Table 4. — Diameter, stem characteristics and volume production by 12 provenances of *Tectona grandis* 17 years after planting at Longuza, Tanzania.

Provenance	Diameter DBH (cm)	Self Pruning (m)	Straight-ness (Scores)	Basal Area (m²/ha)	Volume Production (m³/ha)	Rank**
A – Kihuhwi, Tanzania	19.3 a*	13.7 a	4.1 ab	33.6 bc	280.9 ab	4
B – Mtibwa, Tanzania	19.8 a	13.5 a	4.2 ab	33.9 bc	288.3 ab	2
C – Trinidad	18.8 a	13.7 a	3.9 bc	32.7 bc	270.3 b	7
D – Sudan	19.5 a	14.1 a	4.0 abc	32.7 bc	279.3 ab	5
E – Saigon, Vietnam	20.9 a	17.7 a	4.0 abc	31.6 bc	272.2 b	6
F – Mtibwa, Tanzania	19.7 a	14.5 a	4.3 a	34.8 ab	285.8 ab	3
G – Keravat, New Britain	20.4 a	14.0 a	4.0 abc	27.2 cd	232.7 b	10
H – Lembaya, Java	19.6 a	14.2 a	4.1 ab	31.7 bc	264.6 b	8
I – Eastern Region, Nigeria	18.2 a	14.0 a	4.1 ab	31.0 bc	256.3 b	9
J – Coimbatore, India	21.5 a	14.7 a	4.3 a	39.5 a	333.5 a	1
K – S. Chanda, India	19.9 a	13.4 a	3.8 c	25.2 d	209.3 c	11
L – Hoshangabad, India	19.0 a	13.8 a	4.1 ab	25.8 cd	207.9 c	12

*) Within the same column values with the same subscript are not statistically different, $p < 0.05$.
**) Provenance ranking based on volume production.

(B and F). The least straight was one of the lesser well performing Central Indian provenance from S. Chanda (K). The other provenances were rather uniform with only a few trees being crooked.

The extent of self pruning was not significant between provenances. In general however, all provenances showed good self pruning properties, with most stem boles being more than 50% branch free.

Forking, fluting and buttresses were rare to absent in all provenances. However, buttressing may be expected at a later stage. Flowering started as early as 4 years in the Keravat provenance (G) which was nearly 50% flowering in 1969 (PERSSON, 1971). At 17 years, all provenances held moderate to abundant flowers/seeds. The early initiation of flowers in some provenances does not seem to have negatively affected their stem form as suggested in other studies (EGENTI, 1978).

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Geographic Variation in Cones of Norway Spruce (Picea abies (L.) Karst.)

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Abstract

The geographic variation of Norway spruce (*Picea abies* (L.) KARST.) was studied using (*i*) provenances growing along the Italian Alpine margin; (*ii*) the relic provenance from the Tuscan Apennine (Italy); (*iii*) provenances from the extremes of the Norway spruce European natural range (Bulgaria and Norway).

This research studied seed scale variability in the considered provenances. Within the same geographic provenance, populations from different altitudes were sometimes sampled. Cones were collected either on single trees or, following a systematic sampling, on the ground below the tree crown. Twenty scales were taken from the median cone portion and each scale was classified with respect to several qualitative traits. Absolute frequencies of qualitative trait categories were computed for each cone.

On category frequencies the following statistical analyses were performed: (*i*) calculation of populations mean and standard error; (*ii*) univariate, with variance component estimation, and multivariate nested analysis of variance; (*iii*) calculation of PEARSON correlation coefficients between geographical variables and population means; (*iv*) discriminant and principal component analysis.

The univariate analysis of variance showed a large contribution of trees (in half of the cases greater than 50⁰/₀) to the variation of scale traits so that a genetic control over scale morphology seems to be confirmed. The multivariate analysis of variance showed statistically significant effects of provenances and populations. Discriminant analysis showed: (*i*) good discrimination between "autochthonous" and "artificial" populations within the relic provenance from the Tuscan Apennine; (*ii*) a tendency, for the Tuscan Apennine provenance, to be in a central position with respect to the studied Alpine populations and a closer similarity to Aosta Valley populations with respect to the other western Alpine populations; (*iii*) *a longitudinal geographic variation of Alpine populations interpretable as evidence of postglacial migration pathways along the southern Alpine margin*; (*iv*) differences between Italian, Bulgarian and Norwegian populations.

Key words: Picea abies, geographic variation, postglacial migration, cones, multivariate analysis.

Zusammenfassung

Eine geographische Variationstudie der Fichte (*Picea abies* (L.) KARST.) wurde auf der Basis *i*) der Herkünfte, die sich entlang der italienischen Alpengrenze befinden, *ii*) der relikten Herkunft des toskanischen Appennins (Italien) und *iii*) der Herkünfte der extremen europäischen natürlichen Verbreitungsgrenze der Fichte (Bulgarien und Norwegen) durchgeführt.

