EXPERIENCE WITH SOME *PINUS* HYBRIDS IN QUEENSLAND, AUSTRALIA

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ABSTRACT

Hybridisation has been undertaken extensively in Queensland among and within several *Pinus* species with the aim of discovering and developing high-yielding varieties with suitable wood properties and matched to sites of industrial plantations. The plantations are located on a wide range of sites between 17°S and 27°S. The desired matching requires use of a number of taxa including hybrids. Currently the plantation area of *Pinus elliottii* var. *elliottii* × *P. caribaea* var. *hondurensis* (PEE × PCH) hybrids exceeds 26 000 ha (21% of the lowland, *Pinus* estate). Annual plantings of outcrossed F_2 (best orchard families bulked) and selected F_1 families and clones exceed 3000 ha. Many other pine hybrids are under test.

This paper reviews the domestication of PEE, PCH and other taxa involved in hybridisation, the choice and development of the PEE × PCH F_1 hybrid, and the exploration of a number of other hybrids. The production of PEE × PCH outcrossed F_2 and the first backcross hybrids, and the potential of these and other hybrids locally and internationally are also reviewed. Possible future directions of pine hybrid breeding in Queensland and the main conclusions from the 40-year program, which has been intensive over the past 25 years, are indicated. It is suggested that "useful" hybrid vigour, in an industrial tree plantation program, is the economic (multi-trait) superiority of the hybrid over the higher-performing (high) parent.

INTRODUCTION

In Queensland the State has established 176 000 ha of coniferous plantations (of *Araucaria cunninghamii* and *Pinus* species and *Pinus* hybrids) (Anon. 1999) primarily for sawn wood and plywood products. The *Pinus* plantations (131 000 ha), initiated in the 1930s, are principally in subtropical lowlands around 25 - 27ºS (105 000 ha) with a further 21 000 ha in tropical lowlands (8000 ha around 23ºS and 13 000 ha in forest located between 16º45′S and 18º45′S) (Figure 1). Another 5000 ha are in forests elsewhere, mainly in the southeast.

These plantations encompass a large range of environments with climates varying from subtropical to tropical. Almost all the sites have soils which are low in nutrients and a substantial proportion are poorly drained. The desired matching of species and/or hybrids (with suitable wood) to available locations and sites may require the use of several taxa, either as pure species or as contributors to hybrids. This paper describes the *Pinus* hybrids that have been produced, their performance and their likely future development. Hybrids showing high-parent heterosis, i.e. superiority to the higher-performing parent, are identified, as well as those non-heterotic hybrids which combine desired traits and are thus also potentially useful. Conclusions about pine hybridisation are drawn from the Queensland experience of more than 40 years of which only the past 25 years have seen intensive work. The work has been carried out by the Queensland Forestry Research Institute (QFRI) for the Queensland Department of Primary Industries – Forestry (QDPI-F) or by/for the antecedents of both.

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DOMESTICATION OF SEVERAL *PINUS* SPECIES

An outline of the history of species introduction, domestication and hybrid production in Queensland was given by Nikles (1996). In brief, *Pinus elliottii* var. *elliottii* (PEE) became the principal plantation species in the subtropical southeast, and *P. caribaea* var. *hondurensis* (PCH) in the tropical areas, after extensive testing of a wide range of species. PCH was also planted extensively on well-drained sites in south-east Queensland in the 1980s. However, the PEE × PCH hybrid has almost entirely and entirely replaced PEE and PCH respectively in southeast Queensland, and other hybrids under evaluation could challenge PEE × PCH F_1 in some subtropical areas, and PCH in parts of the tropics. Other aspects of the introduction and domestication of several *Pinus* species are given below.

PEE

The PEE base population derives from seed introduced from north Florida and south Georgia in the 1920s and 1930s. The first clonal seed orchard (CSO) of PEE was established in 1953 and another in 1958-1961; by 1968 Queensland was self-sufficient in PEE orchard seed. A further PEE CSO of improved composition was established in 1974-76. Infusions of select germ plasm have been made from South Africa, the south-east USA and Zimbabwe. Currently the PEE breeding base comprises 450 families or clones of two diverse populations, backed up by a gene conservation population (Toon et al. 1996). Within-species genetic parameters of growth, stem straightness and crown defects (Dieters 1996), and breeding values related to general combining abilities (GCAs) of many parents in Populations 1 and 2 (of three) have been estimated; and general hybridising abilities (GHAs)(Nikles and Newton 1991) with PCH are known for many trees in Population 1 (Dieters and Nikles 1998). PEE is being bred for hybrid production to reduce the incidence of crown defects, to maintain stem straightness and improve growth (Dieters 1996).

