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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References

Allona, I., Casado, R. and Aragoncillo, C.: Biochemical genetics of a 7 S globuline-like protein from *Pinus pinaster* seed. Theor. Appl. Genet. **88**, 454–459 (1994). — Bahrman, N. and Damerval, C.: Linkage relationships of loci controlling protein amounts in maritime pine (*Pinus pinaster* Ait.). Heredity **63**, 267–274 (1989). — Bahrman, N., Zivy, M., Damerval, C. and Baradat, P.: Organisation of the variability of abundant proteins in seven geographical origins of maritime pine (*Pinus pinaster* Ait). Theor. Appl. Genet. **88**, 407–411 (1994). — Bailey, N. T. J.: Introduction to the mathematical theory of genetic linkage. Oxford University Press, London (1961). — Baradat, P. and Marpeau, A.: Le pin maritime. Biologie et genétique des terpènes pour la connaissance et l'amélioration de l'espèce. Thèse doctorat d' Etat ès Sciences, University of Bordeaux 1, Bordeaux. (1988). — Blakesley, R. W., and Boezi, J. A.: A new staining technique for proteins in polyacrylamide gels using Coomassie Brilliant Blue G-250. Anal. Biochem. **82**, 580–582 (1977). — Duff, G. E.: The variaties and geographical forms of *Pinus pinaster* Sol. in Europe and South Africa. Union of South Africa. Africa Forest Dept. Bul. **22**, Pretoria (1928). — Gerber, S., Rodolphe, F., Bahrman, N. and Baradat, P.: Seed-protein variation in maritime pine (*Pinus pinaster* Ait.) revealed by two-dimensional electrophoresis: genetic determinism and construction of a linkage map. Theor. Appl. Genet. **85**, 521–528 (1993). — Giannini, R., Morgante, M. and Vendramin, G. G.: Allozyme variation in Italian populations of *Picea abies* (L.) Karst. Silvae Genet. **40**, 160–166 (1991). — Gil, L., Gordo, J., Alia, R., Catalan, G. and Pardos, J. A.: *Pinus pinaster* Aiton en el paisaje vegetal de la Península Ibérica. Ecología, Fuera de serie **1**, 469–495 (1990). — Laemmli, U. K.: Cleavage of structural proteins during the assembly of the head of bacteriophage T4. Nature **227**, 680–685 (1970). — Mirov, N. T.: The genus *Pinus*. Ronald Press Company, New York (1967). — Nei, M.: Genetic distance between populations. Amer. Natur. **106**, 283–292 (1972). — Sneath, P. H. and Sokal, R. R.: Numerical Taxonomy. W. H. Freeman and Co., San Francisco (1973). — Yeh, F. C. and El-Kassaby, Y. A.: Enzyme variation in natural populations of Sitka spruce (*Picea sitchensis*). 1. Genetic variation patterns among trees from 10 IUFRO provenances. Can. J. For. Res. **10**, 415–422 (1989).

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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Key words: additive genetic variation, *Alnus acuminata,* Costa Rica, genetic correlations, heritability, insect attack, phenotypic selection, progeny testing, provenance variation, resistance, *Scolytodes alni.*

FDC: 232.12; 232.11; 165.3; 165.62; 165.5; 176.1 *Alnus acuminata;* (728.6).

Introduction

Alnus acuminata, a fast-growing, nitrogen-fixing producer of light but versatile timber (LAMPRECHT, 1990), is one of the species most planted by smallholder farmers in the highlands of Costa Rica. One of the limitations both on the productivity of such plantations and their wider adoption by farmers has been the low genetic quality of the available seed (BOSHIER and MESÉN, 1986). For this reason, in 1989 CATIE, a regional organization dedicated to the improvement of smallholder forestry and agroforestry systems in Central America, initiated a programme of genetic improvement of the species.

The present article describes the results at ages up to 34 months of a provenance/progeny test of this species. The principal objectives of the test are to provide a basis for recommendations of appropriate seed sources for reforestation in the breeding zone in question, to identify elite trees for directed seed collections (WHITE, 1987) and, after conversion to seedling seed orchard, to produce improved seed.