Diese Untersuchung analysiert die Zapfenschuppenvariabilität der oben beschriebenen Herkünfte. Innerhalb der gleichen geographischen Herkunft wurden manchmal in verschiedenen Höhenlagen lebende Populationen als Muster genommen. Die Zapfen wurden, entweder auf einzelnen Bäumen oder durch systematische Musterentnahme auf dem Boden unter der Baumkrone, gesammelt. Zwanzig Zapfenschuppen wurden aus dem Mittelteil des Zapfens genommen und jede Zapfenschuppe wurde auf der Basis vieler quantitativer Merkmale klassifiziert. Absolute Frequenzen von quantitativen Merkmalen jeder Klasse wurden für jeden Zapfen kalkuliert.

Die statistische Analyse, die auf der Klassenfrequenzen begründet sind, umfaßten *i*) die Errechnung der Populationsmittel und der Standardabweichung, *ii*) die univariate Varianzanalyse, zusammen mit der Varianzkomponentenschätzung und die multivariate hierarchische Varianzanalyse, *iii*) die Errechnung der Korrelationskoeffizienten von PEARSON unter den geographischen Variablen und die Populationsmittel, *iv*) die Varianzdiskriminantanalyse und die Varianzkomponentenanalyse. Die univariate Varianzanalyse zeigte einen großen Beitrag der Bäume (in den halben Fällen über 50⁰/₀) zu der Variation der Zapfenschuppenmerkmale, so daß es eine genetische Kontrolle der Zapfenschuppenform bestätigt zu sein scheint. Die multivariate Varianzanalyse wies signifikante Effekte der Herkünfte und der Populationen auf die Gesamtvariation auf. Die Varianzdiskriminantanalyse zeigte: *i*) eine gute Diskrimi-

nation zwischen "autochthonen" und "künstlichen" Populationen der relikten Herkunft aus dem toskanischen Appennin, *ii*) die Tendenz der Herkunft des toskanischen Appennins zu einer zentralen Position im Vergleich zu den alpinen Populationen, und eine engere Ähnlichkeit der appenninischen Herkunft mit der aostatalen Populationen im Vergleich zu der anderen westlichen alpinen Populationen, *iii*) eine geographische longitudinale Variation der alpinen Populationen, deutbar als eine nacheiszeitliche Wanderbewegung entlang der südlichen Alpengrenze, *iv*) signifikante Unterschiede zwischen den Populationen aus Italien, Bulgarien und Norwegen.

Introduction

Norway spruce (*Picea abies* (L.) KARST.) is a prominent canopy tree of boreal and montane conifer-dominated forests in Europe. It occurs throughout Fennoscandia and European Russia as well as along the major mountain ranges of central and eastern Europe. Siberian spruce (*Picea obovata* LEDEB.), which reaches the western extremity of its range in Fennoscandia, is now considered as a subspecies, variety or ecotype of *Picea abies* (FRANCO, 1964; SCHMIDT-VOGT, 1974a and 1974b; SCHMIDT-VOGT, 1978).

Despite many studies on the large degree of polymorphism that this species shows throughout its wide natural range, the geographic variation of Norway spruce in Italy has not been widely investigated.

Recently MAGINI *et al.* (1980) performed a geographic variation study considering: (*i*) provenances from Italian Alps; (*ii*) the relic provenance from Tuscan Apennine ("Alpe delle Tre Potenze" provenance (CHIARUGI, 1936a, 1936b; MAGINI, 1972; FERRARINI, 1977)); (*iii*) provenances from Bulgaria and Norway. As in other studies on .the geographic variation of Norway spruce (PRIEHAUSSER, 1956 and 1958; SCHMIDT-VOGT, 1972, 1974a, 1977 and 1978) MAGINI *et al.* (1980) used different seed scale types occurring with different frequencies in the studied provenances. In particular, they proposed a synthetic index based on qualitative scale traits. As these authors point out, the scale traits relative importance, although based on their experience with the material, is arbitrary (MAGINI *et al.*, 1980, pp. 117—123).

Using essentially the same data set as MAGINI *et al.* (1980), the present work pursues, through the simultaneous consideration of scale characteristics by multivariate techniques, the following objectives: (*i*) to confirm previous results by using a strictly objective approach; (*ii*) to discriminate between "autocthonous" and "artificial" populations within the provenance from Tuscan Apennine, in order to improve its gene conservation programme (MAGINI and GIANNINI, 1977); (*iii*) to classify the Tuscan provenance with respect to the Alpine provenances; (*iv*) to investigate the geographic variation of Norway spruce along the southern Alpine margin and classify the Italian provenances with respect to provenances from the extremes of the Norway spruce European natural range, discussing it in relation to the proposed Holocene migration pathways.

