

yellow anthers are subject to the laws of particulate (qualitative) inheritance and behave as a simply inherited Mendelian trait.

Examination of trees planted at Ilanot and of natural populations in northern Israel showed that the leaves can hardly be termed coriaceous and/or subcoriaceous, as stated by several authors (LINGELSHEIM, 1920; Post, 1933; FEINBRUN-DOTHAN, 1978). We also failed to confirm the existence of hairs (Post, 1933; FEINBRUN-DOTHAN, 1978). Confirming to the description of the species by LINGELSHEIM (1920), stomata do indeed occur on the upper leaf surface (Fig. 2).

Standard floras are notoriously short on numerical data describing the range of morphological characters, and those consulted in connection with the present study of *F. syriaca* (BOISSIER, 1879; Post, 1933; VASIL'EV, 1967; FEINBRUN-DOTHAN, 1978; YALTIRIK, 1978; see also LINGELSHEIM, 1920) are apparently no exception.

The number of leaflets listed ranges from 2–6 in LINGELSHEIM (1920) and VASIL'EV (1967) to (1-) 3 (-11) in FEINBRUN-DOTHAN (1978); in our subjects it varies from 3 to 13, with an average of 6.7. The length of the leaflet ranges from 3–6 cm in VASIL'EV (1967) to 1–10 cm in LINGELSHEIM (1920), and in our study from 2.8 to 8.4 cm with an average of 5.6 cm. The width is given as 2–2.5 cm by VASIL'EV (1967) and 0.8–3.5 cm by LINGELSHEIM (1920), with our data ranging from 1.2 to 2.9 cm, with an average of 1.9 cm (Table 6). Similar differences were found with regard to dimensions of the samara. This implied criticism of the data listed in standard floras does, admittedly, not take into account the possibility of geographic variation, a subject apparently not yet investigated.

Factor analysis (Table 7) leads to a much clearer understanding of morphological variation in *F. syriaca* and describes total variation better than a series of correlations or scatter diagrams. Cluster analysis (Table 8) used to indicate groupings among the trees examined, provides

further insight into the structure of the population and shows that 71% of the trees belong to two well defined groups, whereas other groups are represented by single or few trees only.

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## Genotype-Environment Interactions in Tropical Pines and their Effects on the Structure of Breeding Populations

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#### Summary

To the tree breeder the many statistical definitions of genotype-environment interaction (*gei*) can be reduced to the one practical implication that the optimum population or individual on one site is not necessarily the best for others. Various univariate and multivariate techniques are available for detecting and evaluating *gei*; four methods (PLAISTED'S, WRICKE'S, joint regression, principal components) were compared with a limited set of data for maximum wood density of *Pinus caribaea* MORELET and found to provide similar conclusions about the sources of *gei* but joint regression analysis has the potential for predicting genotypic performance on untested sites.

*Gei* effects occur at the level of species, provenance, family or clone (and examples of each in tropical pines are

given) but few field experiments have been specifically designed to estimate them nor have data been analysed to determine the contributing environments and genotypes.

*Gei* reduces heritability and hence gain, necessitates the creation and maintenance of separate breeding populations, and requires the integration of genetic and silvicultural research. It is probably only realistic to expect to detect, explain and use *gei* when a single environmental factor affects an economically important trait in a predictable manner. The decision to use *gei* effects in breeding strategy becomes more complex when two traits are inversely correlated; the breeder also has to decide between seeking homeostasis at the level of population or individual. This is particularly important in relation to the transience of forest environments due to changing management practices and to the increasing use of marginal sites.

A strategy of maintaining multiple populations retains the existence and identity of gene complexes (which can be combined later to regenerate variation), yields highly productive populations for specific environments, provides safeguards against inbreeding and encourages the populations to diverge genetically (by selection for different traits or environments) thus maintaining variability and ensuring future gain at lower cost than the traditional hierarchy of species, provenance and breeding populations.

*Key words:* tropical pines, genotype-environment interaction, breeding strategy, provenance trials, multiple populations.

### Zusammenfassung

Für den Forstpflanzenzüchter können die zahlreichen statistischen Definitionen der Genotyp-Umwelt-Interaktion (hier *gei*) auf die eine praktische Folgerung reduziert werden— daß die optimale Population oder das optimale Individuum auf einem Standort nicht notwendigerweise auch die bzw. das beste auf anderen Standorten sein muß. Verschiedene Uni- oder Multivariate Techniken sind zur Entdeckung und Schätzung der *gei* verfügbar. Vier Methoden, die von PLAISTED, die von WRICKE, die zusammengesetzte Regression und die Hauptkomponentenschätzung wurden mit einem begrenzten Datenset für die maximale Holzdichte von *Pinus caribaea* MORELET verglichen. Dabei wurde gefunden, daß diese für die Ursachen der *gei* ähnliche Schlußfolgerungen liefern, aber die zusammengesetzte Regressions-Analyse hat das Potential, um die genotypische Leistung ungetesteter Standorte vorauszusagen.

*Gei*-Effekte treten auf dem Level der Arten, Provenienzen, Familien und Klone auf, (Beispiele für jede der tropischen Kiefern werden gegeben), aber nur wenige Feldversuche sind speziell dazu angelegt, um sie zu schätzen, noch sind Daten analysiert worden, um die Einflüsse von Umwelt und Genotyp zu bestimmen.

Die *gei* reduziert die Heritabilität und folglich den Gewinn, bedarf der Entwicklung und Aufrechterhaltung separater Züchtungspopulationen und erfordert die Integration von genetischer und waldbaulicher Forschung. Es ist wahrscheinlich nur realistisch, zu erwarten, die *gei* zu entdecken, zu erläutern und zu benutzen, wenn ein einzelner Umweltfaktor ein ökonomisch wichtiges Merkmal in einer vorhersagbaren Art beeinflußt. Die Entscheidung, den *gei*-Einfluß bei Züchtungsstrategien zu benutzen, wird komplexer, wenn 2 Merkmale negativ korreliert sind. Der Züchter hat auch auf der Suche nach Homeostasis zwischen dem Populations- oder Einzelbaumniveau zu entscheiden. Dies ist besonders wichtig in Relation zur Veränderung der forstlichen Umwelt, die auf wechselnde Management-Praktiken und die Erhöhung der Verwendung marginaler Standorte zurückzuführen ist.

Eine Strategie der „multiplen Populationen“ ist die Erhaltung der Existenz und der Identität von Genkomplexen, (die später kombiniert werden, um die Variation zu erneuern), sie bringt hochproduktive Populationen für spezielle Standorte hervor, liefert Sicherheiten gegen Inzucht und regt die Populationen an, genetisch abzuweichen, (durch Selektion auf verschiedene Merkmale oder Standorte hin). So werden die Variabilität erhalten und zukünftige Gewinne zu geringeren Kosten gesichert, als sie bei der herkömmlichen Hierarchie von Arten, Provenienzen und Züchtungspopulationen aufgetreten wären.

### Definitions of Genotype-Environment Interaction

In statistical and genetic terms an interaction between two factors (here genotypes and environments) can be variously defined as a lack of additivity of their individual effects, a differential ranking of levels of the first factor at different levels of the second, or a set of differential differences between levels of the first within the second. The

net effect is a lack of similarity of genetic differences in the various environments or, in simple terms, a good genotype in one environment is not necessarily good in another.

“Environment” itself needs some definition or clarification. It involves all natural biotic, climatic and edaphic factors that influence tree growth and includes annual climatic variations. The effects of each of these can interact with others and all can interact with genetic effects. Thus, although genotype-environment I. (*gei*) is a collective term, it is always desirable to declare the factors of interest that distinguish between environments since it is possible, for a given set of genotypes, to detect *gei* in relation to one environmental factor but not to another. Environment also includes artificially imposed factors such as spacing (see e.g. CAMPBELL and WILSON, 1973), fertilizer (JAHROMI *et al.*, 1976; ROBERDS *et al.*, 1976) and genotypic interaction caused by competition (see e.g. ADAMS *et al.*, 1973; SNYDER and ALLEN, 1971).

