuevo were the worst. These results are in close agreement with those reported by BURDON and BANNISTER (1973). They also found that Guadalupe was the best in straightness in New Zealand and suggested that this population may contribute genes towards straighter stems and tolerance to severe exposure.

Concerning bark thickness, there is significant negative correlation between it and latitude of the seed origin (r=–0.58**). This indicates that bark thickness decreases from south to north. An exception was observed in the Guadalupe and Cedros islands which had the thinner bark (2.77 mm and 2.70 mm, respectively). Ano Nuevo provenances had mean bark thickness 3.78 mm, Monterey 4.19 mm and Cambria 4.15 mm (*Table 3*). Part of the variation in bark thickness is related to variation in growth rate, since these characteristics are interrelated. This may explain the thinner bark of the slowest growing populations of Cedros and Guadalupe islands.

Differences Among The Three Main Populations

Nested analyses of variance of the 3 main natural populations (13 provenances) showed that there are no significant differences between provenances within populations for all characteristics studied in both locations (*Table 7* and *8*). The

Table 7. – Nested analyses of variance of the 3 main populations of *Pinus radiata* grown at Raches experimental planting.

		MEAN SQUARES[1]								
Source of variation	**D.F.**	**HT1**	**HT2**	**HT3**	**HT4**	**HT5**	**HT9**	**DBH9**	**DBH10**	**HT12**
Populations (P)	2	0.006	0.006	0.009	0.020	0.079	0.277	0.748	1.394	0.179
Provenances/P	10	0.003	0.012	0.021	0.043	0.083	0.312	1.105	1.408	1.051
Replications (R)	6	0.001	0.002	0.013	0.020	0.048	0.118	0.484	0.687	0.908
P*R	12	0.001	0.002	0.007	0.007	0.048	0.082	0.401	0.475	0.254
R*Pr/P	60	0.004	0.005	0.016	0.036	0.088	0.388	0.970	1.312	0.752
Source of variation	**D.F.**	**DBH12**	**BTH**	**STR**	**CF**	**WN**	**BN**	**DTB**	**MBD**	**FR**
Populations (P)	2	2.074*	0.354*	0.019	0.285	0.726	0.557	4.136	3.876	0.722*
Provenances/P	12	2.169	0.060	0.496	0.223	1.249	0.251	9.569	5.214	0.094
Replications (R)	6	0.769	0.054	0.287	0.239	0.097	0.454	1.286	2.820	0.117
P*R	12	0.499	0.078	0.072	0.097	0.405	0.522	3.374	5.018	0.084
R*Pr/P	60	1.890	0.149	0.125	0.165	1.036	0.924	7.062	4.147	0.129

[1])*) Statistically significant at 0.05 probability level.
HTi, DBHi total tree height and DBH at the age i years respectively;
BTH bark thickness, STR stem straightness, CF crown form, WN number of whorls,
BN number of branches per whorl, DTB diameter of the thicker branch in the whorl,
MBD mean branch diameter in the whorl, FR frost resistance.

Table 8. – Nested analyses of variance (A) and contrast comparisons for HT9 (B) of the three main populations of *Pinus radiata* grown at Granitsa experimental planting.

A. Analyses of variance

Source of variation	D. F.	MEAN SQUARES[1] HT6	HT9	DBH9
Populations	2	0.134 *	1.349 *	0.838
Provenances / population	10	0.153	0.536	1.585
Replications	9	1.364 **	5.569 **	10.911 **
Populations x replications	18	0.039	0.281	0.341
Error	90	0.117	0.448	0.919

B. Contrast comparisons for HT9 for populations

Comparison	Totals (T) Ano Nuevo 58.2	Monterey 57.4	Cambria 51.5	Li = ΣTλi	Divisor $n\Sigma\lambda^2$	SS = $Li^2/n\Sigma\lambda^2$	D.F.
$\lambda_1 i$	+1	0	- 1	6,7	20	2.245*	1
$\lambda_2 i$	+1	-2	+1	5.1	60	0.434	1
					Total SS	2.679	2

[1]) HT6, HT9, DBH9, Total tree height and DBH at the ages 6 and 9 years respectively.