Materials and Methods

The treatments

The treatments consisted of 45 open-pollinated families of 5 provenances: Palestina de los Altos, Guatemala (15 families); División, Costa Rica (5 families); Los Santos, Costa Rica (7 families); Pacayas, Costa Rica (11 families); Prusia, Costa Rica (6 families). The Guatemalan provenance was obtained through the CAMCORE (Central America and Mexico Coniferous Resources) cooperative (DVORAK, 1990). Geographic and climatic information on the seed collection sites is presented in *table 1.* All the families included are derived from plus-trees, selected primarily on the basis of stem straightness. In Costa Rica, all plus-trees also had diameter at breast height (dbh) and height superior to the stand mean (most stands are believed to be approximately even-aged). All the seed collections were made in natural stands, except for the Prusia provenance, which is a plantation established with seed of unknown origin, and 2 trees of the Los Santos provenance, which were planted with locally collected seed. Two controls consisting of commercially available seed, 1 from the Prusia provenance and 1 from the División provenance, were also included.

The experimental site

The experiment was planted in December 1990 in Santa Cruz de Turrialba, Costa Rica (latitude 9°58' north, longitude 83°47' west, elevation 2300 m a.s.l., mean annual precipitation 2912 mm, mean of 1.5 dry months (< 80 mm) per year). The soil is of sandy loam texture in horizons A and B, both of which have pH of 5.1. By agricultural standards the soil is slightly deficient in phosphorus and magnesium, and deficient in calcium and potassium (BERTSCH, 1986). The topography is undulate and sloping, with some areas of poor drainage. Drainage canals were dug before planting, but these were only partially successful. Before planting the site was under pasture. The few trees remaining of the original forest cover were felled before planting. The trial was cleaned manually every 4 to 5 months during the first 2 years.

Table 1. – Details of provenances included in a provenance/progeny trial of *Alnus acuminata* located in Santa Cruz de Turrialba, Costa Rica.

Provenances[1]	Latitude [north]	Longitude [west]	Mean annual precipitation [mm]	Mean annual temperature [°C]	Elevation [m above sea level]	Mean number of dry months [<80 mm]
División	9°28'-9°32'	83°41'-83°43'	3910	12.7-19.0	1560-2700	2
División (control)	9°31'-9°32'	83°42'-83°43'	3910	17.0-19.0	2340-2610	2
Los Santos	9°38'-9°34'	83°55'-83°58'	2078	14.0-17.4	1850-2450	4
Pacayas	9°55'-9°59'	83°44'-83°51'	1845-3640	14.0-17.0	1680-2220	0-3
Palestina, Guatemala	14°53'	91°36'	unavailable	unavailable	2730-2840	unavailable
Prusia	9°57'	83°53'	1440	11.4-12.0	2560-2840	5
Prusia (control)	9°57'	83°53'	1440	12.0	2500	5

[1] Costa Rica, unless stated

Table 2. – Linear models used in the analysis of covariance of a provenance/progeny trial of *Alnus acuminata* in Santa Cruz de Turribala, Costa Rica.

Hypotheses[1]	Model[2]	Random effects in model	Error term (F-test denominator)
1, 2, 3, 4, 5	$Y_{ijl}=\mu+\phi_i+\lambda_j+\beta(X_{ijl}-\bar{X})+\phi\lambda_{ij}+\varepsilon_{ijl}$	λ_j	$\phi\lambda_{ij}$
6	$Y_{jk}=\mu + \alpha_k + \lambda j + \beta(X_{jk}-\bar{X}) + \varepsilon_{jk}$	λj	ε_{ij}

[1]) see text; [2]Y_{ijl} = the observed value of the response variable 'Y' on the jth tree of the jth block of the ith performance; μ = the population mean; ϕ_i = the effect of the ith provenance; λ_j = the effect of the jth block; β = the regression coefficient of 'X' on 'Y'; X_{ijl} = the value of the drainage covariable 'X' for the lth tree of the jth block of the ith provenance; $\bar{X}$ = the mean value of the drainage covariable 'X'; $\phi\beta_{ij}$ = the interaction of the effects of the ith provenance and the jth block; ε_{ijl} = the residual deviation of the lth tree of the ith provenance on the jth block; Y_{jk} = the observed mean value of the response variable 'Y' on the kth family in the jth block; α_k = the effect of the kth family; λ_j = the effect of the jth block; ε_{jk} = the residual deviation of the kth family in the jth block.

