

Genotype-Environment Interactions in *Pinus caribaea* var. *hondurensis* in Queensland, Australia

I. Population x Site Interactions

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Summary

A large open pollinated progeny test of *Pinus caribaea* var. *hondurensis* planted at eight coastal sites in Queensland, Australia, was studied to determine the importance of genotype-environment interactions. Families were established as groups, or populations, according to their origin and were measured approximately six years after planting.

Among the four populations studied, representing 90 families, statistically significant population x site interactions were found for stem diameter ($P < 0.05$) and straightness score ($P < 0.001$), but not for height. Partitioning of the population x site interaction revealed that 55% of the interaction variance in straightness could be accounted for by differences between populations in the slope of the regression on site means. For diameter, the figure was only 7%. It was considered likely that the large regression component for straightness was due to disparate scoring scales used over the sites.

Least-squares site means for diameter ranged from 13.3 cm to 16.8 cm. At all sites, the Queensland families had the highest mean diameters (15.9 cm), followed by Fiji and New Caledonia families (15.5 cm), Culmi (14.9 cm) and Rus Rus (14.3 cm). Mean heights at each site ranged from 7.8 m to 10.6 m. At each site, populations ranked the same for height as for diameter. Straightness scores ranged from site means of 1.03 to 3.24, with population mean scores of 2.34 for Queensland families (straightest), 2.06 for Fiji and New Caledonia families, 1.61 for Culmi families and 1.79 for Rus Rus families. With one very minor exception, rankings of the populations were consistent across sites. For practical purposes, interactions were of little importance for the traits studied. The breeding strategy adopted for *Pinus caribaea* var. *hondurensis* in Queensland is consistent with this result.

Key words: *Pinus caribaea* var. *hondurensis*, genotype-environment interaction, breeding population, breeding strategy.

Introduction

More than 50 000 ha of *Pinus caribaea* MORELET var. *hondurensis* BARRETT and GOLFARI (Pch) have been established by the Queensland Forest Service, with plantations concentrated in three distinct coastal regions centred around latitudes 18°, 22° and 26° S. Historically it has been standard practice for progeny tests involving Pch to be replicated within and across plantation regions. Given the wide latitudinal range and variety of sites within and

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between regions, the possible importance of genotype x environment interactions has long been a source of concern and subject of investigation. Preliminary studies of genotype x environment interaction from early tests (NIKLES et al., 1978; EISEMANN et al., 1980; EISEMANN and NIKLES, 1983) have not disclosed interactions of any practical importance. Nevertheless, seed production has been regionalized (NIKLES, 1986) to ensure that plantations are well adapted to their environment.

The development of a formal breeding strategy for Pch in Queensland by KANOWSKI and NIKLES (1988) necessitated a review of the importance of genotype x environment interaction in the breeding population. BARNES et al. (1984) suggested that, in the absence of knowledge regarding how genetic groups interact with the environment, consideration should be given to maintaining multiple populations. However, in the case of Pch in Queensland, information at the population and family level is available from the large multi-site experiment used by WOOLASTON et al. (1990) to estimate genetic parameters. In this paper we examine the importance of interactions between planting sites and Pch populations and discuss the likely effects on the breeding programme.

Materials and Methods

The progeny tests on which these analyses were based are part of the Experiment 567 series of the Queensland Forest Service. The series comprises 210 open pollinated families from eight populations, with each population representing a particular seed source. In the field, populations were grouped into three sets according to origin. This grouping into sets enabled each test to be kept to a tractable size (where a test is defined as a set established at a particular location). The experiment was planted in 1980 and replicated at eight locations in coastal Queensland. The composition, location, design and assessment of these tests were described by WOOLASTON et al. (1990). For completeness, the relevant details are summarized here.

Table 1. — Total number of families in each population.

Population	Seed source	Origin	Number of families
Queensland	ortet	Queensland plantations	37
Culmi	ortet	Culmi, Honduras	18
Rus Rus	ortet	Rus Rus, Honduras	9
Fiji & NC	ortet	Fijian and New Caledonian plantations	23

Table 2. — Details of relevant progeny trials in the series.