“Genotype” also is a collective term, including genetic structure at the level of species, provenance, family or individual (seedling or vegetative propagule). Each of these has its own characteristic levels of genetic variation, homeostasis and stability. For the purposes of this paper we assume that replicated plots of randomly selected trees for each population, however defined, are planted in each environment.

“*Gei*” has been studied mainly with agricultural crops and only recently with forest trees (e.g. MORGENSTERN and TEICH, 1969; SQUILLACE, 1970; SHELBOURNE, 1972; BURLEY and KEMP, 1972; MERGEN *et al.*, 1974; SHELBOURNE and CAMPBELL, 1976). Plant breeders tend to ignore or dispose of *gei* effects while geneticists try to explain *gei* in terms of gene action but in fact it offers valuable information that should be used to direct breeding strategy. The major problems lie in designing suitable experiments to estimate *gei* effects, analysing data appropriately to determine the contributing environments and genotypes, and interpreting the results for use in breeding strategy.

### Methods for Detecting and Assessing GEI Effects

In common with data from any experiment for which statistical analysis is planned, *gei* data should be examined graphically to search for anomalies and likely contributors to the interaction. For the full statistical analysis a variety of univariate methods is available including: —

- (i) the normal analysis of variance (ANOVA) of a replicated two-way classification,
- (ii) a modified ANOVA to omit each environment and genotype in turn to determine the individual contributors to *gei* variance (WRICKE, 1962) and the consistency of genotypes over all environments (PLAISTED, 1960),
- (iii) analysis of single degrees of freedom (TUKEY, 1949) or firmness (MANDEL, 1971) to examine the effect of each contributing level of both factors,
- (iv) partitioning of the *gei* variance component (YATES and COCHRAN, 1938; SHUKLA, 1972),
- (v) the so-called joint regression technique wherein genotypic performance is plotted against the mean of all genotypes in each environment separately, or against some external estimator of site quality; the interaction variance is partitioned into two terms, the heterogeneity of regressions between genotypes and the deviation from regression for each genotypes (FINLAY and WILKINSON 1963; FREE-

MAN, 1973; MERGEN *et al.*, 1974; GARCIA DE LEON, 1982; GIBSON, 1982). Joint regression analysis has limitations including the assumption of linearity of response and the choice of an environmental mean value biased by the genotype under consideration (FREEMAN and PERKINS, 1971; HARDWICK and WOOD 1972; NAMKOONG, 1978) but it is valuable for determining a genotype's stability over environments, and

- (vi) the genetic correlation between each genotype's performance on each pair of environments (BURDON, 1977).

While the above methods are essentially univariate analyses, attempts have been made to use principal component and principal coordinate analysis as multivariate methods with firstly genotypes as variables and environments as observations and secondly the reverse (see BURLEY and KEMP, 1972; FREEMAN, 1973; FREEMAN and DOWKER, 1973; GARCIA DE LEON, 1982). The contributing effects of the individual genotypes or environments to the interaction vari-

Table 1. — Partition and significance of the interaction term from joint regression analysis of maximum density at 7 years in 7 provenances of *P. caribaea* over 3 sites including means, percent contribution to the total interaction sums of squares (SS%) and regression coefficient ( $B_i$ ).

Source of variation	d.f.	M.S.	F(sig)
P-S int.	12	0.010521	2.39(* )
Heterogeneity of reg.	6	0.005613	(1.28(N.S.))
Remainder	6	0.015429	(0.36(N.S.))
Residual	66	0.0044	3.51(** )

Prov.	Mean	SSZ	$B_i$
POP	0.8122	36.05	0.8638
MPR	0.7719	24.80	0.5831
GUA	0.7420	14.03	1.3114
BRU	0.7212	1.74	1.0421
MEL	0.7176	1.82	1.0875
SAN	0.7081	7.85	1.0394
ALA	0.6959	13.71	1.0728

Table 2. — Plaisted's analysis of maximum density at 7 years in 7 provenances of *P. caribaea* over 3 sites. Estimates of the remainder provenance-site interaction components of variance when omitting each provenance successively from the analysis.

Prov.	Mean	$ps_{(j)}$	P-S interaction effects		
			JARI	CARDWELL	MELVILLE
POP	0.8130	$6.27 \times 10^{-4}$	-0.0644	0.0702	-0.0072
MRP	0.7703	$9.85 \times "$	-0.0196	0.0611	-0.0518
GUA	0.7416	$13.26 \times "$	0.0152	-0.0461	0.0386
ALA	0.6945	$13.37 \times "$	0.0404	-0.0427	0.0029
SAN	0.7093	$15.24 \times "$	0.0314	-0.0314	0.0000
MEL	0.7101	$16.88 \times "$	-0.0165	0.0050	0.0143
BRU	0.7224	$17.15 \times "$	0.0134	-0.0161	0.0033

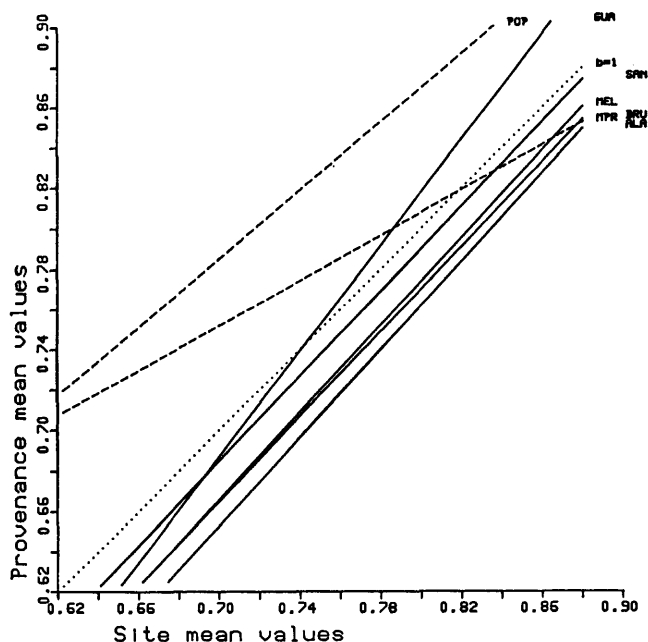


Figure 1. — Joint regression lines for maximum density (g/cc) for 7 provenances of *P. caribaea* on 3 sites at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean ( $b = 1$ ) by dotted line. Site means — Cardwell 0.67, Jari 0.70, Melville 0.88 g/cc.

ance are seen by their loadings in the separate components or coordinates.

Direct comparisons of all these methods are rarely made (see MERGEN *et al.*, 1974) but WRICKE's and PLAISTED's methods were compared with joint regression analysis and principal coordinate analysis for wood density parameters in *Pinus caribaea* MORELET (GARCIA DE LEON, 1982). Two radial samples (8 mm diameter increment cores) were extracted from each of three trees in five replications of seven provenances of *P. caribaea* var. *hondurensis* BARRETT et GOL-FARI growing in seven year old international provenance trials at Jari, Brazil, Cardwell, Queensland, and Melville Island, Northern Territory, Australia. Although only three environments were represented their conditions differed greatly and a combined analysis showed the existence of provenance-environment interaction effects on the maximum density (as determined by X-ray densitometry - see BURLEY *et al.*, 1979).

Joint regression analysis (Table 1), PLAISTED's method (Table 2) and WRICKE's method produced similar results and conclusions. The advantage of joint regression analysis over the other two is that, where there is a generalized response, it also allows the prediction of a genotype's performance in an untested environment. Two inland provenances, Poptun (Guatemala) and Mountain Pine Ridge (Belize), accounted for 60–70% of the interaction variances when analysed by all three methods; in the joint regression analysis their individual regression coefficients indicated above average stability ( $b < 1.0$ ) (Table 1), and hence little adaptability. In this case the overall means were also highest for these two provenances indicating that they could be used for outstanding performance on poor sites and better than average performance on the best sites.