The experimental results are considered to be applicable principally to the upper slopes (above approximately 2000 m a.s.l.) of the Central Volcanic Range of Costa Rica, particularly sites of medium fertility in zones with annual rainfall above 2000 mm and with 0 to 2 dry months.

Experimental design

The experimental design followed the CAMCORE standard (DVORAK and DONAHUE, 1992) where possible; the provenances were randomized within block, and families and controls randomized as 6-tree row plots within their respective provenances.

There are 8 blocks. Two surround rows of material of unknown provenance, acquired from a commercial nursery, were planted. Spacing was 2.5 m x 2.5 m.

Measurements

Total tree height was measured at 12, 16, 22 and 34 months. Dbh was measured at 22 months and 31 months. Height increments (12 months to 16 months, 16 months to 24 months, 12 months to 24 months, 24 months to 34 months) and diameter increment were derived by subtraction. In addition, the following form traits were evaluated: stem straightness (scale of 1 to 4: 1 = straight or nearly so; 2 = straighter than average; 3 = less straight than average; 4 = crooked), basal sweep (present or absent), stem lean (present or absent), basal forking (present or absent), non-basal forking (present or absent); branch angle (scale of 1 to 3: 1 = horizontal or nearly so, 3 = 45° or nearly so; 2 = intermediate) and branch thickness (scale of 1 (thickest) to 3 (thinnest)).

As tree growth was markedly slower in the remaining areas of poor drainage than in the well drained areas, each tree's microsite was scored either 0 ('free drainage') or 1 ('impeded drainage'). This score was used as a covariable (blocks were laid out based on slope rather than drainage patterns).

Hypotheses and statistical analysis

Null hypotheses, together with notes on their associated statistical analyses, are presented below. The underlying models are presented in *table 2.*

Table 3. – Formulae for genetic parameter estimates in a provenance/progeny trail of *Alnus acuminata* in Santa Cruz de Turrialba, Costa Rica.

parameter estimated[1/]	formula for estimator	notes
additive genetic variance (σ^2_A)	$4\sigma^2_F$[2/]	σ^2_F = variance component for half-sib families;
additive genetic coefficient of variation % (AGCV)	$100[\sigma_A / \bar{x}]$,	$\bar{x}$ = experimental mean
h^2 (narrow-sense individual-tree heritability)	$\sigma^2_A / [\sigma^2_E + \sigma^2_{FB} + \sigma^2_F]$	σ^2_E=error variance; σ^2_{FB} =block-family interaction variance
h^2_F(plot mean heritability)	$\sigma^2_F / [\sigma^2_E/b + \sigma^2_F]$	b = number of blocks
$r_{a[x,y]}$ (genetic correlation between traits x and y)	$\sigma_{x,y} / \sqrt{[\sigma^2_x\sigma^2_y]}$	$\sigma_{x,y}$ = family covariance component between x and y[3/]

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1) all parameters include confounded effect of provenance;

2) i.e. open-pollinated families are assumed to approximate to half-sibs;

3) derived from variances of sums of traits (STONECYPHER, 1992)

Table 4. – Analysis of covariance of a provenance/progeny trial of *Alnus acuminata* in Santa Cruz de Turrialba, Costa Rica at ages 12 to 34 months: 'F' values and significance levels for provenance and family-confounded-with-provenance effects and planned comparisons.