PCH

The first tests of PCH were established in the late 1940s using seed imported from the Mountain Pine Ridge (MPR) provenance in Belize. A breeding program was initiated in the 1950s based on selections within plantations of that provenance. Clonal seed stands were first established at Byfield in the early 1960s, and clonal seed orchards later near Cardwell (18º15′S) in the late 1960s to the early 1980s, and at Byfield in the early 1980s. By the late 1970s, Queensland was self-sufficient in the production of PCH orchard seed. This, combined with the development of bare-rooted planting stock and the discovery that wood quality was satisfactory, permitted extension of operational planting of PCH from the tropics to subtropical south-east Queensland where it replaced PEE on well-drained sites until the 1990s, when PCH was in turn replaced by PEE × PCH hybrids.

Results of provenance trials with PCH sponsored by the Oxford Forestry Institute (OFI) (then CFI), UK and established widely in Queensland in 1973 (Nikles et al. 1983), led to the introduction of new PCH material (bulks) of other upland (OUL), coastal (COA) and Guanaja Is. (GUA) regions (Nikles and Newton 1983) and of families in the 1980s. Subsequently superior trees were selected in this material and added to the PCH breeding population (Kanowski and Nikles 1989). Also, infusions of select germ plasm have been made from breeding programs in several other countries (Dieters and Nikles 1997).

Estimates of genetic parameters of PCH show individual tree, narrow-sense heritabilities for diameter, height, stem straightness, latewood percent, basic density and spiral grain to be moderate to high, but low for windfirmness (Harding et al. 1991; Woolaston et al. 1990), despite evidence of improvement in the latter trait having been achieved via phenotypic selection (Nikles et al. 1983). In Queensland PCH has been bred for stem straightness, maintenance of vigour, branching and wood density for both pure-breed and hybrid production. Currently, work is proceeding on estimation of breeding values for all members of the breeding population (more than 1000 select trees) prior to the preparation of a revised breeding plan.

Other taxa domesticated or being domesticated in Queensland lowlands

P. taeda (PTAE) was introduced from north Florida and south Georgia in the 1920s and 1930s and, until the mid 1950s, was domesticated in parallel with PEE (Haley 1957), but planting was discontinued in 1954 in favour of PEE. A small CSO was established in 1967, and a small seedling seed orchard was planted in 1998 with infusions of select germ plasm from South Africa, but a resource of only 700 ha remains.

P. caribaea var. *bahamensis* (PCB) was introduced in the 1960s and 1970s via seed from all the Bahama and Caicos islands on which it occurs. A second introduction of open-pollinated seedlots from 130 parents (from OFI) was planted in 1989. Approximately 1300 ha of plantations of PCB have been established, including areas from local select-tree seed, and this provided the base from which 80 trees were selected and established in clone banks.

P. caribaea var. *caribaea* (PCC) was also introduced in the 1960s and 1970s, mainly via seed that had been collected in Cuba by H.A. Luckhoff in the late 1950s (Luckhoff 1964). Nine natural-stand provenances were also introduced in the 1970s (from the OFI). An estate of some 900 ha (currently 650 ha) was established, including areas from local select-tree seed, within which 120 trees have been selected and established in clone banks.

Relatively small amounts of seed of *P. tecunumanii* (PTEC) (mostly lowland) and *P. oocarpa* (POOC) were introduced, mainly in the 1970s, via the OFI program (Dieters and Nikles 1997), for establishment of provenance trials and provenance resource stands (totalling about 90 ha and 130 ha of PTEC and POOC respectively). A breeding seedling orchard of 96 open-pollinated families of PTEC was established at Cardwell in 1989 from seed supplied by the OFI and CAMCORE. Some 120 plus trees of PTEC and 40 of POOC have been selected across the estates and most are established in clone banks.

The selected ortets and/or clones of these seven taxa (including PEE and PCH) have provided the genetic resources required for hybridisation and other work.

DEVELOPMENT OF PEE × PCH HYBRIDS

Historical development in Queensland

As early as the mid-1950s it was known that PEE and PCH had complementary traits: PEE is straighter, more wind-firm, and tolerates poorly-drained soils better than PCH, while PCH has faster growth, superior branch quality and more uniform wood. In 1955 the first crosses between PEE and PCH were attempted in the hope of producing a hybrid with qualities superior to those of both parents, and the progeny of these crosses were planted in 1958. Extensive field trials of the PEE × PCH F_1 hybrid (PEE is the usual seed parent) have since been established in south-east Queensland and in the southern tropics at Byfield (as well as in New South Wales, and internationally). These trials have demonstrated that the F_1 hybrid is superior in growth and superior or equal in stem straightness to both parent species when grown on sites with very poorly-drained soils in south-east Queensland. The hybrid is superior in growth to PEE on almost all sites on the coastal lowlands of south-east and central Queensland (Nikles et al. 1987; Dieters 1999; Powell and Nikles 1996a; Figure 2). The PEE × PCH F_1 hybrid produces wood of sufficiently high density and strength to satisfy the predominantly structural-products market that has developed (Harding and Copley 2000).