Principle components analysis allowed the identification of

- (i) provenances that contributed most to differences between sites Figure 2A and Table 4B; principal

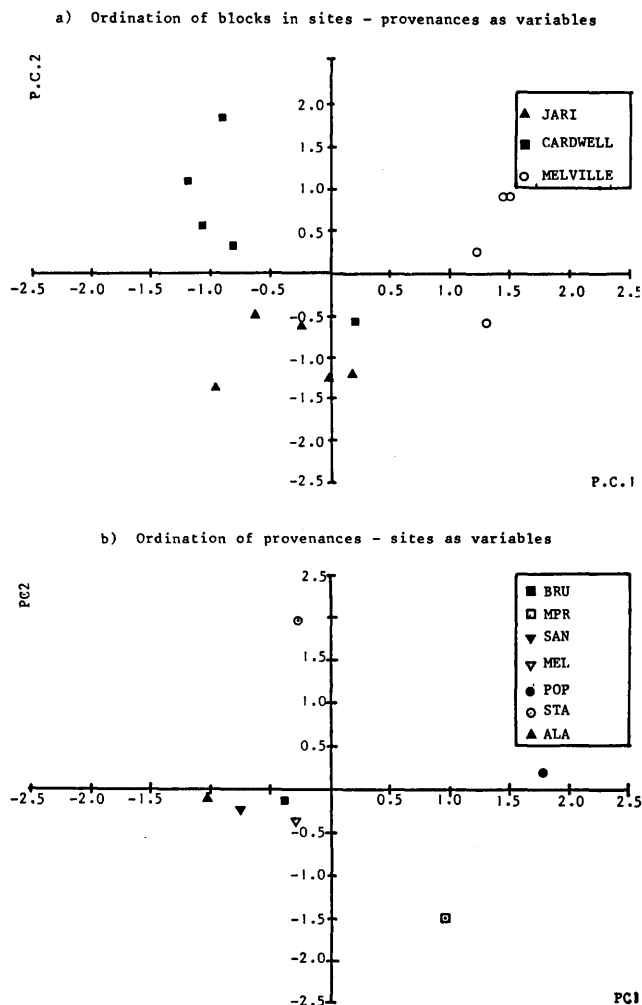


Figure 2. — Ordination of sites (a) and provenances (b) on principal components 1 and 2 for maximum density for 7 provenances of *P. caribaea* on 3 sites at 7 years.

component 1 (which explained 88% of the variation compared with 10% by component 2) is heavily weighted by Cardwell, i.e. the separation between provenances is greatest on this site and (ii) sites that contributed most differences in genotypic responses (Figure 2B and Table 4B; principal component 1 (which explained 72% of total variation compared with 11% by component 2) is heavily weighted by the group Santos, Guanaja, Melinda, Alamicamba and Brus, i.e. site differences are most apparent in coastal provenances.

Principal components analysis is by definition used for building hypotheses on the joint distribution of several variables; no estimate of precision is possible for the individual components. The conclusions drawn in (i) and (ii)

Table 3. — Wricke's analysis of maximum density at 7 years in 7 provenances of *P. caribaea* over 3 sites. Means, sums of squares (SS), percent contribution to sums of squares (SS%) and cumulative percent (Cum%).

Prov.	Mean	SS	SS%	Cum%
POP	0.8122	0.0095644	37.82	37.82
MPR	0.7719	0.0063959	25.29	63.11
GUA	0.7420	0.0038787	15.34	78.45
ALA	0.6959	0.0032582	12.88	91.33
SAN	0.7081	0.0017810	7.04	98.37
BRU	0.7212	0.0003457	1.37	99.74
MEL	0.7176	0.0000640	0.26	100.00

above agree with those obtained from analysis of variance and joint regression analysis of this small set of data and therefore there is no immediately obvious advantage of this type of analysis. However, it may be useful with large number of provenances and sites. Its application in resolving the problem of bias in joint regression analysis is not clear.

Note: The following abbreviations have been used in the Tables and Figures for the *Pinus caribaea* provenance names

- ALA — Alamicamba, Nicaragua
- STA — Santa Clara, Nicaragua
- POP — Poptun, Guatemala
- MPR — Mountain Pine Ridge, Belize
- MEL — Melinda, Belize
- SAN — Santos, Belize
- POT — Potosi, Honduras
- BRU — Brus Lagoon, Honduras
- GUA — Guanaja, Honduras

and the following abbreviations for site names

- ANO A — Puerto Rico A
- ANO B — Puerto Rico B
- BBM — Beerburrum, Queensland, Australia
- BFR — Byfield Ridge, Queensland, Australia
- BTH — Bukit Tapah, Malaysia
- CDL — Cardwell, Queensland, Australia
- CPN — Chumphon, Thailand
- CTI — Chati, Zambia
- HBG — Huey Bong, Thailand
- JRI — Jari, Brazil
- MTI — Mariti, South Africa
- SPO — San Pedro, Ivory Coast

For full details of seed sources and collections see GREAVES, 1978.

### The Importance of Genotype-Environment Interactions in Silviculture and Breeding

The implications of *gei* are three-fold. Firstly, it reduces overall genetic gain (whether obtained by selection of species, provenance or individuals) since the *gei* variance appears in the denominator of all heritability estimates and thus reduces heritability and consequent gain. Secondly, to overcome this, heritability and gain can be maximised

Table 4. — Principal components analysis of maximum density at 7 years in 7 provenances of *P. caribaea* over 3 sites. Eigenvectors, proportionally weighted for each component.

Vector	PROVENANCES							SITES		
	BRU	MPR	SAN	MEL	POP	GUA	ALA	JARI	CARDWELL	MELVILLE
1	0.745	0.432	1.000	0.840	0.526	0.904	0.834	0.069	1.000	0.325
2	-0.057	0.669	-0.315	0.091	1.000	-0.096	-0.552	0.221	-0.413	1.000

within each environment individually; and this requires the creation of separate breeding populations with consequent problems of cost, management, recording and ancestry control. Thirdly, silvicultural and genetic research, which traditionally have been conducted by different organizations or individuals, must be integrated to determine the optimum genotypes and management system for each afforestation site (see e.g. GROSE, 1972; CAMPBELL and WILSON, 1973).

The level at which *gei* effects are important varies with species and character but ignorance of *gei* can cause severe losses of plantation yield through tree death or reduced growth. For example, at the species level, large areas of *P. radiata* D. DON grown at the lower levels of the mist belt of East Africa are virtually eliminated by *Scirrhia pini* FUNK and PARKER; below the mist belt conditions are too dry for both pine and fungus while at higher levels reduced temperatures eliminate the disease but also reduce tree growth rates; other species can be selected for each condition.

Similarly, at the provenance level, *P. caribaea* MOR. var. *hondurensis* BARR. et GOLF. seed from Mountain Pine Ridge, Belize, has been used to establish nearly a million hectares in many tropical countries, largely because it has been the most easily available source; yet differences among provenances of at least 10% have been shown in many sites and for many characters. If in only a quarter of the plantations Mountain Pine Ridge were a sub-optimal source, the total annual loss of yield could amount to a million cubic metres.

At the individual level the differences between genotypes (families or clones) and the effects of *gei* may not be as dramatic. Nevertheless it is important to use them to maximise yield while minimising cost, to obtain the best use of genetically improved stock, and to intensify the use of marginal land. As forests are being established progressively on less desirable land, it will become more necessary to identify adapted and productive genotypes.

Recognising the three levels at which *gei* may occur, it is necessary to decide at what level different breeding populations will be maintained. Obviously separate populations are necessary for different species, although distinctions may blur in the case of naturally introgressed populations; also two species' populations may be combined deliberately in programmes of artificial hybridization.

Among provenances it is desirable to maintain separate breeding populations for control of co-ancestry, for conservation of co-adapted gene complexes, and for controlled inter-provenance hybridization.

Within provenances the extent of partitioning the breeding population must be a balance between (i) the costs of maintaining and using separate groups and (ii) the need to do so as evidenced by the size of *gei* effects. Comparative cost-benefit analysis of different alternative strategies is feasible but has not yet been attempted.