	Provenance	Family[1]	Costa Rican families v. Guatemalan	División v. control	Prusia v. control	All Costa Rican families v. controls
Variable[2]	**F[3]**	**F[3]**	**F[3]**	**F[3]**	**F[3]**	**F[3]**
basal sweep	1.2 NS	1.8**	-	-	-	-
branch angle	1.1 NS	3.5**	-	-	-	-
branch thickness	4.9**	2.5**	13.7**	2.2NS	1.6NS	3.8NS
dbh (22)	2.2 NS	1.6*	-	-	-	-
dbh (31)	6.2 **	1.8**	25.0**	.45NS	.08NS	.8NS
dbh inc. (22-31)	1.4 NS	2.7**	-	-	-	-
forking (basal)	8.9**	2.2**	38.3**	.74NS	1.26NS	.01NS
forking (non-basal)	2.5*	.83 NS	4.6*	2.2 NS	.8 NS	.09NS
height (12)	0.7 NS	-	-	-	-	-
height (16)	0.6 NS	-	-	-	-	-
height (22)	2.0 NS	1.8**	-	-	-	-
height (34)	13.7**	3.7**	65.6**	.3NS	1.23NS	.11NS
height inc. (12-16)	1.7 NS	-	-	-	-	-
height inc. (12-22)	1.8 NS	-	-	-	-	-
height inc. (16-22)	1.4 NS	-	-	-	-	-
height inc, 22-34)	7.4 **	4.0**	31.9**	.3NS	.4NS	0.0NS
number of stems	10.8 **	1.9**	63.5**	1.1 NS	1.22NS	0.0NS
stem lean	3.2*	1.4 NS	14.4**	.1 NS	1.49NS	.3 NS
stem straightness	7.5 **	2.0**	41.3**	0.0 NS	.36NS	0.2 NS

1) Analysis made on Costa Rica families only;
2) at 34 months unless stated;
3) * = significant at p = 0.05, ** = significant at p = 0.01, NS = not significant

Null hypothesis (Ho) 1: there are no differences in the parametric mean values of the different provenances.

Ho 1 was tested using the F test derived from analysis of covariance on individual tree values. The following subsidiary hypotheses were also tested as part of the same analysis using single degree of freedom F tests (STONECYPHER, 1992): Ho 2 (there is no difference between the parametric mean of the 4 Costa Rica provenances as a group and that of the Palestina provenance); Ho 3 (there is no difference between the parametric mean of the División selected provenance and the División control); Ho 4 (there is no difference between the parametric mean of the selected treatments as a whole and the unselected treatments (controls)); Ho 5 (there is no difference between the parametric mean of the Prusia selected provenance and the Prusia control). Hypotheses 3 and 4 were tested only for those form characteristics which showed significant provenance variation under hypothesis 1. Hypothesis 5 was tested for all characteristics with significant provenance variation under hypothesis 1 (as the Prusia site is a plantation, gain would be expected in growth as well as form traits).

Ho 6: There is no additive genetic variation within the reference population sampled by the open-pollinated families.

Hypothesis 6 was tested using the 'F' test derived from analysis of covariance on family plot means. There is no provenance effect in the model (see *table 2*) because this is considered to be irrelevant to the ultimate application of the analysis, i.e. selection of superior families and individuals, independently of whether their superiority is due to provenance or family-within-provenance effects.

For those traits with significant (at p = 0.05) family variation, variance components were derived from observed and expected mean squares and used to estimate family heritability. For the non-dichotomous variables, a separate analysis of covariance on individual-tree values was conducted and used to estimate the additive genetic variance, the additive genetic coefficient of variation (AGCV), heritabilities and genetic correlations (see *Table 3* for details). Phenotypic correlation coefficients based on plot means were also estimated.

Results

Provenance analysis

Results are presented in *tables 4* (significance tests) and *5* (provenance means). At age 22 months, none of the traits showed significant differences at the 5% probability level. However, at ages 31 and 34 months only basal sweep, branch angle and 22 to 31 month diameter increment were insignificant at the same level. Therefore, hypothesis 1 of no differences between the provenance parametric means for all the other traits at ages 31 months to 34 months may confidently be rejected.