Materials and Methods

1. Sampling procedures and seed scales classification

The provenances studied are shown in *Fig. 1*. Geographical background of sites of origin and sampling procedures are summarized in *Table 1*. Cones were collected in natural stands, on single trees ((1), 5 or 10 cones per tree) or on the ground below the tree crown (in most cases 3 cones per tree). In this case sampling points were 5 to 15 m apart from each other and cones were assembled in
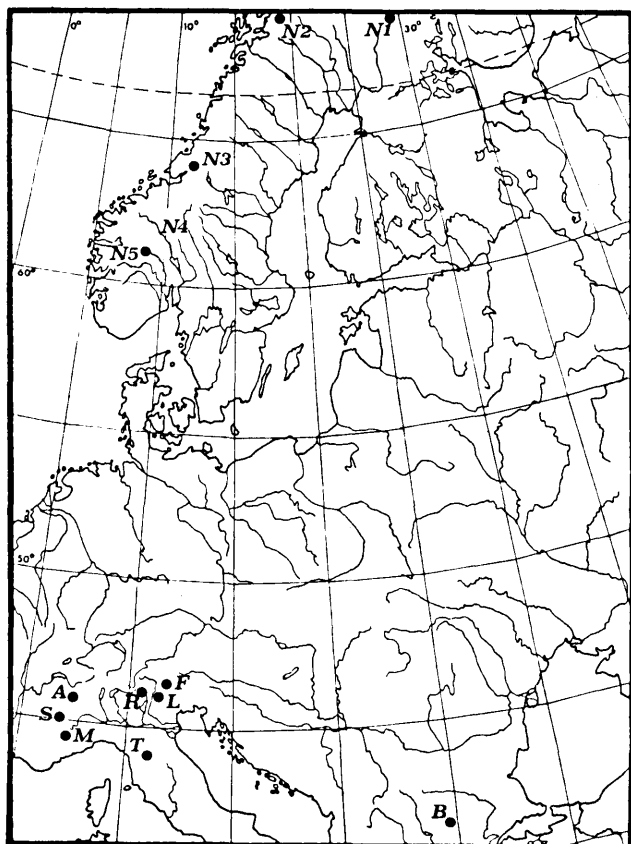
Fig. 1. — Location of the studied provenances.

Table 1: — Geographical background of the considered provenances and characteristics of sampling procedures.

Provenance	Population	Lat. North	Long. East	Alt. m	No. trees	No. cones
T Alpe Tre Potenze-I a)	T1 Lago Bruciate	44°07'	10°33'	1460	-	87
T Alpe Tre Potenze-I	T2 Campolino 1	44°07'	10°33'	1700	10	100
T Alpe Tre Potenze-I	T3 Campolino 2	44°07'	10°33'	1620	10	100
T Alpe Tre Potenze-I	T4 Campolino 3	44°07'	10°33'	1560	10	100
T Alpe Tre Potenze-I	T5 Lago Greppo	44°07'	10°33'	1530	20	200
T Alpe Tre Potenze-I	T6 Doccione	44°07'	10°33'	1350	-	78
T Alpe Tre Potenze-I	T7 Pizzo Alpestre	44°07'	10°33'	1650	19	190
T Alpe Tre Potenze-I	T8 Uccelliera	44°07'	10°33'	1480	5	50
T Alpe Tre Potenze-I	T9 C.348 b)	44°07'	10°33'	1300	-	185
T Alpe Tre Potenze-I	T10 C.407+410+411	44°07'	10°33'	1240	-	182
T Alpe Tre Potenze-I	T11 C.302	44°07'	10°33'	1220	-	53
T Alpe Tre Potenze-I	T12 C.291+303+304 +C.305+306	44°07'	10°33'	1320	-	166
T Alpe Tre Potenze-I	T13 C.113	44°07'	10°33'	1290	-	211
F Val di Fiemme-I	F1 Paneveggio 1	46°18'	11°50'	1900	7	70
F Val di Fiemme-I	F1 Paneveggio 2	46°18'	11°50'	1530	7	70
L Lavarone-I	L1 Lavarone	45°55'	11°20'	1400	-	500
R Val Rendena-I	R1 Pinzolo	46°10'	10°50'	1650	-	500
A Val d'Aosta-I	A1 Morgex	45°45'	07°00'	1950	22	110
A Val d'Aosta-I	A2 Avise	45°45'	07°00'	1450	25	125
A Val d'Aosta-I	A3 Morgex	45°45'	07°00'	1350	20	100
S Val di Susa-I	S1 Salbertrand 1	45°11'	06°50'	1950	50	250
S Val di Susa-I	S2 Salbertrand 2	45°11'	06°50'	1525	50	250
M Val Maira-I	M1 Prazzo	44°28'	06°50'	1400	-	498
N Norway	N1 Sör-Varanger	69°07'	29°05'	175	-	9
N Norway	N2 Mälslev c)	69°08'	18°40'	50	-	231
N Norway	N3 Steinkjer	64°05'	11°50'	80	24	240
N Norway	N4 Gausdal	61°15'	10°00'	600	-	228
N Norway	N5 V.Slidre	61°05'	08°50'	80	-	232
B Bulgaria	B1 Pogonu 1	41°40'	24°40'	1800	24	24
B Bulgaria	B2 Pogonu 2	41°40'	24°40'	1200	13	13

a): I = Italy
b): C.= forest compartments defined by the working plan
(see Cantiani and Bernetti 1963)
c): stand reforested with seed from the central-northern part of Norway.

single lots representing each population. Twenty scales were taken from the median portion of each cone. Each scale was classified with respect to the following traits.

(A) *Apophysis characteristics*

(A1) Scales without apophysis.

(A2) Scales showing a pronounced apophysis, dentate or bifid, with its vertical axis greater than the horizontal one, in correspondence with its basis.