Commercial deployment of the F_1 hybrid was long delayed, however, due to the low numbers of viable seeds produced per cone by controlled crossing, and the difficulty in vegetative multiplication of hybrid seedlings (Nikles and Robinson 1989). In the 1980s two initiatives attempted to overcome the problem of producing PEE × PCH F_1 hybrid seed operationally: (1) extensive, fully-controlled crossing of selected clones in the third PEE clonal seed orchard was undertaken annually for several years resulting in substantial amounts of expensive, sound, F_1 seed; and (2) isolated, monoclonal PEE orchards were established at Byfield in which emasculation and mass pollination i.e. without bagging, were undertaken annually for several years, resulting in the production of up to 80 kg of seed per year, largely comprising F_1 but also putatively pure PEE seed. Also, research on rooting of cuttings resulted in the development of cuttings production from seedling hedges (Haines 1992). This breakthrough permitted restriction of controlled crossing to the production of limited amounts of seed of proven superior F_1 families for use in vegetative multiplication to produce planting stock. These developments have enabled “family forestry” to be practised with the F_1 hybrid since 1991, using a combination of seedlings and rooted cuttings of proven families. They have been accompanied by the gradual introduction of tested clones, and it is anticipated that clonal forestry, using tested clones from superior hybrid families, will be fully implemented in Queensland by 2002 (Walker et al. 1996).

A PEE × PCH, F_2 hybrid bulk seedlot (open-pollinated from a clone bank) performed well in a 3-location trial planted in 1976 (Dieters 1999); and nine- or 10-year results of a 4-location test planted in 1987 show the control-crossed F_2 hybrid (36 families) equals the F_1 hybrid (144 families) in growth at all sites, though it is inferior in stem straightness (data provided by Dr Mark Dieters, QFRI). These families of F_2 and F_1 hybrid from selected parents have similar coefficients of variation for diameter, uncorrelated with the means such that there are high-growth, relatively uniform families (pers. comm., M.B. Powell, 1994); and basic density means, coefficients of variation and ranges in other F_1 and F_2 hybrid populations are similar (Harding and Copley 2000).

These results support the decision to make substantial operational plantings of F_2 hybrids on a range of sites since the 1980s. Seed of the F_2 hybrids is produced in a conventional wind-pollinated clonal seed orchard, composed of selected F_1 clones. A small F_2 seed orchard was established at Byfield in 1983, and continues to produce around 100 kg of seed each year. A second F_2 seed orchard has been established and the seed will be used primarily as a back-up to any shortfalls in the clonal forestry program with F_1 hybrids. The F_2 hybrid predominated in annual plantings until 1993, but a substantial proportion of annual plantings have comprised F_1 hybrids since 1989. Some 26 300 ha of PEE × PCH hybrids have been established in Queensland up to June 1999 (Anon. 1999) – 13 800 ha of F_1 and 12 500 ha of

F_2 (pers. comm., N. Taylor, QDPI-F, 2000). These hybrids currently comprise some 21%, PEE 36% and PCH 40% of a total lowland *Pinus* estate of 126 000 ha.
The potential of the first backcross hybrids PEE × (PEE × PCH) and (PEE × PCH) × PCH (seed parent named first) is being evaluated via 36 full-sib families of each in the same four-location trial series (planted in 1987) as that which includes the parental, F_1 and F_2 factorial arrays (Powell and Nikles 1996a). In addition, a separate population of PEE × (PEE × PCH) is included in a three-location trial planted in 1976 (Dieters 1999); and (PEE × PCH) × PCH is also involved in other trials. Nine- or 10-year results of the 1987 trial series show the PEE × (PEE × PCH) backcross is intermediate to PEE and F_1 for growth at all four sites (superior to PEE but inferior to F_1); and it is superior to both PEE and F_1 in straightness on the two poorly-drained sites, but approximately equal to both parents on the well-drained sites (data provided by Dr Mark Dieters). Twenty-one year growth of the PEE × (PEE × PCH) backcross in the 1976 trial series was intermediate to the parents at two sites, but only equal to PEE at the other site; in 5-year straightness, it was inferior to the F_1 hybrid at all sites, but sometimes better or worse than PEE (Dieters 1999).

The (PEE × PCH) × PCH backcross is superior in growth to the F_1 hybrid at all four sites (1987 series), but it is inconsistent relative to PCH across the sites; it is intermediate to its parents in straightness at all sites (data provided by Dr Mark Dieters).

Yield and viability of seed of both backcrosses are high encouraging their production for use under special conditions, e.g. the first backcross to PEE is being used in Queensland on some very swampy sites, and it could be useful in parts of Florida (Rockwood and Nikles 2000) and elsewhere in areas that are too cold for high survival of the F_1 hybrid.

Performance of Queensland-bred PEE × PCH hybrids overseas

Queensland-bred PEE × PCH F_1 and other hybrids are being tested widely overseas with good results in most cases (Nikles 1996). Additional test results from Florida (Rockwood and Nikles 2000), Zimbabwe (Gwaze 1999) and Parana, Brazil (pers. comm., Romualdo Maestri, Pisa Florestal, 1999) further confirm the promise of the PEE × PCH hybrids in certain areas. At Pisa Florestal, in Parana, a broad sample of F_1 hybrid families had 95% more volume per ha at 5.3 years than Queensland-bred PEE, which was superior to a local PTAE control. In the Zimbabwe tests, conducted at two sites, the small sample of Queensland-bred F_1 hybrid (5 families) showed high-parent heterosis in both volume and straightness at one site, but in volume only at the second site. (The high parent for volume was Queensland-orchard PCH and for straightness was PEE – best local family). Collaborators report that Queensland-bred hybrids also perform well in Argentina, China, South Africa and Uruguay (QFRI records).