At 31 months and 34 months, the Guatemalan provenance was significantly inferior to the Costa Rican treatments as a group (*Table 4*); hypothesis 2 of no difference between the parametric means of the Guatemalan provenance and the Costa Rican provenances as a group may be confidently rejected for all these traits. In each case, the Guatemalan was the worst provenance. In addition, from age 31 months, an attack of the bark beetle *Scolytodes alni* (Coleoptera, Scolytidae) became evident. The attack was confined to trees of the Guatemalan provenance, all except a few of which were attacked.

The evidence for genetic differentiation amongst the Costa Rican provenances was weak. However, the División control provenance was best or second best in all traits except stem lean.

Family analysis

Family results (Costa Rican families only) are summarized in *tables 4* (significance tests), *6* (estimates of genetic parameters) and *7* (correlations). Because of their very poor performance, the Guatemalan families were omitted from the family analysis. To have included them would have given inflated estimates of heritability and genetic gain with no relevance to any likely or meaningful actual selection scenario.

There were significant differences (probability of 5% or less) between all traits except non-basal forking and stem lean. Individual-tree heritabilities ranged from 0.06 (22 month dbh) to 0.34 (height increment between 22 months and 34 months). Estimates of family heritabilities ranged from 0.11 (22 month height) to 0.62 for branch angle. Estimates of AGCV ranged from 7.5% (22 month height) to 13.2% (height increment between 22 months and 34 months) for the growth traits, and from 9.7% (stem straightness) through to 78.8% (basal forking) for form traits. In view of the assumption that the relationship within the open-pollinated families approximates that of half-sibs, these values would be overestimates insofar as the actual average coefficient of relationship is greater than 0.25 (SQUILLACE, 1974).

As, under the adopted evaluation scales, low values for some variables are favourable in terms of product characteristics, genetic correlations are most meaningfully described in terms of their being adverse or favourable, rather than simply their magnitude and direction. In this sense, the estimated values of the genetic correlations between height increment and branch thickness, height increment and stem straightness, height increment and basal sweep were strongly adverse. Other adverse correlations, including basal forking and branch thickness, basal forking and diameter increment, branch thickness and stem straightness, basal sweep and diameter increment, straightness and diameter increment, were moderate or low. The correlations between basal forking and basal sweep, basal sweep and stem straightness were strongly favourable. Other favourable correlations, including basal forking and stem straightness, branch thickness and diameter increment, had moderate or low values. Phenotypic correla-

Table 5. – Least squared provenance means for 8 traits in a provenance/progeny trial of *Alnus acuminata* in Santa Cruz de Turialba, Costa Rica.

	TRAIT AND GRAND MEAN							
Rank[1]	branch thickness[2]	dbh (31 months) (mm)	proportion with basal fork	proportion with non-basal fork	height, 34 months (m)	height inc. 22-34 months (m)	proportion with stem lean	stem straightness[3]
	1.71	7.6	.15	.05	7.7	3.0	.07	3.2
					PROVENANCE, MEAN (σ)			
1	División control 1.95	División control 8.4(.4)	División control .05 (.07)	División control 0.00 (.04)	Prusia 8.4 (.1)	Prusia 3.5 (.1)	Prusia control 0.0 (.04)	Los Santos 3.1 (.06) División 3.1 (.07) División control 3.1 (.14)
2	Pacayas 1.75 (.03)	División 7.8 (.2)	Prusia .1 (.03)	Prusia .03 (.04)	División control 8.2 (.2)	División control 3.3 (.1)	Los Santos .02 (.02)	
3	Prusia control 1.74 (.03)	Prusia control 7.7 (.4) Pacayas 7.7 (.1)	División .11 (.03)	Pacayas .04 (.01) Prusia control .04 (.04)	Pacayas 8.0 (.1)	Prusia control 3.2 (.1)	División .04 (.02)	
4	Los Santos 1.73 (.04)		Prusia control .17 (.06)		División 7.8 (.1) Prusia control 7.8 (.2)	Pacayas 3.1 (.1)	Pacayas .05 (.01)	Pacayas 3.2 (.04) Prusia 3.2 (.04)
5	División 1.72 (.05)	Prusia 7.5 (.1) Los Santos 7.5 (.2)	Pacayas .18 (.02)	Los Santos .06 (.02)		División 3.0 (.1)	División control .06 (.04)	
6	Prusia 1.56 (.03)		Los Santos .19 (.03)	División .07 (.02)	Los Santos 7.4 (.1)	Los Santos 2.7 (.1)	Prusia .07 (.02)	Prusia control 3.3 (.13)
7	Palestina 1.52 (.03)	Palestina 6.4 (.1)	Palestina .28 (.02)	Palestina .08 (.01)	Palestina 6.4 (.1)	Palestina 2.3 (.1)	Palestina .11 (.01)	Palestina 3.5 (.04)