(A3) Scales with an evident apophysis but not showing the characteristics described at point (A2).

(B) *Characteristics of the apophysis margin*

(B1) Scales with integer or eroded margin.

(B2) Scales with dentate margin (teeth longer than 1 mm).

(C) *Scale form*

(C1) Scales with angular form.

(C2) Scales not showing angular form.

(D) *Dimensional ratios*

(D1) Scales with the horizontal axis much greater than the vertical one.

(D2) Scales with the horizontal axis slightly greater than the vertical one.

(D3) Scales with the horizontal axis equal to the vertical one.

(D4) Scales with the horizontal axis slightly smaller than the vertical one.

(D5) Scales with the horizontal axis much smaller than the vertical one.

Within each group of traits (i.e. A, B, C, D), scales were classified into *one* and only *one* category (*i.e.* A1, A2, etc). To deal with quantitative data, for each group of traits the frequency of each category was computed for each cone. All statistics were computed considering these frequencies as elementary values.

2. Statistical methods

For cones collected on individual trees (see *Table 1*), a four-level nested analysis of variance (provenances, populations within provenances, trees within populations within provenances, within trees) was carried out for each trait. Variance components were also estimated.

A three-level nested multivariate analysis of variance (provenances, populations within provenances, cones within populations) was performed on the whole data set.

PEARSON correlation coefficients between geographical variables (latitude, longitude and altitude) and average values of trait frequencies in each population were computed.

Canonical discriminant analysis was performed considering either provenances or populations as *a priori* groups. Discriminant analysis was performed: (*i*) considering the relic provenance from Tuscan Apennine; (*ii*) considering the Italian provenances; (*iii*) on the whole data set. This technique allowed us to graphically display distances between population centroids (multivariate population means), to classify single observations into *a priori* groups, to evaluate the contribution of individual characters to the multivariate differences among groups.

Principal component analysis was also carried out.

All statistics were computed using SAS statistical package (SAS Institute Inc., 1982) implemented on an IBM 4341 computer.

Results and Discussion

Tables 2a and *2b* report descriptive statistics of traits for the populations considered.

The nested analysis of variance showed statistically significant effects of provenances, populations and trees on the variation of all the considered traits (*Table 3*).

Tables 2a and 2b. — Absolute frequencies of different seed scale categories (see text for symbols explanation) in the studied populations; M = mean; SE = standard error.

Pop.		A1	A2	A3	B1	B2	C1	C2	D1	D2	D3	D4	D5
T1	M	.855	.145	.000	.525	.475	.331	.669	.000	.019	.162	.350	.470
	SE	.030	.030	.000	.036	.036	.033	.033	.000	.006	.025	.032	.046
T2		.594	.404	.002	.577	.424	.385	.615	.003	.056	.337	.318	.287
		.042	.042	.002	.026	.026	.032	.032	.003	.013	.030	.023	.034
T3		.782	.218	.000	.739	.262	.304	.696	.008	.039	.272	.270	.413
		.033	.033	.000	.022	.022	.031	.031	.003	.010	.031	.023	.039
T4		.803	.198	.000	.578	.423	.296	.704	.000	.010	.279	.406	.306
		.034	.034	.000	.023	.023	.026	.026	.000	.004	.025	.018	.028
T5		.720	280	.000	.656	.344	.415	.585	.002	.019	.260	.461	.259
		.029	.029	.000	.017	.017	.018	.018	.001	.004	.018	.016	.021
T6		.757	.243	.000	.424	.576	.447	.553	.011	.007	.476	.231	.210
		.038	.038	.000	.025	.025	.036	.036	.009	.021	.045	.034	.042
T7		.699	.301	.000	.535	.465	.616	.384	.000	.007	.128	.266	.599
		.026	.026	.000	.020	.020	.018	.018	.000	.004	.018	.020	.029
T8		.920	.080	.000	.347	.653	.237	.763	.000	.000	.021	.188	.791
		.026	.026	.000	.044	.044	.032	.032	.000	.000	.008	.029	.032
T9		.503	.493	.005	.524	.476	.295	.705	.002	.010	.115	.315	.558
		.031	.031	.003	.023	023	.021	.021	.002	.004	.015	.018	.025
T10		.477	.503	.020	.463	.537	.428	.572	.001	.015	.140	.224	.620
		.032	.032	.009	.018	.018	.027	.027	.001	.005	.019	.020	.031
T11		.374	.626	.000	.575	.425	.277	.723	.000	.023	.258	.290	.430
		.031	.031	.000	.019	.019	.023	.023	.000	.009	.027	.026	.034
T12		.545	.448	.008	.642	.358	.335	.665	.001	.001	.245	.242	.501
		.033	.033	.006	.018	.018	.027	.027	.001	.007	.030	.024	.034
T13		.359	.556	.085	.477	.523	.279	.721	.001	.009	.097	.183	.710
		.030	.031	.018	.023	.023	.019	.019	.001	.003	.016	.016	.024
F1		.810	.180	.010	.375	.625	.269	.731	.001	.004	.547	.291	.157
		.042	.040	.010	.025	.025	.038	.038	.001	.002	.046	.032	.035
F2		.661	.339	.000	.273	.727	.424	.576	.000	.000	.094	.303	.604
		.049	.049	.000	.022	.022	.038	.038	.000	.000	.025	.035	.047