Extensive use of PEE × PCH F_1 hybrids overseas could be achieved either by importation of Queensland-bred material or by producing hybrids locally. In some cases production using locally-adapted, highly-selected seed or pollen parents might be more effective. A research program using locally-adapted seed parents was initiated by the Cooperative Forest Genetics Research Program in Florida in the early 1990s when pollen from select trees of PCH, PCB and PEE × PCH F_1 was shipped from Queensland to Florida for crossing to PEE parents of local breeding populations. Tests have been established with suitable controls on eight sites in north Florida and South Georgia, USA (White et al. 1996 and earlier reports), and 5-year results will be available soon.

Hybrid breeding strategy

An appropriate strategy for hybrid breeding will depend, among other factors, on the correlation of general combining abilities estimated within pure species (GCAs) with those in hybrid combination (GHAs). Powell and Nikles 1996b reported a high overall correlation between GCAs and GHAs for diameter (0.68) and height (0.70), but a low and non-significant correlation (0.35) for straightness, based on a combined sample of 12 PEE and 12 PCH parents and their F_1 hybrids, and similar results for the individual taxa samples. (Also, GHAs of either PEE or PCH were good predictors of hybrid family performance.) Contrary to this result for growth Dieters and Nikles 1998, using data from families of a much larger sample of PEE parents (95), and 10-year-old progeny, found no correlation between GCAs and GHAs for diameter (-0.07); straightness had a significant but low (0.29) correlation. Dieters and Nikles 1998 also found GHAs were good predictors of hybrid family performance for all four traits considered. Hence, parents are currently selected on GHA for crossing to produce superior hybrid families from which to select good clones.

The current breeding strategy aims to improve PEE and PCH breeding populations from which to select F_1 hybrid parents with the highest GHAs. Accordingly, 300 PEE parents are being polycrossed with a 30-parent PCH pollen mix to enable estimation of PEE GHAs. The best 200 or so parents (including those with high GHAs identified in earlier work) will form the PEE breeding population. Similar work to generate a PCH breeding population of 200 parents with highest GHAs is proposed. This strategy for PEE and PCH breeding could be described as reciprocal recurrent selection for GHA (RRS – GHA).

Work continues in Queensland related to definition and implementation of an appropriate breeding strategy to enable long-term, incremental improvement of hybrids. This work includes estimation of genetic parameters in hybrid and parental populations (Dieters and Dungey 2000), simulation of comparative gains from alternative breeding strategies (Dungey et al. 2000; Kerr et al. 2000), and maintenance of genetic diversity of PCH (Kanowski and Nikles 1989) and of PEE (Toon et al. 1996).

DESCRIPTION OF OTHER HYBRIDS PRODUCED

Nikles 1995 listed the numerous *Pinus* hybrids that have been produced in Queensland from six species i.e. *P. caribaea, P. elliottii, P. oocarpa, P. palustris, P. taeda* and *P. tecunumanii*. Hybrids have been produced using both taxonomic varieties of *P. elliottii* (var. *densa* and PEE), and PCB, PCC, PCH, POOC and PTEC. Also, hybrids have been produced between PEE and PTAE and PTAE and PTEC, and among populations of the provenance regions of PCH (Coastal – COA, Guanaja – GUA and Upland including the MPR).

The crossabilities and genetic distances of these taxa are generally related to their geographic proximities (CAMCORE 1999; pers. comm., W. Dvorak, 2000). These distances are also related to the level of heterosis for growth exhibited by hybrids (see below).

Other hybrids of PEE – PEE × PCB, PEE × PCC, PEE × PTEC, PEE × PTAE

The crossability of PEE with PCB is high but it is less with PCC (Bowyer 1985). PEE × PCB and PEE × PCC F_1 hybrids have been evaluated in a 3-location trial planted in 1976 which includes several other hybrids and parental controls (Dieters 1999). The PEE × PCC is the more promising of these two hybrids as it demonstrates high-parent heterosis in volume production and straightness, whereas PEE × PCB shows little or no high-parent heterosis in south-east Queensland. However, the PEE × PCH F_1 hybrid is more highly productive than PEE × PCC in this study (and in an earlier trial series), so there is little need to produce PEE × PCC (nor PEE × PCB) hybrids for operational use in Queensland.

The PEE × PTEC F_1 hybrid has very low average seed viability. The small F_1 hybrid populations planted in 1986 and 1994 are very heterogeneous but include some outstanding trees. In view of the availability of the PEE × PCH hybrid there is no need to pursue the development of this hybrid at present.