*), **) Statistically significant at 0.05 and 0.01 probability level respectively.

Table 9. – Values of the 2 main factors and Mechalanobis distances of 13 provenances of the 3 mainland populations, Ano Nuevo (O1), Monterey (O2) and Cambria (O3).

Provenance	Factor (1)	Factor(2)	Distance(1)	Distance(2)	Distance(3)
o1/1	-7.461	0.965	2.704	13.610	7.509
O1/2	-6.787	3.122	2.443	13.196	8.951
o1/3	-5.403	2.233	2.694	11.709	7.635
O1/4	-7.419	3.321	2.470	13.821	9.376
O2/1	6.664	0.812	13.789	2.766	11.329
O2/2	7.195	0.016	14.324	2.536	11.320
O2/3	5.903	-0.630	13.280	2.887	10.010
O2/4	6.172	1.346	13.282	2.885	11.222
O2/5	4.276	1.105	11.349	2.859	9.461
O2/6	5.617	1.523	12.712	2.873	10.856
O3/1	-2.343	-3.185	7.419	9.399	2.552
O3/2	-2.283	-5.241	9.064	10.338	2.078
O3/3	-4.133	-5.389	8.429	11.933	2.317

differences between populations were significant for DBH at age 12 years, bark thickness and frost resistance at Raches planting (*Table 7*) and for height at the age of 6 and 9 years at Granitsa (*Table 8*). FALKENHAGEN (1991) has also found in South African provenance trials raised from seed of exactly the same collection, significant differences between the three main natural populations and insignificant differences between provenances within the population for growth at ages 4 and 8 years. At Raches, the Ano Nuevo and Monterey populations are not different in DBH at the age of 12 years but both are statistically better from the Cambria population. At Granitsa height and DBH at the age 9 years of the Ano Nuevo and Monterey populations were better than those Cambria. Provenance trials of the 3 mainland population established in Australia Capital Territory in 1942 and 1949 have also shown that Cambria population was the slowest in growth rate (ANONYMOUS, 1963).

Discriminal analysis of variance for the Raches trial based on ten characteristics (total tree height and DBH at age 12 years, bark thickness, stem straightness, crown form, number of whorls, number of branches per whorl, diameter of the thicker branch, mean branch diameter and frost resistance) resulted in perfect classification of the provenances in the populations where they originate. The values of the 2 factors for all provenances and the Mechalanobis distances are shown in *table 9*. The distribution of the provenances in the axes of the factors are graphically presented in *figure 2*. The results verify once again that there are significant differences between the three mainland populations of radiata pine, while the differences between provenances within populations are insignificant.

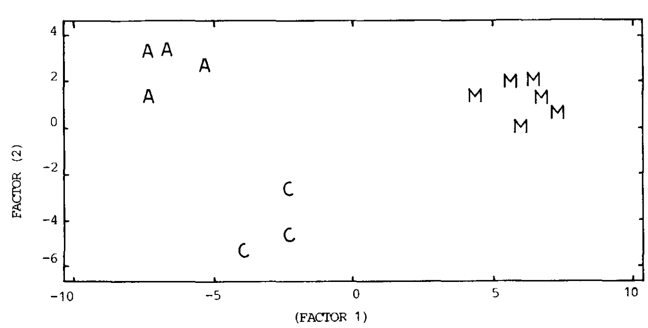

Figure 2. – Distribution of the provenances of the 3 mainland populations of *Pinus radiata* in the axes of the 2 factors (A, M, C indicate provenances from Ano Nuevo, Monterey and Cambria respectively).

