# THE GENETIC IMPROVEMENT OF CARIBBEAN PINE *(PINUS CARIBAEA* MORELET) - BUILDING ON A FIRM FOUNDATION

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Abstract:— *Pinus caribaea* Morelet comprises three geographic varieties or subspecies — var. *bahamensis,* var. *caribaea* and var. *hondurensis.* Variety *hondurensis* incorporates substantial variation between provenances and individuals within provenance; however for the other two varieties, variation is primarily among individuals. As well, var. *caribaea* and var. *hondurensis* especially, have substantial complementarity of characteristics important in commercial plantation forestry. Furthermore, var. *hondurensis* is the fastest growing of the three varieties, and it has been hybridised successfully with the other two varieties, *P. elliottii, P. tecunumanii,* and *P. oocarpa.* Thus genetic improvement of *P. caribaea* can use and is using the wealth of genetic resources contained in some species of the slash—Caribbean—Central American pines complex.

*P. caribaea* is an important species for commercial plantation forestry throughout the tropics and subtropics, with over 1 million hectares established world-wide. The future of this species (and some of its hybrids) in commercial plantations seems assured. Nevertheless the future of the broad range of genetic resources of *P. caribaea* that has been assembled through a series of exploration and seed collection efforts, and established in many *ex situ* plantings, is not assured. The genetic resources of the species has been dispersed across a number of geographic regions and organisations. There is a need to develop a coordinated and collaborative approach to the future conservation and use of the genetic resources that have been collected and developed in *ex situ* plantings.

Keywords: *Pinus caribaea,* provenance variation, breeding strategy, gene conservation

*Pinus caribaea* Morelet is a very important plantation species. Over the last 20-30 years the plantation estate has rapidly expanded, such that there are now over 1 million ha of plantations world-wide. There is still the potential for further expansions in the *P. caribaea* plantation estate. The genetic conservation, testing and breeding of *P. caribaea* has been characterised by a high level of collaboration and cooperation over this same period. This has led to the establishment of a world-wide network of international provenance trials, the exchange of genetic material, and the development of strong relationships between diverse people and organisations. In this paper we will briefly describe the taxonomy and distribution of the species, the history of international collaboration in the collection and testing of genetic resources, the current status of breeding world-wide, some benefits of hybridisation, and the need for continued collaboration to adequately conserve and wisely use the genetic resources of *P. caribaea.* It is our contention that continued international collaboration is vital to the future genetic conservation and sustainable genetic improvement of this species and its hybrids.

## TAXONOMY AND DISTRIBUTION

The name *Pinus caribaea* was first used by Morelet in publications dated 1851 and 1855 to refer to slash pine (now *P. elliottii* Engelm.) growing in the south-eastern USA; its distribution was thought to extend to Central America and Cuba (Anoruo and Berlyn 1993). This resulted in considerable confusion because the name referred to both slash pine and the

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Caribbean pines. Anoruo and Berlyn (1993) describe how Grisebach (in 1864), Seneclauze (in 1867) and Loock (in 1951) attempted to divide the pine species in Central America, Cuba and the Bahamas Islands into three geographic entities; however, Little and Dorman (1952) were the first to effectively separate slash pine from the Caribbean pines. *P. caribaea* was subsequently further separated into three varieties *(bahamensis, caribaea* and *hondurensis)* based on the independent work of Barrett and Golfari (1962) and Luckhoff (1964). The nomenclature of the species has remained unchanged since.

The natural distribution of the Caribbean pines lies between 27°25'N latitude in Grand Bahama and Great Abaco and 12°13'N near Bluefields on the east coast of Nicaragua, while the longitudinal range is from 71°40'W in the Caicos Islands to 89°25'W at Poptun in Peten province of Guatemala (Lamb 1973). However, continued exploration work by CAMCORE (Central America & Mexico Coniferous Resources Cooperative) continues to expand the known distribution of the species slightly. The three varieties of *P. caribaea* are found in three separate geographic regions:

- var. *bahamensis* on the Bahamas and Caicos Islands,
- var. *caribaea* on the western part of Cuba in the province of Pinar del Rio at Cajalban, and at the northern end of Isle of Pines, and
- var. *hondurensis* on the mainland of Central America (Mexico, Belize, Guatemala, El Salvador, Honduras and Nicaragua) and Guanaj a and Roatán Islands off the northern coast of Honduras.