#### **Genotype-Environment Interaction and Improvement Strategy**

Tree improvement strategies range in intensity from simple species selection, through mass selection within species to complex systems in which genetic variances are estimated, multiple selection indices constructed and precisely planned controlled crosses made in a sub-population to maximize genetic advance with each generation of selection. Because of the environmental and economic impact

of forestry, most organizations concerned with tree improvement are national and involved at all levels, from species to individual tree. The presence of *gei* at any level implies the potential to increase productivity but only at the cost of an increase in the complexity of what is usually an already multifaceted programme. A compromise therefore has to be made in adopting strategies which will produce well adapted breeds but at the same time will not result in an unmanageable number of separate populations for special environments with attendant problems of recording and ancestry control; decisions have to be taken at the level of species, provenance, family, tree and individual trait.

To make these decisions, estimates of *gei* at all levels are required and carefully planned experiments are needed to provide the data, as an integrated part of improvement strategy. The more clearly the genotypic behaviour can be related to a specific factor in the environment, the more likely it is that it will be explained by a generalized response and the greater the predictive, as opposed to the empirical, value will be. However, even if only three climatic variables are taken into account, the number of environments required to give a good spread of values for each factor and for the interaction between them already becomes prohibitive in experimental terms. Moreover, different populations of genotypes react differently to a given set of environments and therefore information gained for one set of provenances or families is not necessarily applicable to another; a set of families from ortets selected in one area may not show *gei* to the same extent as a set from ortets selected over a wide range of sites. It is, therefore, not surprising that *gei* has rarely been properly measured in any programme. It is probably only realistic to expect to detect, explain and use *gei* when a single factor in the environment affects an economically important trait in a predictable manner.

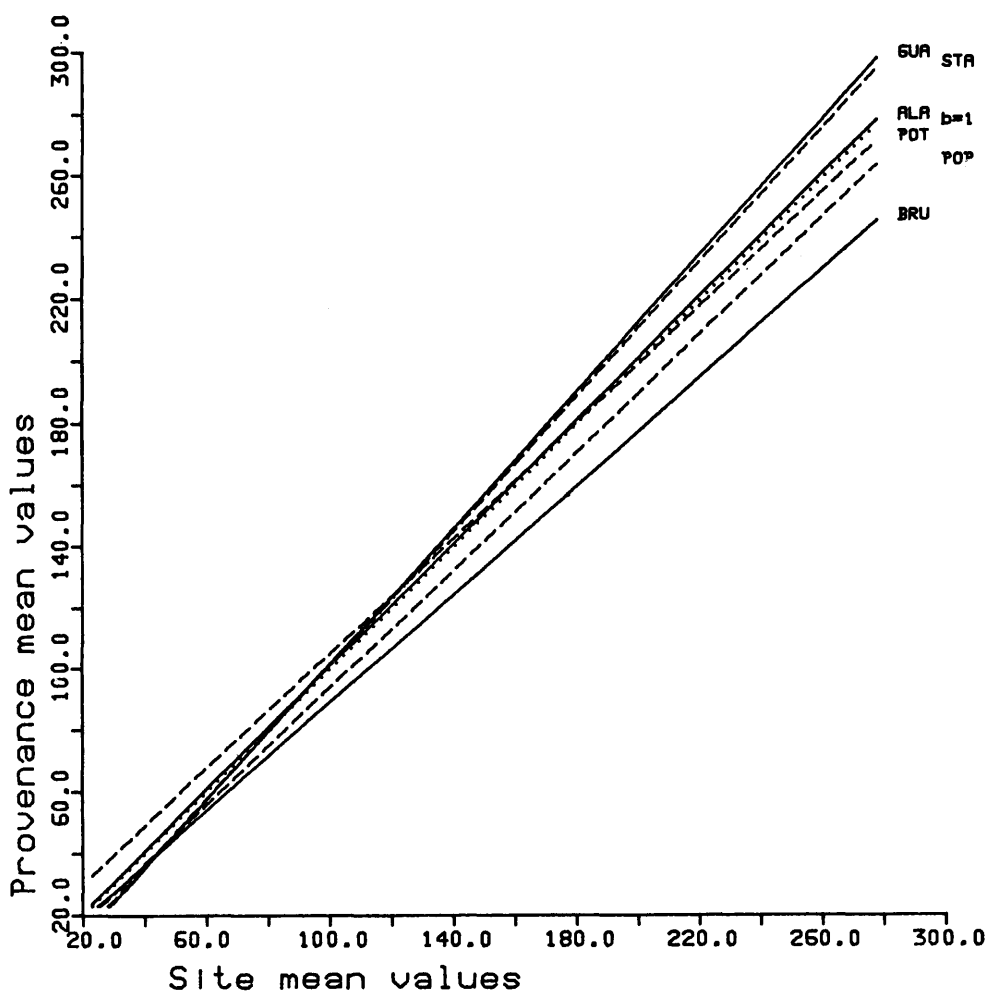
If species or provenance trials, progeny or clonal tests indicate the presence of *gei* there are other points which must be taken into consideration when deciding on a strategy to use it. If the *gei* concerns a single, economically vital trait, the decision may be straightforward but it is more likely that other traits will complicate the issue. If two traits interact with an environmental factor but inversely to each other, a careful cost-benefit analysis may be necessary before a decision can be taken to use *gei* for either of them. If the trait of interest is genetically correlated with another which itself does not interact in the same way with the environment, this could provide a further complication. A more obscure but just as important consideration is whether the breeder should seek homeostasis at the populational or individual tree level (see NAMKOONG, 1979). Breeding for overall adaptability will favour the production of a population in the former state whereas selection for individual environments may make it advisable to maintain heterozygosity at the individual genotypic level and to take active steps to avoid homozygosity. The question of homeostasis is allied to the desirability or otherwise of breaking up co-adapted gene complexes within species. If *gei* is used only between provenances this will not arise but *gei* does frequently occur between families or individual trees as well when there would be a strong incentive to use it at both levels and this would result in provenance "cocktails" which might produce later problems in asynchronous flowering, seed production and segregation. A further complication is that

all forms of gene effect have been found to be associated with *gei* (NAMKOONG, 1979) and special experiments to determine this may be necessary. Lastly, the transience of the environment itself must be taken into account; there is often uncertainty about future forest environments because management practices change them, because there may be other demands on a particular land category or because forestry will be expected to use increasingly marginal sites.

These arguments indicate how difficult it would be to make decisions about using *gei* in the absence of precise information which would be expensive to obtain and is rarely available in any tree improvement programme. This applies mainly at the provenance level or below but there are numerous instances where similar decisions have to be made at the species level. Therefore, of the more subtle

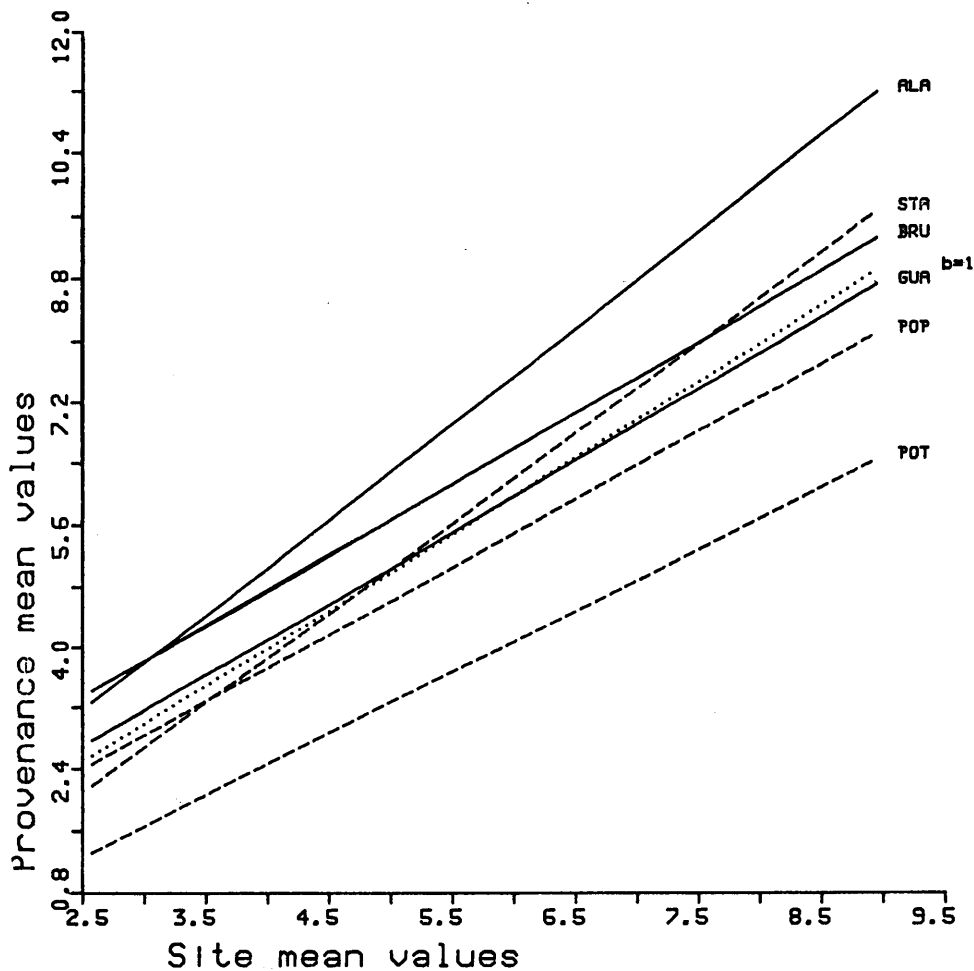
potential of *gei* is to contribute to production, improvement strategy must ensure that it is allowed to express itself and be developed in the breeding process without the necessity for expensive experiments to explain it.