Site name	Code	Latitude and Longitude	Elevation a.s.l. (m)	Annual rainfall (mm)	Establishment date
Cardwell Ridge	cr1	18° 15' S 145° 55' E	20	2122	February 1980
Byfield Ridge	br1	22° 50' S 150° 45' E	50	1625	March 1980
Byfield Swamp	bs1	22° 50' S 150° 45' E	50	1625	March 1980
Wongi Swamp	ws1	25° 27' S 152° 35' E	35	986	March 1980
Tuan Swamp	ts1	25° 30' S 152° 47' E	20	1393	March 1980
Toolara Ridge	tr1	25° 53' S 152° 50' E	50	1369	April 1980
Glasshouse Swamp	gs1	26° 48' S 153° 05' E	10	1590	July 1980
Glasshouse Ridge	gr1	27° 05' S 153° 05' E	20	1337	May 1980

Table 3. — Age in months assessment of the trials, with the range of possible scores for straightness.

Trial	Diameter	Height	Straightness (score)
br1	66	66	66 (5)
bs1	66	66	66 (5)
cr1	74	74	74 (7)
gr1	56	56	57 (5)
gs1	63	63	63 (7)
tr1	62	62	63 (5)
ts1	78	78	78 (7)
ws1	88	88	78 (7)

Population x environment interactions were examined among the populations in one set (Set 1 of WOOLASTON et al., 1990), that containing the most populations and represented at the greatest number of sites. The seed sources and number of families in each population are shown in table 1. All populations derive from Central America, with Rus Rus originating from a coastal area and all other populations from upland areas.

Details of the eight sites included in these analyses are presented in table 2. Each test was established in a randomized complete block design. Blocks contained six trees from each family arranged in single tree plots, with eight blocks at all sites except Glasshouse Ridge, which contained only four blocks.

The age at which the tests were assessed varied from site to site, but the majority were assessed between five and six years after planting (Table 3). Traits studied were stem diameter (over bark at 1.3 m), height and straightness. Straightness was scored on a five or seven point scale, as shown in table 3.

Statistical Methods

As there were some missing data, family means were obtained at each site using least-squares analysis (HARVEY, 1987) by fitting the model:

(Equation 1)

$$Y_{ijk} = U + f_j + b_k + fb_{jk} + e_{ijk}$$

where Y_{ijk} is the measurement on the i th tree of family j and block k

U is the overall least-squares mean
 f_j is the effect of the i th family
 b_k is the effect of the j th block
 fb_{jk} is the family-block interaction
 e_{ijk} is a random error, mean zero.

Least-squares family means were then used in cross-site analyses by fitting the model:

(Equation 2)

$$Y_{jlm} = U + p_l + f_{jl} + s_m + ps_{lm} + e_{jlm}$$

where Y_{jlm} is the mean of the j th family in population 1 at site m

U is the overall least-squares mean
 p_l is the effect of the l th population
 f_{jl} is the effect of the j th family of population 1
 s_m is the effect of the k th site
 ps_{lm} is the population-site interaction
 e_{jlm} is a random error, mean zero.

It was not possible to include a term for the interaction between families and site in the above model because of missing subclasses. Joint regression analysis (FREEMAN, 1973; HILL 1975) was used to examine the regression of performance of each population at each site on the overall mean at each site. Thus the population x site interaction variance was partitioned into two orthogonal components: regression variance and deviations from regression variance. Linear regression coefficients and their standard errors were estimated for each population. Thus the population x site interaction effect (ps_{jk}) was expressed as:

(Equation 3)

$$ps_{lm} = B_l \cdot s_m + d_{lm}$$

where B_l is the linear regression coefficient of the l th population on the site means
 s_m is the effect of m th site
 d_{lm} is the deviation of the l th population at the m th site from the fitted regression line for the l th population.

Results

A summary of the analyses of variance is shown in table 4. The effects of population, family and site were highly significant ($P < 0.001$) for all traits and the population x site interaction was significant for diameter ($P < 0.05$) and straightness ($P < 0.01$). Partitioning of the population x site interaction revealed that only 7% of the interaction variation in diameter was accounted for by differences between populations in the slope of the regression on site means. For height and straightness score the respective figures were 6% and 55%. The relatively high proportion of the interaction variation left

Table 4. — Summary of analyses of variance for population x site interactions for diameter (cm²), height (dm²) and straightness score (score²), showing the components of the population x site interaction effects as estimated by joint regression.