Interrelationship Between Characteristics

PEARSON and SPEARMAN'S rank correlation coefficients between all combinations of the characteristics are shown in *table 10*. As it was expected, year to year correlations for height growth were strong between consecutive years and their values gradually decreased, as the time between measurements increased. The correlation coefficient for height at ages 2 and 3 years was strong ($r = 0.80$), while that between 1 and 12 years reduced to $r = 0.63$. Similar trend were observed in the values of SPEARMAN'S rank correlations. FALKENHAGEN (1991) has also found strong age to age correlation in height growth in radiata pine grown in South Africa. Characteristics related to tree size (i. e., total tree height, DBH, bark thickness and branch diameter) are highly correlated (*Table 10*). Straightness and crown form are loosely correlated with the growth characteristic, while they are moderately intercorrelated ($r = 0.64$). The number of whorls per tree is positively correlated with the growth characteristics, indicating that the faster growing trees are forming more whorls. As a result of this relationship, when selection for growth is practiced, multinodal trees are favored. Similar results have been reported at 4.5 years stands grown in Australia (FIELDING, 1966), 10 years provenance tests grown in Greece (MATZIRIS, 1979a) and 5 years grown in New Zealand (SHELBOURNE and THULIN, 1974). Branch diameter is positively correlated with the number of whorls ($r = 0.49$). This value is slightly lower than that reported by RAYMOND and COTTERILL (1990) in progeny tests grown in New Zealand. The number of branches per whorl is also positively correlated with growth characteristics with r values ranking from 0.38 to 0.47 (*Table 10*).

Frost resistance is positively correlated with total tree height, indicating that the taller trees are more damaged by frost. This is because the crowns of the taller trees are exposed to freezing winds, while shorter trees were protected within the trial.

Conclusions

From the analyses of a 12 year-old provenance test of *Pinus radiata* grown in Greece, the following conclusions can be drown:

Table 10. – Product moment (above diagonal line) and Spearman rank (below diagonal line), correlation coefficients of 18 characteristics of *Pinus radiata* at Raches experimental planting.

Char.[1]	HT1	HT2	HT3	HT4	HT5	HT9	DBH9	DBH10	HT12	DBH12	BTH	STR	CF	WN	BN	DTB	MBD	FR
HT1		0.88	0.82	0.79	0.75	0.67	0.73	0.73	0.63	0.71	0.58	-0.06	0.18	0.53	0.42	0.42	0.56	0.38
HT2	0.81		0.94	0.90	0.86	0.74	0.79	0.79	0.69	0.76	0.64	-0.15	0.09	0.65	0.45	0.67	0.61	0.39
HT3	0.76	0.70		0.95	0.93	0.80	0.81	0.80	0.75	0.76	0.61	-0.05	0.13	0.70	0.45	0.66	0.58	0.29
HT4	0.69	0.85	0.92		0.97	0.85	0.85	0.85	0.80	0.81	0.63	-0.11	0.15	0.73	0.46	0.70	0.63	0.30
HT5	0.66	0.80	0.89	0.96		0.86	0.84	0.84	0.82	0.79	0.60	-0.09	0.16	0.75	0.45	0.69	0.62	0.24
HT9	0.48	0.56	0.68	0.77	0.80		0.91	0.91	0.87	0.88	0.60	-0.21	0.03	0.74	0.44	0.74	0.69	0.18
DBH9	0.54	0.64	0.68	0.77	0.77	0.83		0.99	0.83	0.97	0.75	-0.18	0.16	0.71	0.47	0.84	0.80	0.35
DBH10	0.55	0.64	0.67	0.78	0.77	0.83	0.97		0.82	0.98	0.76	-0.17	0.18	0.71	0.47	0.85	0.80	0.34
HT12	0.46	0.53	0.66	0.73	0.76	0.84	0.76	0.74		0.79	0.53	-0.06	0.10	0.65	0.38	0.62	0.59	0.11
DBH12	0.52	0.59	0.61	0.72	0.71	0.79	0.94	0.97	0.71		0.73	-0.16	0.18	0.69	0.43	0.83	0.79	0.28
BTH	0.43	0.53	0.47	0.49	0.47	0.39	0.61	0.63	0.34	0.58		-0.10	0.24	0.45	0.36	0.73	0.64	0.58
STR	0.03	-0.04	0.08	0.00	0.01	-0.16	-0.16	-0.15	-0.02	-0.16	-0.08		0.64	-0.25	-0.08	-0.13	-0.16	-0.13
CF	0.24	0.15	0.17	0.21	0.22	0.02	0.19	0.22	0.09	0.19	0.25	0.60		-0.13	0.00	0.27	0.25	0.12
WN	0.32	0.51	0.57	0.63	0.62	0.63	0.61	0.60	0.57	0.59	0.34	-0.16	-0.12		0.34	0.49	0.43	0.11
BN	0.31	0.33	0.37	0.37	0.39	0.29	0.28	0.29	0.25	0.24	0.28	0.00	0.07	0.21		0.41	0.18	0.24
DTB	0.45	0.55	0.55	0.61	0.60	0.63	0.79	0.80	0.51	0.77	0.66	-0.14	0.28	0.40	0.30		0.89	0.40
MBD	0.43	0.50	0.48	0.55	0.55	0.61	0.77	0.78	0.53	0.75	0.56	-0.15	0.24	0.35	0.10	0.87		0.35
FR	0.35	0.40	0.27	0.27	0.22	0.06	0.24	0.24	0.00	0.19	0.56	-0.13	0.10	0.10	0.22	0.36	0.29	