Most tree breeding programmes have adopted the classical breeding approach of using a hierarchy of populations e.g. gene pool, breeding population and seed production population, through which material is transferred to the commercial plantations. Avoidance of inbreeding in this system is difficult and restricts the breeder's freedom. An alternative strategy is to develop an array of populations within the total breeding population for a species (NAMKOONG *et al.*, 1980) within which it is possible to retain the existence and identities of gene complexes, e.g. provenances, which can be combined later to regenerate variation. This system provides safeguards against inbreeding and



Site name	HBC	ANOB	BFR	MTI	ANOA	CDL	BTH	CPN	BBM	JRI	SPO	CTI	
$\bar{x}$	21.0	99.1	109.1	113.4	114.9	118.3	132.1	146.1	165.5	209.0	292.9	297.7	
Source (df)	Analysis of Variance and Variance Components (%)												
Provn (5)	7.3	9.3	1.3	0.0	15.8	6.3	0.0	10.5	39.2	26.2	33.3	58.0	
sig F	NS	NS	NS	NS	NS	NS	NS	NS	**	*	**	***	
Repln (4)	23.3	33.7	85.7	25.6	14.8	0.0	78.4	51.8	4.0	17.7	15.1	8.1	
sig F	*	**	***	*	NS	NS	***	***	NS	*	NS	NS	
Resdl (20)	69.4	57.0	13.0	74.4	69.4	93.7	21.6	37.3	56.8	56.1	51.6	35.9	
Total	$s^2$	104.8	1173	1782	857.8	1759	295.4	1362	2811	467.6	1719	1807	2262

Figure 3. — Regression lines for 6 provenances of *P. caribaea* over 12 sites for volume over bark (cubic decimetres) at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean ( $b = 1$ ) by dotted line.



Site name	CTI	MTI	BBM	BFR	ANOA	JRI	ANOB	SPO	CDL	BTH
$\bar{x}$	3.29	3.32	4.27	5.53	6.65	7.53	7.60	7.64	7.92	8.92
Source (df)	Analysis of Variance and Variance Components (%)									
Provn (5)	38.1	22.9	19.8	50.5	31.7	46.5	32.2	57.7	57.8	12.7
sig F	*	NS	NS	***	*	**	*	***	***	NS
Repln (4)	3.7	4.4	0.0	10.6	0.0	10.2	0.0	9.8	0.0	42.0
Sig F	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Resdl (20)	58.2	72.7	80.2	38.9	68.3	43.3	67.8	32.5	42.2	45.1
Total $s^2$	1.34	1.57	1.92	4.91	5.64	3.33	7.91	4.92	4.36	3.78

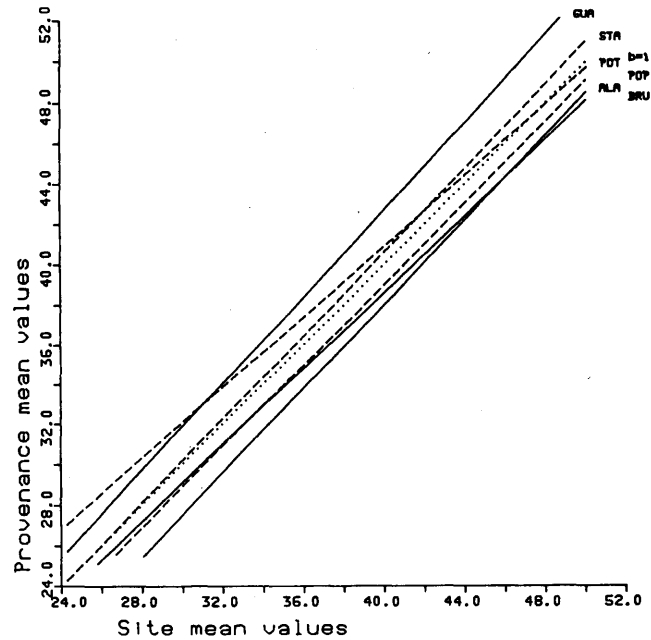
Figure 4. — Regression lines for 6 provenances of *P. caribaea* over 12 sites for stem straightness (weighted rating) at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean ( $b = 1$ ) by dotted line.

allows the breeder more latitude. An underlying concept in this strategy is that the multiple populations diverge in their genetic constitutions. This can be brought about by selection for different attributes and/or for different environments. The multiple population strategy could have a dual advantage, therefore, in that broad, empirical indications of *gei* could be used to develop and build up populations matched to environments. In this system the prime reason for developing a population for a particular environment does not involve a difficult decision to exploit *gei* but an intuitive guess that it might be worth exploiting; it could result in the development of highly productive populations for specific environments and at the same time increase the potential for maintaining variability in the species to ensure long-term gain. In terms of gain, it will encourage parallel rather than unequal development of a number of populations thus ensuring that a broad genetic

base is maintained. This strategy is being used for an international plan for the genetic improvement of *P. caribaea* (see Figure 8).

#### Evidence for Genotype-Environment Interaction in Tropical Pines

There are about 25 pine species which occur naturally in the tropics and most, plus three or four more that grow just outside the tropics, have been widely introduced as exotics throughout the tropical world. Of these, six species have, at various times, been the subjects of intensive international programmes to sample provenance variation over their entire natural ranges and to distribute seed for trials throughout the tropics. Genetic improvement programmes for two species, *P. caribaea* and *P. patula*, are sufficiently advanced in a number of countries for there to have been international exchange of half-sib, full-sib



Site name	SPO	CPN	JRI	CTI	CDL	BBM	BFR	ANOA	ANOB	BTH	MTI	HBG
$\bar{x}$	26.92	30.50	30.77	33.23	33.43	33.93	34.38	35.02	37.31	39.95	41.66	49.97
Source (df)	Analysis of Variance and Variance Components (%)											
Provn (5)	53.7	27.9	16.8	1.0	5.5	43.7	5.2	26.7	32.8	38.5	2.7	1.4
sig F	***	*	NS	NS	NS	**	*	*	**	*	NS	NS
Repln (4)	5.0	8.8	1.0	10.0	27.9	0.6	81.0	9.9	27.3	28.2	2.8	55.0
sig F	NS	NS	NS	NS	*	NS	***	NS	**	*	NS	***
Resdl (20)	41.3	63.3	82.2	89.0	66.6	55.7	13.8	63.4	39.9	33.3	94.5	43.6
Total $S^2$	5.64	10.67	9.68	4.04	9.61	4.74	46.09	19.21	15.47	18.67	7.72	32.02

Figure 5. — Regression lines for 6 provenances of *P. caribaea* over 12 sites for bark thickness (percent) at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean ( $b = 1$ ) by dotted line.

and clonal material of individual genotypes. In other words, there has been, within the genus, wide distribution of material at the species, provenance, family and individual tree levels and therefore there should be the opportunity to observe *gei* in the pines in its broadest sense.