Source of Variation	Diameter		Height		Straightness	
	df	Mean Squares	df	Mean Squares	df	Mean Squares
Population	3	64.6667 ***	3	11.9170 ***	3	15.1371 ***
Family:Population	87	2.5384 ***	87	0.5377 ***	87	0.1979 ***
Site	7	91.2471 ***	6	66.4986 ***	6	27.0877 ***
Population x Site	21	0.6032 *	18	0.0602 ns	18	0.6157 ***
Regression	3	0.2745 ns	3	0.0237 ns	3	2.0263 **
Deviations	18	0.6580 *	15	0.0675 ns	15	0.3336 ***
Remainder	448	0.3669	385	0.0566	372	0.0419

*** $P < 0.001$ ** $P < 0.01$ * $P < 0.05$ ns not significant

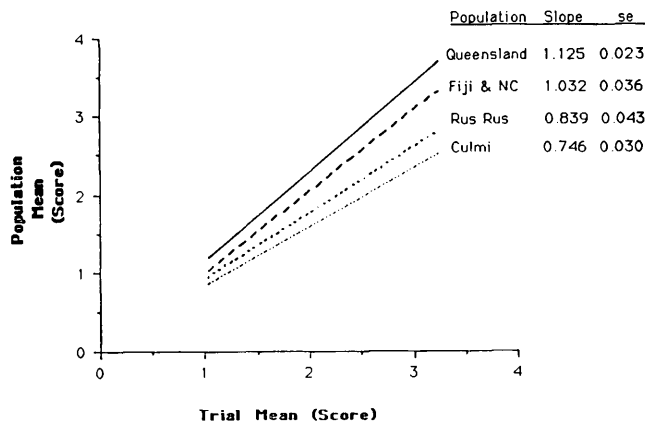


Figure 1 — Fitted regression lines for straightness score of each population at each site on the overall site means, with their slopes and standard errors.

unexplained in the diameter and height analyses meant that the linear regression coefficients were not significantly different from each other. Thus for diameter and height, most of the interaction variance appeared to be unpredictable and not systematically related to the environment at each site, as measured by the respective site mean. In contrast, the magnitude of the regression variance for straightness indicates that over half of the interaction variance for this trait was systematically related to the site means.

Predicted changes in straightness scores of each population with changes in environment are shown in figure 1, together with the estimated regression coefficients. The regression coefficients do not average unity because, firstly, the data were unbalanced and, secondly, some families that contributed to the site means were not classified into any of the four populations. Regression estimates for diameter and height are not presented because the regression did not account for a significant proportion of the interaction variance (Table 4).

Population mean diameters at each site are shown in figure 2. Least-squares site means for diameter ranged

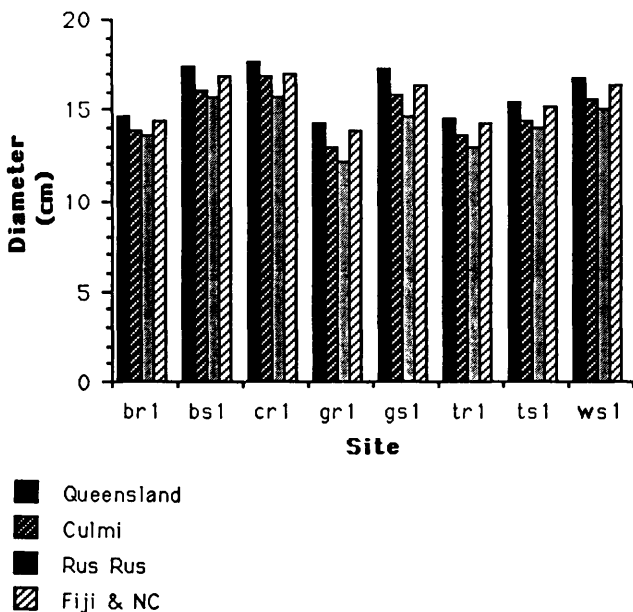
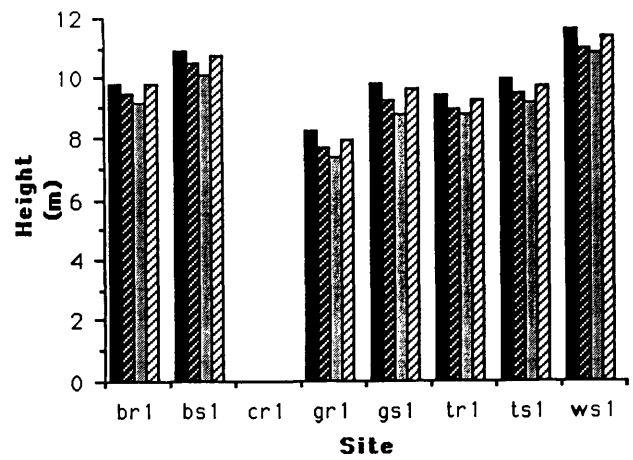
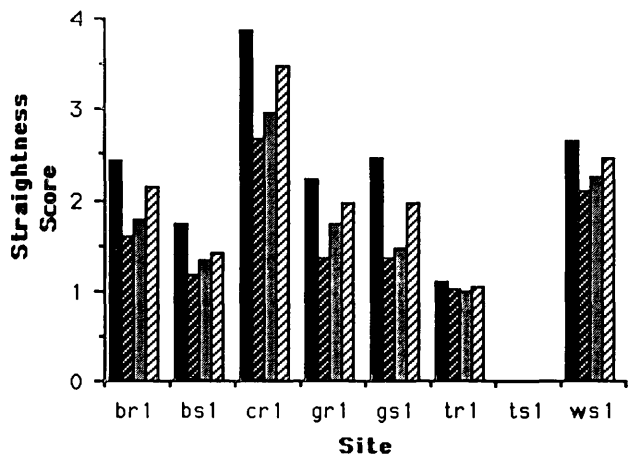