## EXPLORATION, COLLECTION AND INITIAL DOMESTICATION

The first recorded exports of seed are from Belize to California and South Africa in 1927 (Luckhoff 1964). A stand of 2.4 ha was established in 1929 at Dukuduku (on the Zululand coast), South Africa at a latitude of 28°30'S (Lamb 1973). In 1930, a stand of *P. caribaea* was established in Queensland, Australia near Imbil at latitude 31°S which Nikles (1966) confirmed to be var. *caribaea.*

However, it was not until after World War 2 that more substantial and comprehensive introductions of *P. caribaea* were made. There were broadly two waves of post-war introductions. The first wave in the 1950s and 1960s, involved introductions of var. *hondurensis* and then var. *bahamensis* and *caribaea* primarily to Australia (Queensland) and South Africa. These introductions elicited great interest because of the superior growth of *P. caribaea* when compared to *P. elliottii* (Luckhoff 1964, Nikles 1962, Slee and Nikles 1968). In 1955 a small scale breeding program had commenced with var. *hondurensis* in Queensland (Slee and Nikles 1968), and in South Africa by the 1960s. Seed collections (and exports) were almost exclusively from upland sources of var. *hondurensis* from Belize prior to 1960 (Greaves 1978) and the establishment of the Tropical Silviculture Unit of the Commonwealth Forestry Institute (now Oxford Forestry Institute, OFI) in 1963 (Lamb 1973). The first replicated provenance trial that included the *bahamensis* and *caribaea* varieties was established in South Africa in 1959 (Lamb 1973). However, a provenance test of var. *hondurensis* planted in 1956 in Queensland contained one plot of var. *bahamensis* (Nikles 1962, Slee and Nikles 1968). These trials revealed the superior stem straightness of var. *bahamensis* and var. *caribaea* compared to var. *hondurensis,* and stimulated interest in the

further exploration and testing of these two varieties. Preliminary breeding programs did not commence with these two varieties until the late 1960s and early 1970s.

The recent history of the genetic improvement of *P. caribaea* has been characterised by collaboration. The second post-war wave of introductions was precipitated by the 1962 report of the Committee on Silviculture to the Eighth Commonwealth Forestry Conference — Greaves (1978) quotes the following resolutions passed by the Conference in response to this report:

"(i) A special study be initiated into the races and provenances of *Pinus caribaea*.
(ii) Countries interested should make arrangements for coordinated seed collection and provenance trials.
(iii) The above projects be initiated and coordinated by the Commonwealth Forestry Institute."

Subsequently, the OFI with funds provided by most Commonwealth countries and the British Overseas Development Ministry (now Overseas Development Administration, ODA) collected seeds between 1963 and 1969 from natural stands of *P. caribaea* and *P. oocarpa* (Greaves 1978). Distribution of the *P. caribaea* seed commenced in 1971 from a total of 35 natural provenances (19 of var. *hondurensis,* 10 of var. *caribaea* and 6 of var. *bahamensis)* and one improved collection of var. *hondurensis* from a clone bank at Byfield, Queensland (Greaves 1980). Birks and Barnes (1990, page 1) state, "By the end of the 1970s many hundreds of trials [of *P. caribaea* and of *P. oocarpa* Schiede (incorporating what is now known as *P. tecunumanii* Eguiluz)] had been established with representation of 20 to 30 provenances of each species in over 50 tropical countries".

A second round of collections were initiated in the late 1970s and 1980s by OFI and CAMCORE respectively. The identity of individual open-pollinated families was retained and the results from the earlier OFI-sponsored provenance trials were used to help determine collection priorities (Crockford et al. 1990, Dvorak and Donahue 1992). The OFI collections were restricted to the most promising provenances (Crockford et al. 1989, 1990) with the objective of providing a selection base for the creation of breeding populations. However, CAMCORE sampled many provenances that had not previously been represented in international provenance trials including some remote/isolated sources, and OFI/ODA collected additional seed from Guanaja Island in the mid-1980s (Dvorak 1992). The DANIDA Tree Seed Centre was also involved in assembling and distributing *P. caribaea* seed from natural stands during this period (Nikles 1996). FAO facilitated the establishment of conservation stands of two provenances (Poptun and Alamicamba) of var. *hondurensis* in several tropical countries (Wood and Burley 1983). These new provenance introductions, and extra seed of some them, provided a much broader genetic basis for breeding (Nikles et al. 1983).