Although species introduction plots are usually numerous and widespread, replicated trials repeated over environments are not normally established for species because *gei* at this level is usually detectable without a formal statistical approach. Nevertheless, it is of interest to record the nature of *gei* at the species level since most pines have been domesticated for only one or two generations and many still contain population and tree to tree variation which is almost as great as that between species. Soil moisture availability (from drainage to drought) and temperature (annual means, monthly means and extremes) are the factors in the environment with which species interact most commonly. In this respect they can affect wind resistance, productivity, stem and branch morphology, wood density and reproductive behaviour. For example, *P.elliottii* ENGELM. is severely affected by wind throw on well drained soils where mean annual temperatures are below 16° C whereas *P. patula* is unaffected by wind (BARNES and MULLIN, 1976). As temperatures rise above (16° C, the roles are reversed and *P. patula* becomes subject to severe wind breakage. On well drained soil in areas with mean annual rainfall in the region of 800 mm, *P. caribaea* var. *hondurensis* and *P. kesiya* will produce more than *P. elliottii* but not if drainage is impeded under similar

rainfall conditions. Where there is no annual cessation of growth imposed by temperature or soil moisture deficit, *P. caribaea* var. *hondurensis* will grow continuously and produce sinuous stems, irregular branching (foxtails) and very low density wood (BARNES *et al.*, 1977) with no late-wood, whereas *P. elliottii*, *P. taeda* or *P. patula* will maintain their periodic growth habit under these conditions and produce no such defects. At mean annual temperatures over 18° C *P. elliottii* has a normal flowering behaviour whereas *P. patula* becomes asynchronous in production of male and female strobili. On the other hand, at temperatures below 16° C, *P. patula* produces no pollen at all (BARNES and MULLIN, 1974).

These well documented examples of *gei* at the species level have come to be associated with certain macro-factors in the environment and a species' performance is generally predictable, partly because of the large differences between species but also because of the wide distribution of planting. At the provenance, family and individual tree levels, differences are on a progressively smaller scale and although trials and tests have been much more often replicated, the site coverage has not been as great. Prediction at this level becomes dependent upon knowledge of the effects of micro-factors of the environment and many more sites are needed to cover their ranges and interactions

At the provenance level, the most extensive *gei* work with pine species in the tropics has been the international provenance trials of *P. caribaea* and *P. oocarpa*; assessment

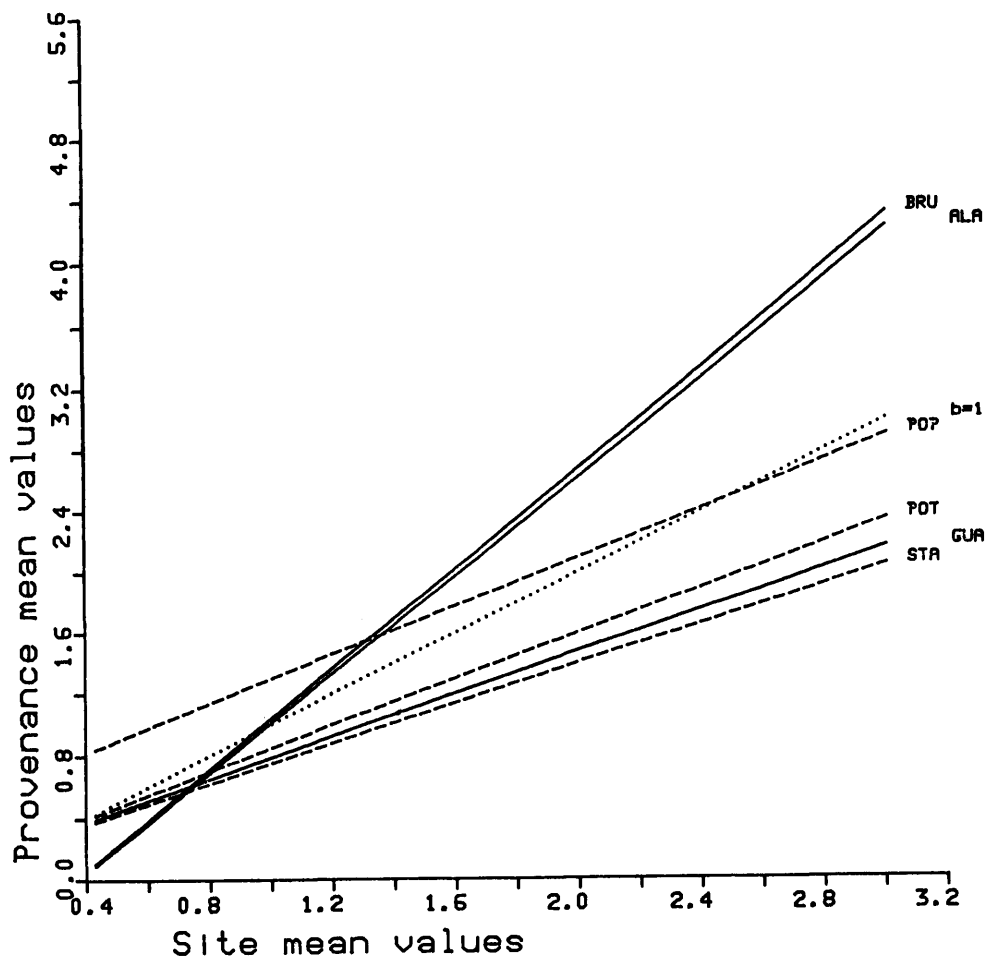


and interpretation has just begun. In an investigation of 6 provenances over 12 sites at 7–9 years of age (GIBSON, 1982), ranking for volume varied over sites but the statistically significant *gei* was attributable to frequent small unpredictable changes in provenance performance over sites and this did not lead to any meaningful change in the slope of the regression lines (Figure 3). However, differences between provenances within trials become statistically more significant at the sites where the trees are larger (sites 9, 10, 11 and 12 in Figure 3) and there are almost complete reversals of the rankings of Alamicamba (coastal) and Poptun (inland) provenances at Chati (inland) and San Pedro (coastal) sites, an interaction that might be expected. The interaction variance was very small compared with that for provenance in stem straightness and bark thickness (Figures 4 and 5) whereas for longest internode (an index of foxtailing) (Figure 6) and

flowering (Figure 7) the *gei* variance was very substantial but almost entirely attributable to heterogeneity of the regression lines which indicated good predictability (Table 5) and the regression lines generally diverge and do not cross indicating a difference in scale of response with little change in ranking between sites.

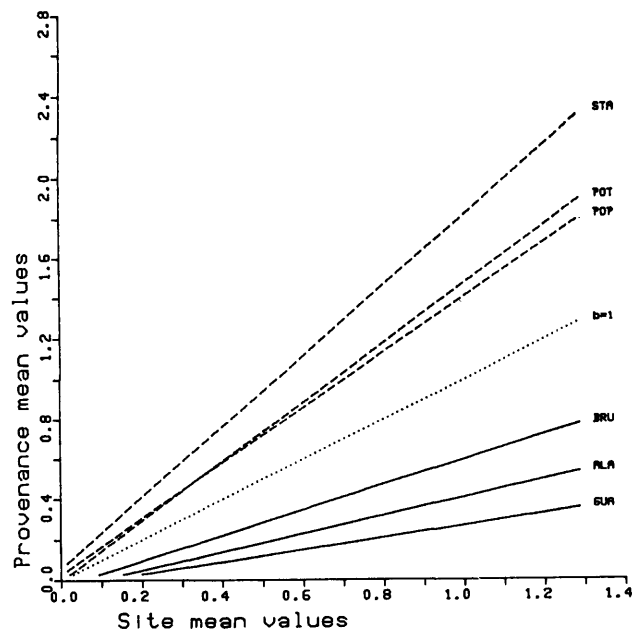
Studies of *P. caribaea* provenances planted over a wide range of sites have shown no evidence of *gei* for mean tree wood density at 6 years (BARNES *et al.*, 1977 and 1980). However, in a densitometric study of radial cores of seven provenances over three sites at seven years, *gei* was detected in within-tree maximum and range of wood density (GARCIA DE LEON, 1982).