The PEE × PTAE F_1 hybrid has very low seed yield and viability; however, the reciprocal cross had higher viability (Barnes and Mullin 1978). This hybrid is very heterogeneous in Queensland (based on few families), and fails to show high-parent heterosis even though some outstanding trees are produced. The yield of outcrossed F_2 hybrid seed is high (Nikles et al. 1999), paralleling the PEE × PCH F_2 hybrid.There is no practical interest in the PEE × PTAE hybrid anywhere in the world at present.

PCH × PTEC and PCH × POOC hybrids

These taxa have moderately high crossabilities, especially when PCH is used as the seed parent (Nikles 1989). Since 1985 many trials of these hybrids (and some reciprocal crosses) have been established in eastern, coastal lowlands between 18º30′S and 27ºS, covering a range of climatic and edaphic conditions. Data from a number of trials in south-east Queensland suggest there are no reciprocal effects for growth, and that PCH × PTEC maintains its growth superiority over both parental taxa and is superior to PCH × POOC in both growth and wind firmness, but is inferior in wind firmness and straightness to PCH (QFRI, unpubl. data). At Cardwell in north Queensland, 10-year data show PCH × PTEC and PCH × POOC are about equal in growth and wind firmness, and both hybrids are superior to PCH in volume on a well-drained site, but inferior on a swamp site (data provided by Dr Mark Dieters). Thus PCH × PTEC seems the better of these two hybrids and it has greatest potential for use on well-drained sites in north Queensland, if straightness and wind firmness can be improved. This might be achieved through intensive selection for these traits within PTEC for subsequent hybrid production, and/or by hybridising PTEC and PCH × PTEC with PCC or PCH × PCC, utilising the good straightness and strong wind firmness of PCC.

Phenotypically-superior trees have been selected in both PCH × PTEC and PCH × POOC F_1 hybrid families. Based on the success of outcrossed F_2 hybrids of PEE × PCH in south-east Queensland, F_2 clonal orchards of the PCH × PTEC and PCH × POOC hybrids were established in north Queensland in 1999.

Queensland-bred PCH × PTEC and/or PCH × POOC F_1 hybrids are also showing promise in other countries. In a replicated trial established near Agudos, SP, Brazil with 12 PCH × PTEC F_1 hybrid families and Brazilian orchard PCH controls, all the hybrid families were superior at age 4.5 years to the best control in diameter, 10 were superior in height, 11 were superior in basal area and their average superiority in basal area was 62% (pers. comm., R. Chaves, Duratex, 1997). Similarly, in Parana, Brazil, a broadly-based population of PCH × PTEC families exceeded local PCH by 36% in volume per tree and 20% in volume per ha at

5.3 years, although survival of both PCH and PCH × PTEC was only 70%, presumably due to cold (pers. comm., Romaldo Maestri, Pisa Florestal, 1999). In Zimbabwe (Gwaze 1999) families of PCH × PTEC (29) and PCH × POOC (26) hybrids showed marked hybrid vigour of growth at age 5 yr. The PCH control comprised a Queensland orchard bulk, the PTEC control was wild-stand material and the POOC control was a Zimbabwe-bred orchard bulk. High-parent heterosis in volume shown by the PCH × PTEC hybrid was greater than that achieved by the PCH × POOC hybrid at both test sites, while for straightness the relativity varied with site. The same hybrids are promising in Swaziland also (author's observations).

Other hybrids of PCH – PCH × PCB, PCH × PCC

The PCH × PCB F_1 hybrid is represented in Queensland by two series of multilocation trials in the subtropics and tropics, one planted in 1976 at Byfield (southern tropics), and at Tuan and Beerburrum (subtropics); and another planted in 1991 at Cardwell (northern tropics) and Tuan. This hybrid showed no superiority to the better-performing parent for growth in the northern tropics (PCH), but varying levels of superiority were expressed in the southern tropics and in the subtropics; in the trial planted on swamp sites in 1976 in the southern tropics and subtropics, the PCH × PCB hybrid was superior to PCH (and the PEE × PCH F_1 hybrid) in growth (but not in wind firmness nor straightness) (Dieters 1999). In the trial planted on a well-drained site at Tuan in 1991, the PCH × PCB hybrid had 10% greater volume than the best-performing PCH, and it showed superior straightness (Dieters et al. 1998). Thus the PCH × PCB hybrid has potential on some sites and warrants further testing.

The PCH × PCC F_1 hybrid is being evaluated in several trials including one planted in 1988 on three sites at two locations in the northern tropics (Cardwell) and southern tropics (Byfield). It is also included in a trial planted in 1991 at Cardwell and at Tuan (subtropics), and in early trials at Byfield and Beerburrum. This hybrid was superior to the high parent (PCH) for growth at nine years on a poorly-drained site in the northern tropics only, where it even surpassed PCH × PTEC (Dieters et al. 1998). Experience in Queensland shows that the PCH × PCC F_1 hybrid can be expected to improve in relative performance with age, reflecting the growth curve of PCC. This hybrid also has a generally lower incidence of crown defects and has greater wind tolerance than PCH. Thus PCH × PCC also warrants further testing.