[1]) HTi, DBHi total tree height and diameter at the age i years, respectively; BTH bark thickness, STR stem straightness, CF crown form, WN number of whorls, BN number of branches, DTB diameter of the thicker branch, MBD mean branch diameter of the whorl, FR frost resistence. Values greater than 0.174 and 0.228 are statistically significant at the 0.05 and 0.01 probability level, respectively. Degrees of freedom for all values = 124.

1. There are significant differences between natural populations of radiata pine, in growth and branching characteristics and resistance to frost, while the differences between provenances within populations are insignificant.

2. The fastest grown populations in Greece are the Ano Nuevo and Monterey while the slowest, that is completely unadapted, is the population of Cedros island.

3. Guadalupe population is the best in stem straightness and can be used as gene donor for the improvement of stem straightness of the fastest grown trees of Ano Nuevo and Monterey populations.

4. Natural populations are suffering from the negative effect of inbreeding depression and heterosis is increased by interpopulation crossing.

5. Bark thickness decreases as the latitude increases. This is probably an adaptation to natural conditions and mainly to higher fire hazzards in the more xeric southern environments.

6. The number of whorls produced is higher in the faster growing trees, so multinodal trees are favored when selection for height growth is practiced.

7. There is strong positive correlation between frost resistance and the latitudes of the natural range of the provenances and populations. An exception is the Guadalupe population which, although from a low latitude, ranks in the top for frost resistance.

8. The population of radiata pine already grown in Greece outperforms in growth all natural populations of the species. Therefore the breeding materials of radiata pine are already present in Greece. Enlarging the genetic base by introducing new materials of Ano Nuevo and Monterey origin is highly recommended.

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Pollen Sizing in Jack Pine (*Pinus banksiana* Lamb.) with a Hemocytometer

By G.-É. CARON[1]) and G. R. POWELL[2])