In various assessments of up to 15 provenances and 10 sites in Queensland, *gei* was judged to be of little importance in height, diameter, volume, stem straightness and foxtailing of *P. caribaea* (EISEMANN *et al.*, 1980). In these



Site name	HBG	SPO	CPN	BFR	BTH	CDL	ANOA	JRI	ANOB	BBM	MTI	CTI
$\bar{x}$	0.8	1.27	1.45	1.59	1.62	1.77	1.79	1.92	2.22	2.41	2.53	2.79
Source (df)	Analysis of Variance and Variance Components (%)											
Provn (5)	0.0	26.7	58.6	23.5	43.0	54.6	32.8	38.2	40.3	26.3	33.3	68.0
Sig F	NS	*	***	*	*	***	**	**	**	*	*	***
Repln (4)	33.3	0.0	0.0	32.4	20.9	4.8	21.3	0.0	0.0	19.2	0.0	0.0
Sig F	*	NS	NS	**	*	NS	*	NS	NS	*	NS	NS
Resdl (20)	66.7	73.3	41.4	44.1	36.1	40.6	45.9	61.8	59.7	54.5	66.6	32.0
Total $s^2$	0.045	0.15	0.58	0.34	0.86	0.29	1.22	0.34	2.16	0.99	0.99	1.72

Figure 6. — Regression lines for 6 provenances of *P. caribaea* over 12 sites for longest internode length (metres) at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean ( $b = 1$ ) by dotted line.



Site name	MTI	CTI	BBM	CDL	BFR	HBG	BTH	SPO	ANOA	ANOB	JRI
$\bar{x}$	0.0	0.0	0.013	0.029	0.064	0.143	0.165	0.337	0.402	0.605	1.083

Source (df)	Analysis of Variance and Variance Components (Z)										
Provn (5)		5.3	0.7	36.5	45.0	62.0	21.0	53.6	50.7	68.0	
sig F		NS	NS	*	**	***	NS	***	***	***	***
Repln (4)		10.6	0.0	0.9	0.0	0.8	4.9	0.0	4.5	1.4	
sig F		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Resdl (20)		84.1	99.3	42.6	55.0	37.2	74.1	46.4	44.8	30.6	

Total  $s^2$  0.002 0.005 0.022 0.040 0.048 0.081 0.280 0.670 0.437

Figure 7. — Regression lines for 6 provenances of *P. caribaea* over 12 sites for conelet frequency (class) at 7 years. Coastal and insular provenances shown by solid line, inland provenances by broken line and the mean (b = -) by dotted line.

trials neither was there evidence of provenance-fertilizer interaction within sites.

An examination of height data of seven *P. kesiya* ROYLE ex GORDON provenances from the Philippines over 10 sites in several countries at four years showed that although some provenances performed well on poor sites and poorly

on good sites, on the whole *gei* was not great (ARMITAGE and BURLEY, 1980).

Although the international provenance trials of *P. caribaea* are not designed to investigate *gei* below the provenance level, there are indications of its significance where individual tree data have been used in the analyses. For

Table 5. — Joint Regression Analysis for five traits of six provenances of *P. caribaea* over 12 sites at 7 years. Bark percentage (BKP); Stem volume over bark (VOB), Stem straightness (STR), Length of longest internode (LIL), Conelet frequency (CLN).

Source	df/1	BKP		VOB		STR		LIL		CLN	
		Sig of F	VC%	Sig of F	VC%	Sig of F	VC%	Sig of F	VC%	Sig of F	VC%
Sites	11	***	78.7	***	87.1	***	50.0	***	28.7	***	41.7
Reps in sites	45	***	1.1	***	0.6	NS	0.2	**	0.4	NS	0.2
Provenances	5	***	5.0	*	0.7	***	17.9	***	22.1	***	17.6
P x S	55	NS	0.3	***	3.0	*	3.4	***	10.1	***	16.6
Het of Reg <sup>n</sup>	5	NS		**		*		***		***	
Remainder	50	NS		***		*		*		NS	
Residual	223		14.9		8.6		28.5		36.7		23.9

/1 The number of degrees of freedom refer to traits assessed over 12 sites, viz. BKP, VOB and LIL. STR was assessed on 10 sites and CLN on 9 sites and the degrees of freedom for sites, reps. PxS, remainder and residual are 9, 37, 45, 40, 184 and 8, 34, 40, 35, 169 respectively.

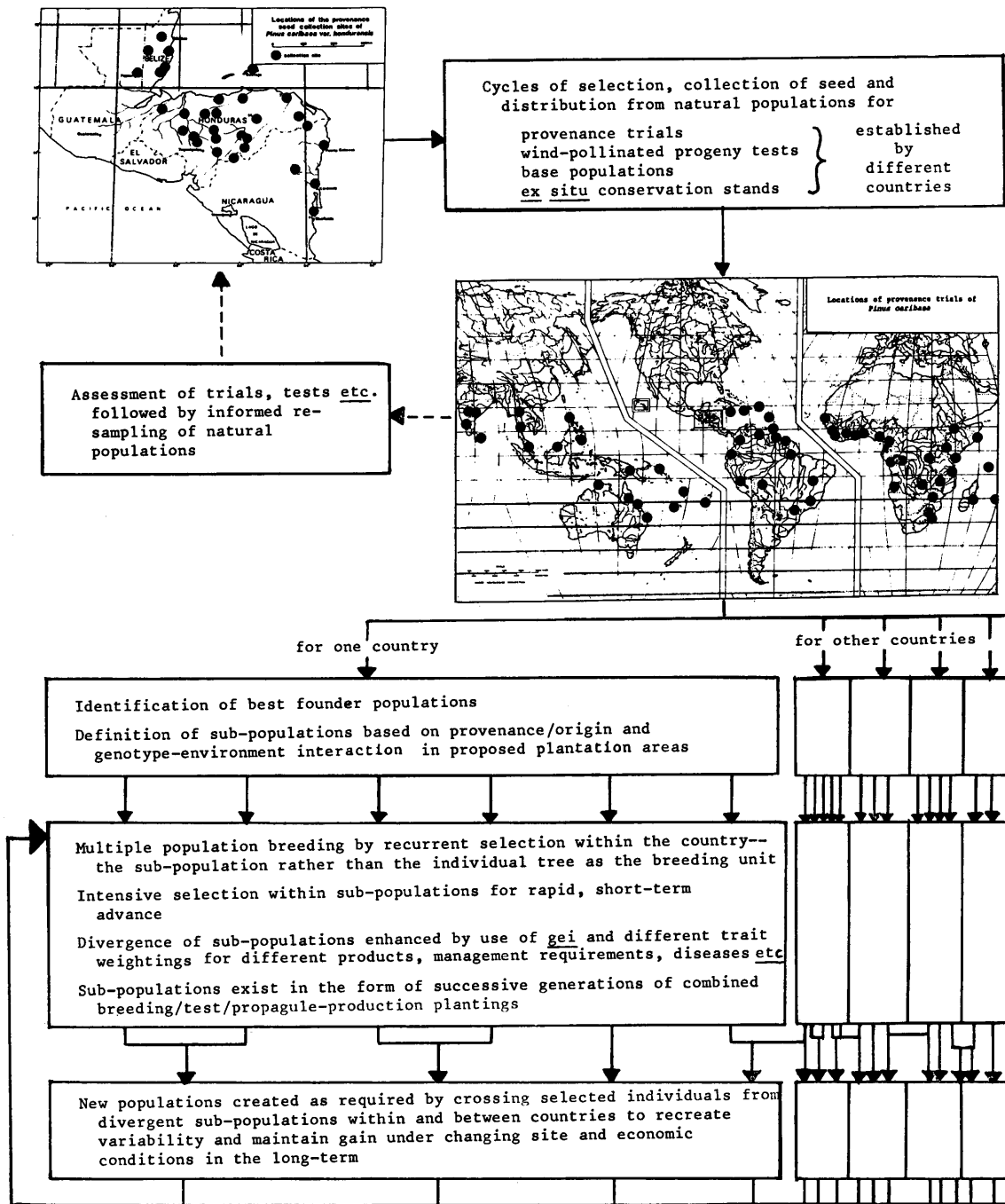


Figure 8. — Schematic flow chart for an international breeding plan for *Pinus caribaea*.

example, at Jari, Brazil, the Santa Clara and Alamicamba provenances had similar mean volumes (211 and 221 dm<sup>3</sup> respectively) but, over five replications, the mean biggest tree in Santa Clara (516 dm<sup>3</sup>) was the largest of all provenances whereas for Alamicamba (287 dm<sup>3</sup>) it was the smallest (BARNES *et al.*, 1980). At other sites the differences were not significant and the rankings were often reversed.