Figure 2. — Least-squares population means for diameter at each site.



■ Queensland
 ▨ Culmi
 ▩ Rus Rus
 ▧ Fiji & NC

Figure 3. — Least-squares population means for height at each site.



■ Queensland
 ▨ Culmi
 ▩ Rus Rus
 ▧ Fiji & NC

Figure 4. — Least-squares population means for straightness score at each site.

from 13.3 cm (gr1) to 16.8 cm (cr1). These means differ slightly from those given in WOOLASTON et al (1990) because the within-site analyses did not adjust for imbalances in the distribution of families across sites, as was the case here. At all sites, Queensland families had the highest mean diameters (15.9 cm overall), followed by Fiji and NC families (15.5 cm), Culmi (14.9 cm) and Rus Rus (14.3 cm).

Least-squares mean heights ranged from 7.8 m at gs1 to 10.6 m at bs1 (Figure 3). Heights were not recorded at Cardwell (cr1). Populations ranked the same at all sites, with overall mean values 9.97 m for Queensland, 9.79 m for Fiji and NC, 9.48 m for Culmi and 9.19 m for Rus Rus families.

Straightness scores ranged from site means of 1.03 (lr1) to 3.24 (cr1), with population mean scores of 2.34 for Queensland families, 2.06 for Fiji and NC families, 1.61 for Culmi families and 1.79 for Rus Rus families (Figure 4). The population rankings were consistent over all sites except lr1, where Culmi and Rus Rus families had the same least-squares means.

Discussion

When considering genotype-environment interactions, a decision must be made about the extent to which the interactions will be tolerated in a breeding programme. In this case, interactions between populations and sites, although statistically significant for diameter and straightness, were of little practical importance. This accords with MATHESON and RAYMOND (1986), who after reviewing provenance x environment interactions in tropical species, concluded that interactions are often statistically significant but seldom have a great effect on the overall gains to be made from selection of provenances. In our data, the population x site interaction only accounted for a very small proportion of the total variance in the traits studied (Table 4) and its magnitude was negligible compared with the main effects of population and site. With one very minor exception involving straightness score, no changes in ranks occurred across sites. Much of the apparently large statistical interaction for straightness score could be simply explained by scale effects, as shown by the partitioning technique. It is impossible to determine from the data whether these scale effects were due to actual site differences in mean straightness, or whether the differences have been artificially imposed by the subjective scoring system. Clearly, the three tests with the seven point scales (cr1, gs1 and ws1) had higher means, and two of the three had greater between-population differences than the other tests (Figure 4). It would be possible to convert all scores to a five point scale but this would be inappropriate as there was no effort made to standardize the scores over sites. Rather, the scorers were instructed to maximize the changes of detecting differences by using all of the available points categories. When GIBSON et al. (1983) used a standardized straightness scoring system over a wide range of sites in *Pinus caribaea* provenance material, differences between provenances in the slope of the regression on site means accounted for only 16% of the interaction variance. This suggests that the scale effect observed in the present tests was largely an artifact of the scoring system used.

The main conclusion from these studies is that the populations ranked essentially in the same order for diameter, height and straightness at all sites. For the purposes of the Queensland Pch breeding programme these studies indicate that reliable rankings of these populations should be possible at any of the eight sites studied, at least for the main traits of interest. This is consistent with the results reported by GIBSON et al. (1983), who found only small changes in rankings of diverse provenance material planted at Cardwell, Byfield and Beerburum (Glasshouse) with respect to diameter, height and to a lesser extent, straightness. In the present study, with a much narrower range of genetic material, the interactions were of little consequence for any one trait. However, if the traits are considered simultaneously, as one would do when using an index, the rankings for Culmi and Rus Rus may or may not change from site to site,

depending on the relative weights given to each trait. In this instance, it may be necessary to vary the relative weight given to straightness from site to site, depending on whether the scale effects apparent in the data are due to real differences in straightness or merely a peculiarity of the scoring system. This exemplifies the difficulty of assigning relative economic values to growth and form traits when scoring standards are intentionally varied from site to site in an attempt to increase heritabilities as advocated by, for example, COTTERILL and DEAN (1990).