Between 1982 and 1993 CAMCORE sampled 23 provenances and 1178 mother trees of var. *hondurensis* in Central America and Mexico (Dvorak et al. 1993), and established 94 tests in six countries (Dvorak and Donahue 1992). CAMCORE has continued their exploration and collection work, with the first collection of *P. caribaea* from El Salvador occurring in 1996

and they now estimate that 99% of the genetic diversity of this species has been sampled (CAMCORE 1996, pages land 24).

As a result of the early work and these internationally-sponsored collections and establishment of trials, as well as other *ex situ* conservation facilities, there is an unprecedented wealth of genetic resources of *P. caribaea* var. *hondurensis* (and also *P. oocarpa* and *P. tecunumanii)* available for exploitation in breeding programs. Furthermore, in the 1970s and 1980s there were considerable exchanges of plus-tree seed and/or scions and pollen (e.g. Pottinger and Barnes 1989) among many of the organisations which developed active breeding programs with var. *hondurensis.* Thus, for example, the Queensland breeding populations of var. *hondurensis* now include a number of plus-trees selected in imported families (170) and imported clones (30).

Much of the exploration and seed collection work described above has concentrated on the more widely distributed var. *hondurensis.* Other than the early collections of Luckhoff (1964) and Nikles (1966) the genetic resources of var. *bahamensis* (particularly) and var. *caribaea* have, by comparison, been subject to only fairly limited exploration and collection. As noted above in the initial 1970's OFI collections 6 and 10 provenances of var. *bahamensis* and var. *caribaea* respectively, were sampled. However, the performance of only 1 and 7 provenances of var. *bahamensis* and var. *caribaea* respectively are reported in Birks and Barnes (1990). Subsequently, exploration and collection activities concentrated primarily on var. *hondurensis* because of its better growth in international provenance trials (Baylis and Barnes 1989, Birks and Barnes 1990).

In the late 1980's OFI, funded by the ODA, initiated a project to collect and distribute seed of var. *bahamensis* following recognition of the possible value of this variety (and var. *caribaea)* due to its greater insect and disease resistance compared to var. *hondurensis.* Tip moth has devastated some plantings of var. *hondurensis* in south-east Asia, and further spread could mean that var. *bahamensis* and var. *caribaea* (or hybrids with these varieties) may become the most important softwood species in the low altitude/latitude tropics (Baylis and Barnes 1990). In total, seed was collected from 10 individual trees in each of 14 provenances throughout 4 islands of the Bahamas. However, no seed was collected from the Caicos Is., the most southerly occurrence of var. *bahamensis.* Seed from most of these families was used to establish family-in-provenance studies on one site in southern China in 1991 (Zheng et al. 1994) and another site in south-east Queensland in 1990.

An extensive seed collection across the natural range of var. *caribaea* was undertaken by the Edinburgh Centre of Tropical Forests and the Institute of Ecology and Resource Management at the University of Edinburgh, in 1994 (Zheng 1966, page 2-31), as part of an ODA UK-China project. The overall aim was to form a base population for future breeding of this variety in China. Seed was collected from 195 trees in 12 natural provenances and one seed orchard population in Cuba (Zheng 1996, pages 2-31,32). This seed, along with land-races from Brazil and China, has been used to establish a base population of 220 open-pollinated families in southern China (Zheng 1996, page 6-145).