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[1]) 1 = best, 7 = worst in potential productivity and quality of sawtimber

[2]) 1 (thickest) to 3 (thinnest)

[3]) scale of 1 (straightest) to 4 (least straight)

Table 6. – Individual-tree heritabilities, family heritabilities and additive genetic coefficients of variation of 11 traits in a provenance/progeny test of *Alnus acuminata* locates in Santa Cruz de Turrialba, Costa Rica (Costa Rican families only).

Variable (34 months unless stated)	Individual-tree heritability	Family heritability	Additive genetic coefficient of variation %
basal sweep	-	.56	20.6
branch angle	.28	.62	16.2
branch thickness	.16	.54	16.4
dbh (22 months)	.06	.15	9.8
dbh (31 months)	.08	.18	9.2
diameter increment (22-31 mths)	.19	.41	12.8
forking (basal)	-	.47	78.8
height (22 months)	.09	.11	7.5
height	.29	.45	9.6
height increment (22-34)	.34	.54	13.2
stem straightness	.12	.26	9.7

Table 7. – Additive genetic (above diagonal) and phenotypic (below diagonal) correlation coefficients between 5 traits in a provenance/progeny test of *Alnus acuminata* in Santa Cruz de Turrialba, Costa Rica[1]).

VARIABLE (34 months)	height inc.[2]/	basal forking	branch thickness	basal sweep	stem straightness	dbh inc.[3]/
height inc.[2]/		-.17	-.73	1.32	.54	.04
basal forking	.001 NS[4]/		.21	.86	.21	.07
branch thickness	.05 NS	.03 NS		-.07	.32	.37
basal sweep	.11 NS	.16*	-.10		1.43	.21
stem straightness	-.03 NS	.24***	.07 NS	.49***		.14
dbh inc.[3]/	.47***	-.09 NS	.33***	-.13*	-.19**	

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[1]) Estimates based on confounded family and provenance effects;

[2]) 22 to 34 months;

[3]) 22 to 31 months;

[4]) * = significant at p = 0.05, ** = significant at p = 0.01, *** = significant at p = 0.001, NS = not significant

tions were generally weaker and sometimes of different sign to genetic correlations.

Discussion

The results conclusively demonstrate the inferiority of the Palestina provenance to the Costa Rican provenances; it grew relatively slowly and succumbed to the attack of a pest by which the local provenances were unaffected. Although the reason for the inferiority of the Palestina provenance cannot be elucidated from the evidence presented here, it is perhaps the result of poor adaptation to the local conditions. Whatever the causal factors involved, they may be present also in other Guatemalan seed sources of *A. acuminata* (e.g. macro-environmental variables such as day-length). As such, it would be prudent to avoid import to Costa Rica not only of *A. acuminata* seed from Palestina but *A. acuminata* seed from Guatemala in general.

The inferiority of the Palestina provenance is also a striking illustration of the danger in general of indiscriminate seed movements, even within relatively small regions such as Central America. It would be rash to assume that seed deficiencies of a given species in one country or ecological zone can be made up with imports from another.

The results suggest that any of the Costa Rican provenances, with the possible exception of Los Santos, are suitable for planting within the zone. The Prusia provenance is much used at present because of ease of seed collection and access (the plantations are located in a small country park close to urban centres). The results presented here do not suggest any reason for discouraging continued use of this convenient provenance in the case that improved seed from the best mother trees or from the test itself is unavailable.