Other interspecific hybrids produced

Crosses of PTAE with PTEC have very low seed viability but a few families have been established in the field (1986). The hybrid is very heterogeneous with some excellent individual trees, but is unlikely to rival the PEE × PCH F_1 hybrid in Queensland lowlands. *P. palustris* and *P. elliottii* hybrids have also been produced but are of no practical interest because of lesser potential than hybrids involving *P. caribaea* mentioned above.

Crosses among the regional provenances of PCH

Six-year results of a study of inter-regional crosses planted at two locations in Queensland in 1992 are now available (data provided by Dr Mark Dieters). Populations involved are: (1) Upland (mostly MPR) as (a) open pollinated families from a CSO and (b) controlled crosses i.e. OUL × OUL; (2) MPR × COA; (3) COA × COA; and (4) COA × GUA. The MPR parents represented had been selected much more intensively than the COA, GUA and OUL parents. Although the cross MPR x GUA could not be included in the study, the results suggest no marked, high-parent heterosis is likely to be obtainable via interregional crossing. However, there could be advantages from including COA and GUA trees in the breeding population in Queensland, as planned, to broaden the base and infuse genes for wind firmness and (from GUA) for higher basic density (Kanowski and Nikles 1989).

DISCUSSION

The main hybrids developed in Queensland are listed in ascending order of genetic distance (either known – CAMCORE 1999; W. Dvorak, pers. comm., CAMCORE, 2000; or presumed – on the bases of crossabilities or taxonomic affinity) in Table 1. In constructing Table 1 genetic distances and crossabilities were given more weight than current taxonomic affinity e.g., PCH and lowland PTEC (genetic distance 0.130 and with relatively high crossability) are considered fairly closely related, though presently classified respectively in subsections *Australes* and *Oocarpae* of Section *Pinus* (Critchfield and Little 1996); and PCH and PCB are more distantly related (genetic distance 0.172) than PCH and PTEC though currently placed together in subsection *Australes* (Critchfield and Little 1966).

In general, there seems to be some correspondence between genetic distance and level of heterosis (Table 1). For example, marked high-parent heterosis is not exhibited in crosses between the regional provenances of PCH (presumed to have small genetic distances), nor clearly exhibited in the PEE × PCB cross (small genetic distance of 0.032). On the other hand, high-parent heterosis is often exhibited by combinations involving larger genetic distances e.g. PCH × PTEC (0.130), PCC × PCH (0.139), PCH × PCB (0.172).

However, genetic distance (and environment of test) does not seem to be the only factor determining the expression of hybrid vigour for growth. For example, PCH × PCB (genetic distance 0.172) represents a wider cross than PEE × PTAE (genetic distance 0.153), yet the former cross has moderate viability and can show high-parent heterosis for growth, while PEE × PTAE has low seed viability and is not a promising hybrid (possibly a case of outbreeding depression).

Even where high-parent heterosis is not exhibited the breeding of one taxon could still benefit from infusion of genes for particular characteristics from another. For example, PEE breeding populations might be enhanced by infusion of genes from PCB, potentially increasing growth capability, drought hardiness and tropical adaptation. In yet other cases, hybridisation does not appear to confer any substantial benefit, e.g. PEE × PTAE.

Results of Queensland studies show that outcrossed PEE × PCH F_2 hybrid seedlings from selected parents can grow as well as F_1 hybrid seedlings, and F_2 hybrid seed can be produced by open pollination in CSOs. This provides opportunity to produce F_2 hybrid seedlings cheaply and/or, more expensively, to vegetatively multiply selected families or clones, extending the options for deployment. It will be very interesting to discover whether outcrossed F_2 hybrids of other heterotic combinations (such as PCH × PTEC) exhibit similar effects – and whether outcrossed F_2 hybrid growth is also good in hybrids among some eucalypts and in other genera.

The first backcross hybrids from PEE × PCH are superior to their recurrent parents in growth or straightness, sometimes both. There could be niches for such hybrids.

A number of other hybrids besides PEE × PCH have considerable potential on certain Queensland sites, especially following improvement of one or more parental taxa for wind firmness, straightness or branch quality or even, possibly, through crossing with a third taxon characterised by high levels of the desired characteristics. These hybrids include PCH × PTEC, PCC × PCH, PCH × PCB and perhaps PEE × PCC. Some other hybrids would appear worthy of further testing e.g. PCC × PCB, or production and testing e.g. PCC × PTEC. Some advanced hybrids thought worthy of testing include (PCH × PTEC) × PCC (to add better wind firmnes), (PEE × PCH) × PCC and (PCC × PCH) × PTEC.

Some interspecific hybrids are very heterogeneous and, although not exhibiting high-parent heterosis for growth, may include outstanding individuals which, if propagable, could be very useful. Examples may include PEE × PTAE and PEE × PTEC.