## PROVENANCE VARIATION

Gibson et al. (1983) and Birks and Barnes (1990) present comprehensive summaries of the results of the initial OFI international provenance trials with *P. caribaea,* and a review of the wood properties of var. *hondurensis* across 8 countries and 11 tests is given by Wright (1990). Crockford et al. (1990, chp. 7) provide a summary of the initial results from the var. *hondurensis* family-in-provenance studies. Numerous authors have reported the results of individual trials (mostly originating from OFI collections), for example: Slee and Nikles (1968), Brigden et al. (1983), Eisemann et al. (1983), Nikles et al. (1983), Haines (1984), Rider et al. (1984), Tozer and Haines (1984) and Wright et al. (1994) in Australia, Zheng et al. (1994) and Pan and Nikles (1996) in China, Bird (1984) in Costa Rica, Das and Stephen (1984) and Tavitayya (1984) in India, Otegbeye and Shado (1984) and Otegbeye (1988) in Nigeria, Kha et al. (1989) in Vietnam and Wright et al. (1986) in Zambia. A summary of the CAMCORE provenance trials established in Brazil, Colombia and Venezuela with var. *hondurensis* provenances from Honduras and Guatemala is given by Dvorak et al. (1993). A more comprehensive analysis of the CAMCORE tests has recently been completed by Dr. Gary Hodge; however, a copy of this report was not available at the time this paper was prepared.

In provenance trials where the three varieties have been compared the following general trends are evident:

- Variation between trees within provenance was at least as great as variation between different provenances.
- Little variation amongst provenances of varieties *bahamensis* and *caribaea* has been reported to date (Nikles 1996); however this may be due to less environmental variation across the range and/or to less intensive sampling of these varieties. However, by contrast substantial variation has been reported among var. *hondurensis* provenances.
- Across a range of sites and countries var. *hondurensis* consistently out-performs the other two varieties in terms of early growth. However, the growth of var. *bahamensis* may exceed that of var. *hondurensis* at slightly higher latitudes and/or altitudes (Luckhoff 1964, Gibson et al. 1983, Baylis and Barnes 1989).
- Varieties *bahamensis* and *caribaea* exhibit generally better stem straightness, greater resistance to wind-damage (as measured by stem lean), and a lower incidence of "fox-tails" than var. *hondurensis* (Birks and Barnes 1990). Note: there was only one var. *bahamensis* provenance (Andros) in the OFI-sponsored tests, and this provenance was similar to the var. *caribaea* provenances in stem straightness and lean (Birks and Barnes 1990). Brigden et al. (1983), Rider et al. (1984) and Pan and Nikles (1996) report similar findings for stem straightness.
- Variety *hondurensis* is markedly inferior to the *bahamensis* and *caribaea* in terms of resistance to insect attack. In Vietnam var. *caribaea* is reported to have superior resistance to insect attack (Kha et al. 1989). In China (Pan and Nikles 1996) var. *hondurensis* had a substantially lower survival (75% compared to near 100%) and higher susceptibility to tip moth *(Rhyaciona* and *Dioryctria* spp.) attack and brown needle disease *(Ceroseptoria pini-densiflorae)* than var. *bahamensis/caribaea* and slash pine. Baylis and Barnes (1989) and Zheng et al. (1994) also note varieties *bahamensis* and *caribaea* may prove to be more suitable for use in south-east Asia because of their resistance to tip moth attack.

Var. *hondurensis:* Birks and Barnes (1990) define three provenance regions of var. *hondurensis:* upland (UPL), coastal (COA) and island (i.e. Guanaja, GUA). In Queensland, these provenance regions can be clearly delineated in terms of wind-firmness (Nikles 1996): the COA provenances show considerably less wind-damage following cyclones than UPL provenances, while GUA material tends to be intermediate (Nikles et al. 1983). Coastal provenances on average also tend to be straighter than upland sources (Eisemann et al. 1983, Birks and Barnes 1990), but have a higher susceptibility to fox-tailing (Birks and Barnes 1990). In terms of growth rates, the Guanaja Island provenance performed well in the OFI trials (Birks and Barnes 1990, Crockford 1990) and provenances with good growth rates can be found amongst both UPL sources (e.g. Belize Mountain Pine Ridge and Poptun) and COA sources (e.g. Laguna el Pinar, Karawala, Alimicamba). The coastal provenance El Limon from Honduras (as distinct from the upland provenance Los Limones from Honduras, in the OFI-sponsored trials) has performed well on a number of sites in the CAMCORE tests (Dvorak et al. 1993); however, in Queensland the stem form of this provenance is inferior to a number of other high-growth provenances. All provenances of var. *hondurensis* tend to be susceptible to attack by tip moth in south-east Asia (Birks and Barnes 1990).