Values of additive genetic variation and heritabilities within the Costa Rican provenances for growth, stem straightness and the branching traits are within the ranges typically found in forest trees (CORNELIUS, 1994). Other form traits showed moderate to high genetic variation. In general, considering that the families are derived from various provenances, higher levels of genetic variation might have been expected due to confounding of provenance and family effects. This feature of the results would appear to be a reflection of the low level of genetic differentiation between the Costa Rican provenances included.

The estimated values of heritability and genetic variation confirm the potential for improvement of *A. acuminata* in Costa Rica. Breeding programmes could be complicated by the existence of unfavourable genetic correlations, particularly between height and stem straightness and basal sweep. However, the correlations between dbh and these form characteristics are considerably weaker and would probably permit reasonable progress in selection for individual-tree volume without undue negative effects on mean straightness of final crop trees or the proportion of unmerchanteable trees.

Judging from the comparison between the División and Prusia provenances and their controls, the time-consuming phenotypic selection of the mother-trees for stem straightness appears to have been ineffective. However, in spite of the apparent ineffectiveness of phenotypic selection in the natural stands and the Prusia plantation, the heritability values for some of the form traits, particularly basal sweep, branch angle and basal forking, suggest that these should be retained as selection criteria in phenotypic selection. It is also worth stressing that the controls themselves, in accordance with commercial collection norms, were taken from phenotypically above average individuals. Although plus-tree progeny did not differ significantly from controls, this does not imply that form can be disregarded or, specifically, that collections can safely be made from poorly-formed individuals.

Conclusions

1. When planted in the upper slopes of the Costa Rican Central Volcanic Range, trees derived from the Palestina, Guatemala provenance are inferior in most traits of economic importance, including growth rate, most aspects of form and susceptibility to *Scolytodes alni* attack. This provenance should therefore not be planted in this area or in Costa Rica in general. Furthermore, it would in general be prudent to avoid Guatemalan and other seed sources from distant or environmentally very distinct zones of origin, until their potential has been examined through field-testing.

2. There is enough additive genetic variation in growth and most of the form traits such as stem straightness to permit worthwhile genetic gains both from directed seed collection from the best mother trees and from converting the test to a seedling seed orchard.

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References

BERTSCH, F.: Manual para interpretar la fertilidad de los suelos de Costa Rica. San José, Costa Rica, Oficina de Publicaciones de la Universidad de Costa Rica. 76 pp. (1986). — BOSHIER, D. H. and MESEN, J. F.: Proyecto de Mejoramiento Genético Forestal del CATIE. Estado de Avance y principales resultados. Paper presented to the I National Forestry Congress, San José, Costa Rica. 10 to 14 December 1986 (1986). — CORNELIUS, J. P.: Additive genetic variation and heritabilities in forest trees. Can. J. For. Res. **24** (2): 372–379 (1994). — DVORAK, W. S.: CAMCORE: Industry and governments' efforts to conserve threatened forest species in Guatemala, Honduras and Mexico. For. Ecol. Manage. **35**: 151–157 (1990). — DVORAK, W. S. and DONAHUE, J. K.: CAMCORE (Central America and Mexico Coniferous Resources Cooperative). Reseña de Investigaciones 1980 to 1992. North Carolina State University, 94 pp. (1992). — LAMPRECHT, H.: Silvicultura en los trópicos. Translated by Antonio Carrillo. Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), Eschborn, Germany. 335 p. (1990). — SQUILLACE, A. E.: Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. **23**(5): 149–156 (1974). — STONECYPHER, R. W.: Computational Methods. Pp. 195–228. In: L. FINS, S. T. FRIEDMAN and J. V. BROTSCHOL (Eds.). Handbook of quantitative forest genetics. Dordrecht, Kluwer Academic Publishers. 403 p. (1992). — WHITE, T. L.: A conceptual framework for tree improvement programmes. New Forests **4**: 325–342 (1987).