Pop.		A1	A2	A3	B1	B2	C1	C2	D1	D2	D3	D4	D5
L1	M	.739	.262	.000	.295	.705	.284	.716	.007	.003	.147	.166	.647
	SE	.017	.017	.000	.009	.009	.012	.012	.002	.004	.009	.008	.016
R1		.889	.111	.000	.595	.405	.341	.659	.001	.035	.313	.348	.303
		.011	011	.000	.012	.012	.011	.011	.001	.004	.014	010	.015
A1		.784	.216	.000	.667	.337	.556	.444	.015	.093	.398	.280	.214
		.031	.031	.000	.027	.027	.040	.040	.009	.021	.034	.028	.034
A2		.554	.446	.000	.716	.284	.289	.711	.000	.010	.226	.287	.477
		.038	.038	.000	.020	.020	.021	.021	.000	.005	.033	.028	.037
A3		588	.412	.000	.690	.311	.311	.690	.019	.073	.369	.269	.271
		.046	.046	.000	.024	.024	.029	.029	.009	.020	.041	.033	.038
S1		.803	.197	.000	.769	.231	.272	.728	.123	.107	.605	.081	.084
		.032	.032	.000	.017	.017	.026	.026	.021	.015	.035	.017	.021
S2		.566	.434	.000	.677	.323	.347	.653	.126	.101	.562	.094	.116
		.027	.027	.000	.014	.014	.022	.022	.016	.010	.025	.014	.017
M1		.715	.285	.000	.780	.220	.437	.563	.052	.061	.684	.075	.129
		.017	.017	.000	.008	.008	.016	.016	.006	.005	.016	.007	.013
N1		1.000	.000	.000	1.000	.000	.706	.294	.000	.172	.400	.361	.067
		.000	.000	.000	.000	.000	.065	.065	.000	.028	.073	.064	.040
N2		.215	.726	.060	.334	.666	.060	.940	.000	.000	.002	.005	.993
		.019	.019	009	.012	.012	.006	.006	.000	.000	.013	.000	.004
N3		.671	.305	024	.727	.273	.280	.720	.000	.000	.038	.109	.853
		.027	.026	.009	.015	.015	.018	.018	.000	.000	.010	.013	.018
N4		.629	.309	.061	407	.593	.220	.780	.000	.002	.061	.063	.875
		.028	.025	.013	.016	.016	.016	.016	.000	.001	.012	.009	.017
N5		716	.284	.000	.669	.331	.135	.865	.000	.000	.000	.055	.945
		.023	.023	.000	.017	.017	.008	.008	.000	.000	.000	.009	.009
B1		.058	.473	.469	.702	.297	.129	.871	.000	.000	.063	.225	.713
		.038	.093	.098	.046	.046	.035	.035	.000	.000	.045	.071	.083
B2		.019	.588	.392	.485	.515	.119	.881	.000	.000	.058	.142	.800
		.016	.122	.126	.105	.105	.042	.042	.000	.000	.058	.078	.102

A large contribution to traits variation is due to trees (in 7 out of 10 cases this is the largest contribution and in 5 out of 10 cases it is greater than 50%) and to cones within trees. The large contribution of trees to the variation of

Table 3. — Nested analysis of variance and variance component estimation. See text for symbols explanation.

Traits		Source of variation a)			
		Prov.	Pop. within prov.	Trees within pop.	Cones within trees
A1	Mean square (x10^2)	356.6	158.9	73.5	4.2
	Variance comp.%	4.0	3.7	67.0	25.4
	F		NS b)	*	***
A2	Mean square (x10^2)	79.1	160.4	74.0	4.2
	Variance comp.%	-1.7	3.9	71.0	26.8
	F	NS	*	***	
A3	Mean square (x10^2)	142.0	0.5	3.7	0.1
	Variance comp.%	43.2	-3.1	52.2	7.7
	F	***	NS	***	
B1,B2 c)	Mean square (x10^2)	434.4	86.0	20.6	2.9
	Variance comp.%	15.4	7.2	38.4	39.0
	F	*	*	***	
C1,C2	Mean square (x10^2)	153.0	184.5	39.9	3.1
	Variance comp.%	-1.6	11.8	58.8	31.0
	F	NS	***	***	
D1	Mean square (x10^2)	111.1	0.3	6.8	0.7
	Variance comp.%	19.3	-3.5	50.3	34.0
	F	***	NS	***	
D2	Mean square (x10^2)	60.4	6.7	3.6	1.0
	Variance comp.%	11.0	1.4	24.7	62.9
	F	***	*	***	
D3	Mean square (x10^2)	1257.3	153.1	37.3	4.8
	Variance comp.%	24.9	6.4	35.5	33.1
	F	***	***	***	
D4	Mean square (x10^2)	480.8	61.6	18.9	3.7
	Variance comp.%	29.2	12.8	36.8	21.2
	F	***	***	***	
D5	Mean square (x10^2)	1981 9	329.0	46.4	3.9
	Variance comp %	29.2	12 8	36.8	21.2
	F	***	***	***	
	Degree of freedom	5	10	300	1674
	Test against entry	B	C	D	

a): Prov.=provenances; pop.=populations
b): NS=not significant; *=p<0.05; **=p<0.01; ***=p<0.005
c): alternative traits (B1,B2; C1,C2) have the same variability.