Several possible hybrids (among the six taxa most involved in hybrid production in Queensland) have not been produced yet. These are: PEE × POOC, PCB × POOC, PCB × PTEC, PCC × POOC, PCC × PTEC and POOC × PTEC. Based on experience gained, the only hybrids among these likely to be interesting are PCB × PTEC and PCC × PTEC. These might have moderate seed viability and combine the good windfirmness of PCC and PCB with the great growth capacity of PTEC.

The importance of additive effects in hybrid populations, such that GHAs are good predictors of family performance, whereas GCAs and GHAs are often poorly correlated, suggests reciprocal recurrent selection for GHA might be appropriate in PEE and PCH. However, more work of the kind in progress in QFRI (references given under Hybrid breeding strategy, above) needs to be done to determine the optimal hybrid breeding strategy.

Considering the results of Queensland studies reviewed in this paper and the diversity of sites presented in plantation areas in Queensland, it is evident that more than one natural taxon is required for optimal matching of taxa and sites and procurement of desired wood properties. The development of the PEE × PCH hybrid has enabled QDPI-F to plant a high-yielding, wind-firm taxon with wood of high density across a large part of the spectrum of sites in the south-east region since the early 1990s, thus realising economic gains when compared to cultivation of PEE or PCH in the region. Yet PEE and/or the first backcross to PEE are better matched to certain "problem" sites. And other hybrids e.g. PCH × PCC and PCH × PTEC are promising in other regions in Queensland where PCH is planted currently.

Hybrids are sometimes judged simply on the basis of performance in relation to midparent for a single trait such as growth. For industrial forestry a more useful basis for judging hybrid potential is "economic superiority" to the high parent reflecting a combination of yield and wood quality offset by the extra costs of producing hybrids. A hybrid may be preferred to a pure breed even if it does not exhibit high-parent heterosis for volume production. For example, in the four-location test of PEE × PCH hybrids and controls in Queensland (Powell and Nikles 1996a) nine- and 10-year results show the F_1 hybrid exhibits high-parent heterosis for stem straightness at three sites and is equal to the best parent at the fourth site; however, it does not exhibit high-parent heterosis for volume production at any of the sites in this series (data provided by Dr Mark Dieters). Yet, because of its favourable combination of these two traits, its strong wind firmness, good wood properties (Harding and Copley 2000) and silvicultural features, the hybrid is preferred for planting on almost all sites in south-east Queensland, as well as on swamp sites in central coastal Queensland lowlands.

CONCLUSIONS

The following main conclusions can be drawn from Queensland experience with a number of *Pinus* hybrids over the past 40 years:

1. Besides the PEE × PCH F_1 and outcrossed F_2 hybrids which are in operational use in Queensland, some other hybrids have considerable potential in particular areas, and certain hybrids not yet made are likely to be viable and possibly useful.
2. PEE × PCH outcrossed F_2 and F_1 hybrids from selected parents are equally vigorous though the former are less straight; such F_2 hybrids may prove similarly viable and vigorous among other *Pinus* species and in other genera.
3. Hybrid breeding for operational F_1 deployment usually requires vegetative propagation for mass production of selected families or clones.
4. Queensland-bred PEE × PCH, PCH × PTEC and PCH × POOC hybrids have demonstrated considerable promise in several countries. However, it seems likely that use of locally-bred parents, of at least one of the taxa in a hybrid, would be desirable.
5. Expression of useful hybrid vigour appears to depend on the parental taxa, there being “considerable” genetic distance between them, the GHAs of parents, and the environment. However, too great a genetic distance may lead to outbreeding depression.
6. Complementarity of desirable attributes provides a good starting point for choosing pairs of taxa to consider for a *Pinus* hybridisation program.
7. GHAs of parents are good predictors of family performance in PEE × PCH, PCH × PTEC and PCH × POOC hybrids; but GCAs and GHAs may be poorly correlated.
8. Further work on development of an appropriate strategy for hybrid breeding is required and is in progress at QFRI.
9. In industrial plantation forestry, overall economic superiority of a hybrid compared to its parents or alternative taxa is more important than high-parent heterosis for a single trait.

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Table 1: Summary of experience with the main *Pinus* hybrids produced in Queensland.