Considerable variation has been reported in wood density (DEN), and variation in wood density (VAR) between provenances of var. *hondurensis* (Wright et al. 1986, Birks and Barnes 1990, Wright 1990, Wright et al. 1994). The Guanaja, Poptun and Santa Clara provenances have consistently demonstrated above average density across a range of sites, and Guanaja had a very low variation in density (Wright 1990).

Var. *caribaea* and var. *bahamensis:* The OFI-sponsored tests reported by Birks and Barnes (1990) include only one provenance of var. *bahamensis*, and therefore provide no information on provenance variation in this variety. Generally, differences among var. *caribaea* provenances have not been found to be statistically significant for most economically important traits (Nikles 1966, Rider et al. 1984, Birks and Barnes 1990, Pan and Nikles 1996). The *bahamensis* variety tends to be more variable than var. *caribaea* as might be expected from its more disjunct distribution across 4 islands of the Bahamas and 2 of the Caicos Islands (Nikles 1996). For var. *bahamensis* growing in southern China, Zheng et al. (1994) found significant differences between region (i.e. islands), provenances within region, and families within provenances for all traits examined (height, diameter and crown width) at 2.5 years of age. Zheng et al. found a 11% difference in height and diameter between the fastest and the slowest growing regions, with the northern sources (Abaco Island) generally performing better than the southern sources. All three traits were significantly correlated with the latitude of provenance origin, and hence rainfall distribution (Zheng 1996, page 5-119). However, Zheng's study did not include the most southerly Caicos Island sources. Nevertheless, most (> 40%) of the variation was between individuals within provenances (Zheng et al. 1994), as has been noted above for *P. caribaea.*

## BREEDING PROGRAMS

*P. caribaea* has been introduced to over 50 countries since the early 1970s; however, very few of these countries now maintain an active plantation program with the species. Tables 1

and 2 summarise the countries with major *ex situ* plantings of *P. caribaea* (all three varieties) and some aspects of the silviculture. Despite the potential to make large gains through breeding in this species (Nikies 1996), of those countries using *P. caribaea* as a commercial plantation species, even fewer are now actively involved in the genetic improvement of the species (Table 3). Further, it is clear that var. *hondurensis* is the most important variety in plantation forestry, followed by var. *caribaea.* There is clearly great potential for the commercial deployment of this species:

- Very large areas have been planted in South America (almost 1 million hectares, Table 1), and the total world-wide plantation area could eventually approach that of other major conifer species such as *P. radiata.*
- The *bahamensis* and *caribaea* varieties have much greater resistance to tip moth than var. *hondurensis,* therefore offering opportunities for the expansion of plantations with *P. caribaea* in east Asia. The plantation estate in south China is expected to increase 3-fold over the next 15 years (Zheng 1996, page 1-20), primarily using these two varieties.
- There is great interest in the use of *P. caribaea* hybrids, including inter-provenance hybrids, inter-variety hybrids, and inter-specific hybrids (Table 3). The use of some hybrids has the potential to increase the area over which *P. caribaea* and its derivatives may be deployed commercially.

Genetic gains from breeding: Dean et al. (1986) indicate that substantial genetic gains are possible from recurrent cycles of breeding with var. *hondurensis.* Subsequently, a number of other authors have also reported moderate levels of additive genetic variance associated with traits of economic importance (e.g. Woolaston et al. 1990, Zheng et al. 1994, Telles dos Santos et al. 1996, Vásquez and Dvorak 1996) and hence the opportunity to achieve economic gain through breeding.

Nikles (1996) highlighted the gains that have been demonstrated in the OFT-sponsored provenance tests. Both the first- and second-stage tests included an "improved" source of var. *hondurensis* that was derived from the early stages of the Queensland breeding program. Birks and Barnes (1990) reported: "The best performer [in productivity] across sites among the var. *hondurensis* provenances was the Byfield (Queensland) seed orchard which itself was derived from the Mountain Pine Ridge (Belize) origin" (Birks and Barnes 1990, page 32). This result is clearly demonstrated in Figure 1.