scale traits may be due to a relevant genetic control of seed scale morphology. Our results are in accordance with previous reports: ROCHE (1969) found genetic control over the characters of cone scale morphology in *Picea glauca* (MOENCH) VOSS, *Picea engelmanni* (PAREY) and *Picea sitchensis* (BONG) CARR.; in *Picea glauca* KHALIL (1974) found that scale length and width are under strong genetic control, weakly controlled by environmental factors and not associated with phenotypic superiority in growth; in *Picea mariana* (MILL.) B.S.P. KHALIL (1983) observed that the length and width of the middle scale are under strong genetic control.

A significant (p < 0.01) relationship with altitude (r = − 0.50) was found only for the trait D5. This is the only instance in which our results agree with the claim by SCHMIDT-VOGT (1974a, 1978), that scale traits reflect a complex of properties which are adaptations to the climate.

Therefore the scale characteristics seem suitable traits for the study of their phylogenetic relationships and in particular of the migration processes that the populations might have undergone.

The nested multivariate analysis of variance showed statistically significant effects of provenances and populations to the overall variation.

Discriminant analysis was first carried out within the relic provenance from the Tuscan Apennine considering populations as *a priori* groups (*Fig. 2*). Good agreement between the hypothesized population origin (*Table 4*) and population centroids along the first canonical axis was found (*Fig. 2*). It is worth noting that populations with a probable mixed origin (*ie* populations *T8, T9, T10* and *T12*)
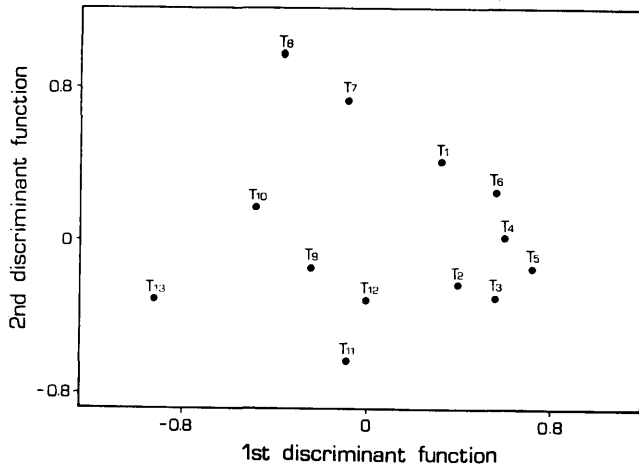
Fig. 2. — Provenance from the Tuscan Apennine: scatter of populations centroids in the plane of the first two canonical functions (38.1% and 19.9% of total variation). Population symbols are those used in *Table 1*.
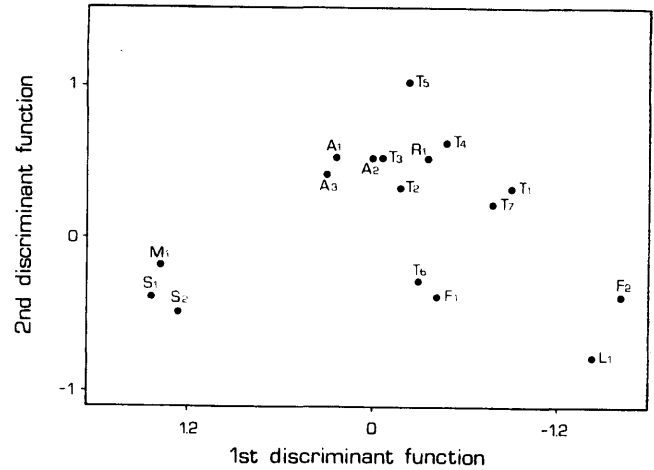

Fig. 3. — Italian provenances (only "natural" populations from the Tuscan provenance): scatter of populations centroids in the plane of the first two canonical axis (62.9% and 17.7% of total variation). Population symbols are those used in *Table 1*.

were found in a median position between population T13 ("artificial") and populations from *T1* to *T4* ("autochthonous"). Only for population *T7* does the position along the first canonical axis not agree with its hypothesized origin. The second discriminant function generated a variability which is difficult to explain, but in the plane of the first two discriminant functions it becomes acceptable to include *T7* among the "autochthonous" populations. In fact no population is between the cluster of "autochthonous" populations and *T7*. Discriminant analysis performed considering only two population groups (the "autochthonous", from *T1* to *T7*, and the "artificial" ones, from *T8* to *T13*) produced 68% of cases correctly classified.

Only populations from *T1* to *T7* were included in further analysis.

When all the Italian populations were used in the discriminant analysis, population centroids appeared ordered by longitude (one exception is represented by population *F1*) along the first canonical axis, with the "autochthonous" populations from Tuscany showing a tendency to be in a central position (*Fig. 3*). A significant linear correlation (r = −0.82, p < 0.01) was found between longitude and population means on the first canonical variable.