Hybrid[1]	Type (current taxonomy)[2]	Putative width of cross (genetic distance)[3]	Crossability[4]	No. of tests	Remarks on performance	
					High-parent heterosis for growth?	Other remarks
PCH – MPR × COA	Intraspecific – between regions of provenance (subsection Australes)	Very narrow (?)	High	4	No	A good cross demonstrating the new COA germ plasm can be infused usefully into MPR for the tropics.
PCH – COA × GUA	As above	Very narrow (?)	High	2	No	A good cross for growth in the tropics but straightness requires improvement.
PEE × PCB	Interspecific (intra subsection Australes)	Narrow (0.032)	High	3	No	PCB germ plasm could be infused into PEE with positive results for growth and stem quality in the subtropics.
PEE × PCC	Interspecific (intra subsection Australes)	Moderately wide (?)	Moderate	5	Yes	Hybrid has potential in central-SE coastal Queensland, but is surpassed by PEE × PCH. Infusions into PEE could be useful where PEE is the preferred species.
PCH × PTEC (lowland PTEC)	Interspecific (inter subsections Australes, Oocarpae)	Moderately wide (0.130)	Moderate	Many	Yes – on well drained sites	Hybrid has potential in north-central coastal Queensland after improvement of wind firmness of PTEC – or perhaps via crossing with PCC. Promising internationally.
PCC × PCH	Intraspecific – between varieties (intra subsection Australes)	Moderately wide (0.139)	Moderate	7	Yes – on swamp sites only	PCC and its hybrids often improve in productivity with age; considered to have substantial future potential in the tropics.
PCH × POOC	Interspecific (inter subsections Australes, Oocarpae)	Wide (?)	Moderate (but lower than PCH × PTEC)	Many	Yes	Potential somewhat less than PCH × PTEC – unless wood is much better, and wind firmness can be improved.

Hybrid[1]	Type (current taxonomy)[2]	Putative width of cross (genetic distance)[3]	Crossability[4]	No. of tests	Remarks on performance	
					High-parent heterosis for growth?	Other remarks
PEE × PCH	Interspecific (intra subsection Australes)	Wide? (?)	Low	Many	Yes – on very swampy sites only	Currently the taxon of choice for most plantation sites in central-SE coastal Queensland, and promising internationally. Outcrossed F_2 highly viable and vigorous.
PEE × PTEC	Interspecific (inter subsections Australes, Oocarpae)	Wide? (?)	Very low	2	?	Hybrid heterogeneous. Promise uncertain at this stage. No need to pursue this hybrid.
PEE × PTAE	Interspecific (intra subsection Australes)	Wide (0.153)	Very low	2 (few families)	No	Hybrid heterogeneous. No promise in USA; potential value exotically not high. Outcrossed F_2 highly viable and vigorous.
PCH × PCB	Intraspecific-between varieties (intra subsection Australes)	Wide (0.172)	Moderate	5	Yes	Promising in the subtropics. Wind firmness requires improvement.

[1]PCH, PCB, PCC – *P. caribaea* var. *hondurensis*, var. *bahamensis*¸ var. *caribaea*; MPR – Mountain Pine Ridge (Belize); COA – coastal; GUA – Guanaja Is; OUL – other upland; PEE – *P. elliottii* var. *elliottii*; POOC – *P. oocarpa*; PTAE – *P. taeda*; PTEC – *P. tecunumannii*. The combinations stated do not necessarily specify the direction of the cross.
[2]Based on Critchfield and Little 1966.
[3]"Genetic p-distance derived from RAPD based markers" (CAMCORE, 1999; pers. comm., W. Dvorak, CAMCORE, 2000), or on crossability (Bowyer, 1985; Nikles 1989; QFRI, unpubl. records).
[4]Based on Bowyer 1985, Nikles 1989 and other research at the Queensland Forestry Research Institute, Gympie
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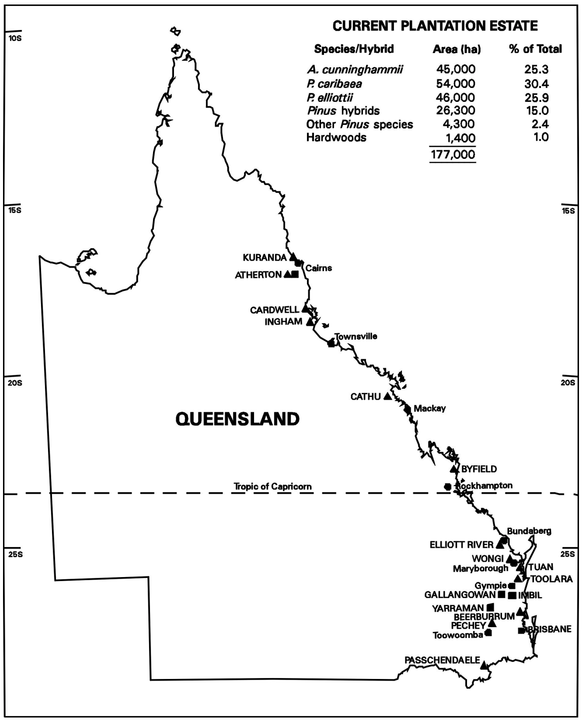

Figure 1: Regional distribution and extent of plantations of *Araucaria cunninghamii* - ■, introduced *Pinus* species (including hybrids) - ▲ and locations of some major cities - ● in Queensland.

Figure 2: A typical row of *Pinus elliottii* var. *elliottii* (PEE) × *P. caribaea* var. *hondurensis* (PCH) F_1 hybrid (left) and of inferior PCH of the same level of parental selection (right) on a mounded swamp site. Location: Tuan State Forest, coastal lowlands, south-east Queensland. Age: 13.5 yr.   PEE (not shown) is inferior in growth on almost all sites in the region.