In two series of half- and full-sib progeny tests of *P. caribaea* covering sites in Queensland, Northern Territory and Fiji, 4- and 7-year volume and stem straightness data showed some family-site interaction but it accounted for substantially less than 50% of the family variance across sites (EISEMANN and NIKLES, 1980). The conclusion was that *gei* was not a dominant feature across a wide

range of sites and cultural regimes and that undifferentiated local and imported selected material could be used in programmes catering for a wide range of climatic and edaphic site conditions without risk of serious loss through lack of adaptation.

In 1.5-year-old full-sib progeny tests of *P. patula* over four sites in Zimbabwe, *gei* did not seriously affect ranking of parents for many traits but variation between sites in the scale of family differences contributed to large discrepancies in heritability estimates, e.g. 0.12 to 0.55 for height (BARNES and SCHWEPPENHAUSER, 1979). *P. taeda* is grown in southern Africa and there have been reciprocal exchanges of half-sib families with indigenous selections of the United States. Overall, correlations between families

are low but the top performers are generally among the highest-ranked in both regions (ANON., 1976).

### How should we use Genotype-Environment Interaction in Tropical Pines ?

Trials, and plantations established over rotation-length periods, have provided ample evidence of *gei* between species of tropical pines and it is being used to increase productivity through selection for a whole range of traits from physiological adaptation through wind-firmness, stem form and wood characteristics, to reproductive behaviour. However, even at this level there are frequently dilemmas in deciding whether to forfeit superiority in one desirable character for excellence in another when moving a species away from optimum environmental conditions or sometimes whether just to avoid changing species.

Trials at the provenance level are better designed but less well distributed and younger. Qualitative characters and reproductive behaviour seem to be subject to considerable *gei* but it is due to variation in scale of differences and slope of the regression line and is therefore interpretable and predictable. *Gei* in production traits has not yet been shown to be substantial but there are indications that it is present at the population level and that it might become more pronounced with age; this has been observed at the species level.

At the family level there are frequently parents that produce trees of extraordinary stability over environments and parents that produce trees which undergo a complete reversal of ranking in productivity from one site to the next.

There is therefore evidence of *gei* in tropical pines at all levels and it provides potential to increase productivity. With identification of genetically distinctive populations and individual trees and development of clonal techniques (see BARNES and BURLEY, 1982), well designed experiments to evaluate *gei* much more precisely can be established. Site coverage is expensive but international coordinating programmes could help to attain far wider environmental representation than any one country could achieve on its own. Nevertheless, there remains the daunting prospect for most organizations involved in tree breeding to have to face a hierarchy of decisions at the levels of site, species, provenance, family, clone and trait. If breeding strategy remains traditional and inflexible the enormous increase in cost of a dichotomy at any one of those levels to use *gei* would almost certainly be prohibitive. As a consequence, trees would be bred for broad coverage and variability and much potential increase in adaptability and productivity would be lost. The multiple population concept at all levels may provide a strategy that allows expression and development of *gei* with a minimal increase in cost.

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## Inheritance of leaf oil terpene patterns in selfed Progeny and some crosses of coastal Douglas-fir

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### Summary

The leaf oil terpene composition of Douglas-fir parent trees or their clones and some of their  $S_1$  and  $S_2$  progeny propagated by ORR-EWING (4), as well as outcrosses within these families, and some narrow and wide coastal variety crosses was determined. Considerable variation in terpene percentages was recorded in all crosses except the dwarf form of the  $S_2$  generation. In the latter uniform terpene patterns were found in members of the same family, but different families had different terpene patterns. It could be confirmed that the coastal variety pattern type B is the quantitative intermediate between types A and C. There was only minor evidence for female dominance in terpene inheritance.

*Key words:* *Pseudotsuga menziesii*, Coastal Douglas-fir crosses, selfed progeny, leaf oil terpene composition.

### Zusammenfassung

Bei Douglasien-Mutterbäumen bzw. deren Klonen und einigen Abkömmlingen aus der von ORR-EWING durchgeführten Kreuzung dieser Klone, d.h. aus deren  $S_1$  und  $S_2$  Nachkommenschaft, sowohl aus Fremdung als zugleich innerhalb der Familien sowie bei einigen enger oder weiter entfernt verwandten Küstenvarietäten wurde die Zusammensetzung der Terpene im Öl der Nadeln untersucht. Dabei konnte in allen Kreuzungen eine beträchtliche Variation festgestellt werden, außer in Zwergformen der  $S_2$  Generation. Letztere enthielten innerhalb der Familien einheitliche Terpenmuster. Bei der Vererbung der Terpen-Zusammensetzung war nur in geringem Maße weibliche Dominanz festzustellen.

### Introduction

ORR-EWING (1977) was remarkably successful in inbreeding coastal Douglas-fir, *Pseudotsuga menziesii* var. *menziesii* (MIRB.) FRANCO., to the  $S_3$  generation. A particular feature in some of the selfed progeny is a segregation into normal ("tall") and dwarf forms. Clones of the parent trees and many of the  $S_1$  and  $S_2$  inbreds propagated by ORR-EWING are still growing at the Cowican Lake Forest Experiment Station, Vancouver Island, and they presented a unique opportunity to explore further the mode of inheritance of the leaf oil terpene patterns in Douglas-fir. Previously, we have reported on inheritance of such patterns in four full-

sib families of  $F_1$  intervarietal crosses (two coastal variety and four interior or Rocky Mountain variety, var. *glauca*, parents) as well as in wind-pollinated progeny (VON RUDLOFF and REHFELDT, 1980). Some pertinent conclusions especially regarding the natural intergrading of these two varieties could be drawn. Whereas the leaf oils of both varieties contain 21 major and at least 8 minor monoterpenes (VON RUDLOFF and REHFELDT, 1980) (VON RUDLOFF, 1972, 1973, 1975), as well as 9–12 sesquiterpenes (3,8), such geographic variation can be described by the relative amounts of  $\beta$ -pinene, the terpinene — sabinene group ( $\alpha$ - and  $\gamma$ -terpinene, terpinolene, terpinen-4-ol,  $\alpha$ -thujene, and sabinene), the camphene group (santene, tricyclene, camphene, borneol, and bornyl acetate), and limonene (VON RUDLOFF and REHFELDT, 1980). The various quantitative terpene patterns can be designated as coastal type A (> 50%  $\beta$ -pinene), coastal type C (> 50% terpinene group), Rocky Mountain or interior type (> 50% camphene group) and the various intermediates thereof (VON RUDLOFF, 1973). Furthermore, the relative amounts of the camphene group are apparently controlled by a single dominant gene, whereas the other terpenes showed quantitative inheritance (i.e. their relative amounts are under the control of several genes (VON RUDLOFF and REHFELDT, 1980). Earlier we had shown that the leaf oil terpene composition of conifers is under strong genetic control during the quiescent and dormant season (VON RUDLOFF, 1972, 1975).

In addition to the leaf oils of the selfed families, we also analyzed those of some narrow and wide crosses between coastal variety parent trees (HEAMAN, 1970). In inheritance studies, grafts rather than the parent trees are sometimes only available for sampling. To ensure that ramets are strictly comparable to the ortets, we analyzed two sets of clones and their parents, and also possible variation within the crown of older and younger trees of the coastal variety, as this had been done previously only with interior Douglas-fir and one younger coastal variety tree (VON RUDLOFF, 1972).

### Materials and Methods

Leaf samples (30–150 g. each) were collected during late fall and winter 1981 and 1982 from trees at the Cowican Lake Forest Experiment Station as listed in Table 1. Other