When Bulgarian and Norwegian provenances were considered (*Fig. 4*) the classification of Italian populations was not substantially altered. It is worth noting that (*i*) Bulgarian populations form a separate cluster; (*ii*) the provenance from the north-eastern part of Norway (provenance *N1* from Lapland) is clustered apart from the other Norwegian provenances (provenances from *N2* to *N5*).

Table 4. — Hypothesized origin of populations from the Tuscan Apennine (from MAGINI *et al.*, 1980).

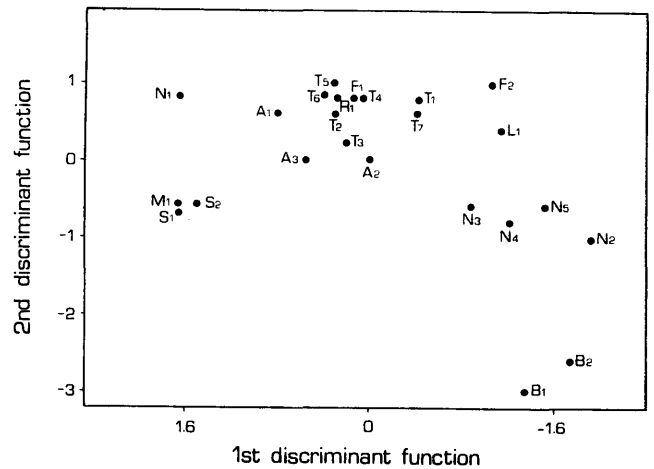| Pop.	Hypothesized population origin
T1	Autochthonous
T2	Autochthonous
T3	Autochthonous
T4	Autochthonous
T5	Autochthonous
T6	Autochthonous
T7	Autochthonous
T8	Largely made up by introduced trees
T9	Largely made up by introduced trees
T10	Largely made up by introduced trees
T11	Artificial
T12	Largely made up by introduced trees
T13	Artificial

Fig. 4. — Whole data set: scatter of populations centroids in the plane of the first two discriminant functions (respectively 49.0 and 19.7% of total variation). Population symbols are those used in *Table 1*.

Principal component analysis was also performed on the various data sets but no substantially different ordering was obtained in the results.

The loadings of the considered traits on the first two canonical functions are reported, for the different analyses performed, in *Table 5*. Traits related to the apophysis characteristics and scale dimensional ratios appear as the most strictly associated with the canonical variables.

A discussion of our results in relation to migration pathways followed by Norway spruce in the postglacial period is now needed.

According to many authors, after the latest glaciation Norway spruce recolonized: (*i*) northern Europe moving out from refugia located in the middle part of Russia; (*ii*) central Europe from refugia located at the foot of the Carpathians and Transylvanian Alps; (*iii*) the Alpine range from refugia located around the Dinaric Alps (BERTSCH, 1953; ZOLLER and KLEIBER, 1971; KRAL, 1977; SCHMIDT-VOGT, 1977 and 1978).

During the Holocene, Norway spruce expanded steadily along the European mountains at rates of 80—240 m yr^{-1}. At 4000 BP the westward expansion of spruce in the Alps produced for the first time a continuous area of spruce-

	Range of standardized canonical coefficients					
	0.-0.20	0.21-0.40	0.41-0.60	0.61-0.80	0.81-1.00	>1.00
1st data set						
CAN1	D1,D2,C1 + + −		D3,D4 + +		A2 +	A1,B1,B2 + + +
CAN2	D1,D2,D4 − − −		C1,D3 + −	A2 +		A1,B1,B2 + − −
2nd data set						
CAN1	A1,A2,C1 − + + D2,D4 + −		D1 +	B1 +	D3 +	
CAN2	C1,D2,D3 + + −	D1 −	A1,A2 + +	B1 +	D4 +	
3rd data set						
CAN1	D2 +	C1,D4 + +	A1,A2,B1 + + + D1 +			D3 +
CAN2	D2,D3 + +	D1,C1 − +	B1 −	D4 +		A1,A2 + +

dominated forests along the European mountains from the western Alps to the western Carpathians and around the Carpathian arc. The westward expansion in Scandinavia occurred later (between 3000 and 2500 BP) but more rapidly, with a rate of up to 500 m yr⁻¹ (HUNTLEY and BIRKS, 1983).

With regard to the Italian peninsula recolonization process, the hypothesis of a westward expansion along the Alpine range, from refugia in the Balcan peninsula, is widely accepted (KRAL, 1978; SCHMIDT-VOGT, 1977 and 1978; ZOLLER and KLEIBER, 1971). The Norway spruce from Tuscan Apennine may be considered as a relic forefront of the ancient Norway spruce natural range in Italy (KRAL, 1977; MAYER, 1977). However, while the migration processes along the northern Alpine range are quite well documented (KRAL, 1977; ZOLLER and KLEIBER, 1977), the ones along the southern Alpine margin and the Italian peninsula have not been widely investigated. Hypotheses on the existence of glacial refugia at the foot of the northern Apennine (FIRBAS and ZANGHERI, 1934, 1954; MARCHETTI and TONGIORGI, 1936;

Table 6. — Italian provenances: classification results by discriminant analysis.