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Abstract

Evaluation of pollen viability and pollen size variation is instrumental in polycross testing. Polymixes used for polycross should be adjusted so that they are composed of equal numbers of viable pollen grains from each male. In this study, yearly and clonal variation in jack pine (*Pinus banksiana* LAMB.) pollen size is evaluated for pollen collected from 15 clones and 25 clones in 1992 and 1993, respectively; 13 clones were common to both years. *In vitro* pollen viability was assessed by using agar with 5% sucrose. Pollen sizing was achieved with a hemocytometer, commonly used by medical technologists to count various blood cells. Pollen viability averaged 70%, 86%, and 90% for 1992 freshly collected pollen, 1992 pollen stored for 1 year, and 1993 freshly collected pollen, respectively. Clonal viability varied between 54% and 90%, 67% and 95%, and 75% and 98% for 1992 freshly collected pollen, 1992 pollen stored for 1 year, and 1993 freshly collected pollen, respectively. The number of pollen grains per mg (MG) or ml (ML) of dry pollen was quite variable between years and among clones. ML averaged 16.4 million and 17.7 million in 1992 and 1993, respectively. The highest clonal ML value in 1992 and 1993 was 1.8 times and 1.7 times that of the smallest value, respectively. No pollen morphometric measure was valid in estimating reliably ML or MG. Adjustments to obtain equal numbers of viable pollen grains for each male parent in a polymix are recommended.

Key words: Pinus banksiana, pollen viability, pollen size, hemocytometer, polymix, polycross.

FDC: 161.6; 164.6; 165.53; 181.521; 174.7 *Pinus banksiana.*

Introduction

A strategy for the genetic improvement of jack pine (*Pinus banksiana* LAMB.) suggests the use of polycross tests (FOWLER, 1986). In the polycross mating design, each selected tree is crossed with a mix of pollens (polymix) from a number of unrelated trees. The polycross test is used to assess general combining ability (GCA) of selected trees and, in turn, to identify full-sib families having high GCA parents (FOWLER, 1986; FOWLER and WISELOGEL, 1993). If the polycross is to provide an accurate estimate of additive genetic variance and GCA, the pollen parents used in the polymix must be equally successful in the pollination-fertilization process (FOWLER and WISELOGEL, 1993). Random mating occurs in polymix pollinations of loblolly pine (*Pinus taeda* L.) (WISELOGEL and VAN BUIJTENEN, 1988). However, differential male reproductive success has been indicated in other species (see MORAN and GRIFFIN, 1985; CHELIAK *et al.*, 1987; MULCAHY and MULCAHY, 1987; APSIT *et al.*, 1989). Hence, some controversy exists over the use of polymixes (see FOWLER, 1987), and this is related to whether the reproductive bias is real and can result in serious distortion of the genetic parameters being estimated.

Polymixes used for the polycross should be adjusted so that they are composed of equal numbers of viable pollen grains from each male. Pollen viability and pollen size variation must therefore be considered. Various tests are available to evaluate *in vitro* pollen viability (see GODDARD and MATTHEWS, 1981; JETT *et al.*, 1993, etc). Pollen sizing has previously been determined by weighing and counting a standard volume (POHL, 1937), with a microscope (SZIKLAI, 1963), or with electronic particle counters (HO and OWENS, 1974; ADAMS, 1982; LUTIER and VAISSIÈRE, 1993). Pollen sizing can also be achieved using a hemocytometer. The hemocytometer, herein proposed for forestry application, is commonly used by hospital laboratory technologists to count various blood cells (PLATT, 1969; HUDSON and HAY, 1980; SIEVERD, 1983).

In the present study, yearly and clonal variation in pollen size was evaluated with the use of a hemocytometer for pollen collected from 15 and 25 jack pine clones in 1992 and 1993, respectively; 13 clones were common to both years. *In vitro* pollen viability was assessed. Adjustments required to obtain equal numbers of viable pollen grains for each male parent in a polycross will be discussed.

[1]) École de sciences forestières, Université de Moncton, 165 Boulevard Hébert, Edmundston, New Brunswick, Canada E3V 2S8

[2]) Faculty of Forestry and Environmental Management, University of New Brunswick, Bag Service No. 44555, Fredericton, New Brunswick, Canada E3B 6C2

Materials and Methods

Pollen collection and storage

Pollen was collected and extracted by J. D. Irving Ltd. in late May of 1992 and 1993 at their clonal seed orchard situated 45