The two improved populations (Queensland and Fiji and NC) consistently ranked above Culmi and Rus Rus for mean diameter, height and straightness score. This suggests the introduction of improved material from Fiji and NC could be of immediate benefit to the breeding programme, whereas introductions of new material from natural stands may need to undergo a generation of local selection before its incorporation into the breeding population.

The breeding strategy proposed for Pch in Queensland by KANOWSKI and NIKLES (1988) continued the practice of testing populations in each of the major plantation regions, primarily for reasons of security and selection intensity. However, it allowed the transfer of selected individuals between regions, and did not emphasize the regionalization of seed production. This strategy is consistent with the results reported here.

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Genotype-Environment Interactions in *Pinus caribaea* var. *hondurensis* in Queensland, Australia

II. Family x Site Interactions

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Summary

Family x site interactions were investigated in a large open pollinated progeny test of *Pinus caribaea* var. *hondurensis* planted at eight coastal sites in Queensland. Families were classified into populations according to their origin and were measured approximately six years after planting. Of the 210 families in the experiment, 85 were involved in this study, representing the three largest populations. Between-site genetic correlations for straightness score were high (average 0.83) compared with those for diameter (0.59). Diameters at the northernmost site were poorly correlated genetically with those at other sites (average 0.39) and this may have been due to heavy grass competition. Had individual selection been based at this site for planting at any of the other sites, the estimated genetic gain would have been only 29% to 57% as efficient as a selection programme based at the plantation site. Similarly, a selection programme based at any of the other sites would have been only 25% to 45% effective in improving diameter at the northern site. No one site was consistently superior as a selection site.

With the possible exception of the northernmost site, family x location interactions were not of sufficient magnitude to justify the formation of sub-populations for each latitudinal region. Selection index calculations indicated that for the purposes of estimating breeding values pertaining to the entire plantation, there is little need to establish more than three replicates of a progeny test.

Key words: *Pinus caribaea* var. *hondurensis*, genotype-environment interaction, genetic parameters, breeding strategy.

Introduction

The 50 000 ha of *Pinus caribaea* MORELET var. *hondurensis* BARRETT and GOLFARI (Pch) plantations in Queensland span a wide latitudinal range and include a variety of soil types (WOOLASTON et al., 1991). Historically, the Pch breeding population has been replicated in a variety of sites to safeguard against losses from localized phenomena such as cyclonic winds and to allow a flexible response to any important family x environment interactions. As

part of a major review of the Pch breeding strategy in Queensland (KANOWSKI and NIKLES, 1988), an assessment of the importance of family x site interactions was necessary.

In a companion paper, WOOLASTON et al. (1991) found that the populations into which the Queensland Pch families are grouped appeared to rank similarly across all sites examined. However interactions must also be examined at the family level, to determine the relevance of progeny tests at any particular site to the overall breeding programme. As the progeny tests also serve as source of selections for the ensuing generation, the likely effects of interactions on individual selection are also of interest.

An informative method for interpreting interactions was devised by FALCONER (1952) and applied to tree breeding by BURDON (1977, 1979), whereby performance at each site is treated as a separate, genetically correlated trait. Although an individual tree can obviously be planted at only one site, this methodology allows one to estimate the genetic correlation between its performance at that site and its performance at another site, had that same tree been planted there. Using conventional selection index theory, genetic gains from individual selection can be predicted from the genetic variance — covariance matrix. Similarly, gains can be predicted when individual selection is augmented by family information from any site, or when family information is used in a progeny test. With appropriate economic weights, gain can be predicted at any or all plantation sites, depending on the breeding objective. Sites which are not representative of the target plantation locality can be accorded an economic weighting of zero. As a refinement of this approach, economic weights can be defined according to the degree to which each test site reflects the characteristics of the plantation site.

In this paper we use this methodology to estimate the relevance of genotype x environment interactions to both individual selection and progeny tests and consider the implications for the breeding programme.

Materials and Methods

The progeny tests on which these analyses were based are part of the Experiment 567 series of the Queensland

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