No	Actual group		Predicted group membership						
			1	2	3	4	5	6	7
1	Val di Fiemme-F	N	54	42	14	6	2	11	11
		%	38.6	30.0	10.0	4.3	1.4	7.9	7.9
2	Lavarone-L	N	87	314	45	28	12	2	12
		%	17 4	62.8	9.0	5.6	2.4	0.4	2.4
3	Val Rendena-R	N	68	79	163	69	4	68	49
		%	13.6	15.8	32.6	13.8	0.8	13.6	9.8
4	Val d'Aosta-A	N	20	42	46	98	15	69	45
		%	6.0	12.5	13.7	29.3	4.5	20.6	13.4
5	Val di Susa-S	N	15	11	26	51	171	206	20
		%	3.0	2.2	5.2	10.2	34.2	41.2	4.0
6	Val Maira-M	N	2	13	17	51	91	293	31
		%	13.8	15.5	21.7	21.6	2.0	9.1	16.4
7	Tuscany-T	N	118	132	185	184	17	78	140
		%	13.8	15.5	21.7	21.6	2.0	9.1	16.4

37.1% of cases correctly classified

DUBOIS and ZANGHERI, 1957) with a recolonization of the Alpine range moving out from these latter ones (FIRBAS, 1949, 1952; BERTSCH, 1953; GIACOMINI, 1958) was also proposed.

A longitudinal variation pattern was shown by our analysis, in accordance with previous results (MAGINI et al., 1980). This seems a good confirmation of the occurrence of migration processes along the southern Alpine margin. The direction of migration (East- or Westward, or both) cannot be ascertained from this study.

From their position in the plane of first and second discriminant functions (Fig. 3) and from classification results by discriminant analysis (Table 6), the Tuscan provenance seems much closer to the Aosta Valley provenance (provenance A) than to provenances from the western sector of Italian Alps (provenances S and M). This result may support the interesting hypothesis advanced by MAGINI et al. (1980), suggesting that Norway spruce, in its recolonization process, reached the northern Apennine directly by crossing the Monferrato and Langhe hills without going through the western Alpine arc. An interesting question arising from our study, but which remains unanswered, is the strong diversity of western Alpine populations (M1, S1, S2).

In agreement with ALEKSANDROV (1984) the southernmost glacial refugium of Norway spruce in Europe was in the Central Rhodope mountains (Bulgaria). For that reason the genetic structure of Bulgarian populations was probably least influenced during the last glacial period and it is not the result of migration processes on an Eurasian scale. Our results confirm the genetic diversity of the studied populations from the Rhodope mountains ones (Fig. 4).

Provenances from Norway (with the only important exception of provenance N1) are clustered together. A single recolonization pathway of Scandinavian peninsula, from North to South has been proposed (MOE, 1970; SCHMIDT-VOGT, 1977). On the contrary, the provenance from Lapland seems to have a highly differentiated genetic structure. It may be worth noting that a recolonization pathway from Siberia throughout the Urals to Lapland and Fennoscandinavia is also hypothesized (PRAVDIN, 1985).

Conclusions

The multivariate analysis of seed scale traits substantially confirmed the results obtained by MAGINI et al. (1980).

Good discrimination was achieved between "artificial" and "autochthonous" populations within the relic provenance from the Tuscan Apennine.

The position of the "autochthonous" populations from the Tuscan Apennine showed the tendency to be rather central with respect to the Alpine populations. A closer affinity links Tuscan populations with Aosta Valley populations than with populations from the western Alpine sector.

Some evidence of clinal geographic variation in the studied Alpine populations was found. This may be a further confirmation of the occurence of postglacial migration pathways along the southern Alpine margin.

Populations from Bulgaria and Norway were clustered apart from Alpine populations. This seems to indicate a substantial genetic diversity and confirms the existence of several pathways in the Norway spruce European recolonization process.

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Probability of Equal Mating in Polymix Pollinations of Loblolly Pine (Pinus taeda L.)

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Summary

The assumption that each pollen parent has an equal probability of mating is the basis for using polymix pollinations to estimate general combining abilities. If the above assumption is true, then any particular ovule has an equal chance of being fertilized by any particular pollen in the polymix providing that an equal number of viable pollen grains of each pollen are used in the polymix and that gametic selection is not taking place. Pollinations with a polymix consisting of nine pollens were performed on four clones. Electrophoresis techniques were used to resolve allozymes at 14 isozyme loci.

Deviations from probability of equal mating by each pollen parent in the polymix crosses were tested in two ways: by examining the allozyme frequencies at individual loci and by attempting to identify the male parent of each seed produced.

Of the 56 allozyme frequencies examined only one was significantly different from the expectation. This is actually fewer than would be expected on the basis of equal probability of mating.

The distribution of male parents in the polymix crosses was also consistent with the equal probability of mating hypothesis.

On the basis of these results it was concluded that general combining ability and other statistics produced from polymix crosses are valid with regard to the equal probability of mating assumption.

Key words: allozymes, isozymes, polycross, Hardy-Weinberg.

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184