Breeding strategies: Broadly, there are currently three groups involved in the genetic improvement of *P. caribaea:* CAMCORE (active) members, countries associated with CIRAD of France and non-aligned organisations. CAMCORE is currently in the process of developing a cooperative, regionalised, multiple-population, breeding strategy which will allow individual members to participate in the improvement of *P. caribaea* var. *hondurensis* at varying levels of intensity (CAMCORE 1996). In the other two groups (within and between which some collaboration has taken place), the breeding strategies employed fall broadly into two classes: low and high intensity breeding. High intensity work is characterised by the maintenance of full-pedigree information, controlled crossing and intensive progeny testing. The low intensity breeding work is typified by the use of "breeding seedling orchards" (BSO), where the functions of breeding, testing, selection and seed production are combined in the one facility (Barnes 1984). The breeding program with var.

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*hondurensis* and var. *caribaea* in Queensland would fall into the high intensity group, while work with var. *hondurensis* in Fiji, var. *bahamensis* in Queensland, and var. *caribaea* and *bahamensis* (Zheng 1996) in China would fall into the low intensity category. However, Zheng (1996) indicated that breeding with *P. caribaea* in China may become more intensive following one or two generations of improvement via the simple BSO strategy.

An additional group which could be added to the above three groups is the "Center of Genetic Conservation and Breeding of Tropical Pines" (CCGMT) in Brazil which is a cooperative association of university and industry groups (Telles dos Santos 1996). CCGMT maintains breeding programs of all three varieties of *P. caribaea,* grafted 150 ha of clonal seed orchards (which include all 1000 members of the breeding program), and established over 50 progeny tests in Brazil and Argentina (Telles dos Santos 1996). However, we are not aware of the current intensity of breeding activities within this program.

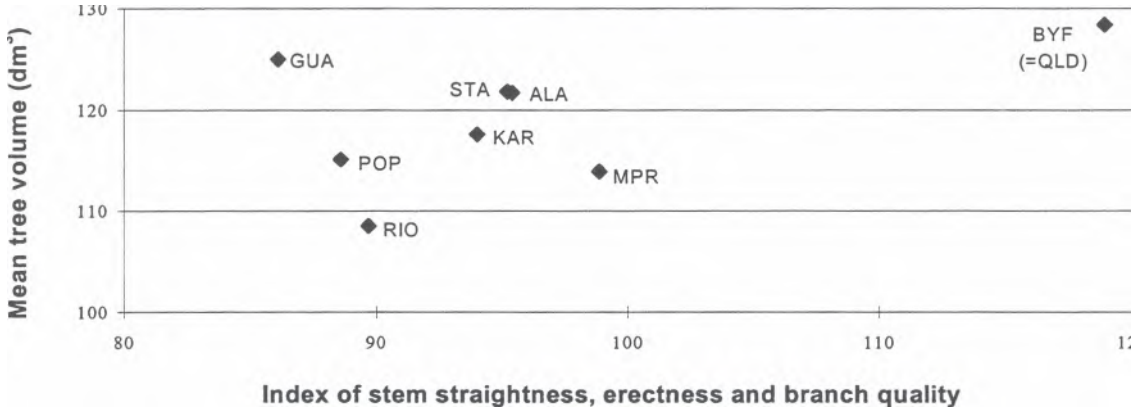


Figure 1: Relationship of provenance means across 9 tests world-wide for mean tree stem volume under bark ($dm^3$) and, across 11 trials, of an index of mean tree stem straightness and branching for provenances of *P. caribaea* var. *hondurensis* (ALA, KAR, RIO – coastal provenances; MPR, POP, STA – upland; GUA – island) and BYF, an early, Queensland (QLD) improved variety derived from MPR. Data based on 6 year assessments reported by Birks and Barnes (1990). Figure taken from Nikles (1996).

Constraints to breeding: There are a number of constraints to the breeding of *P. caribaea* throughout the world (Table 3). These constraints can be categorised as biological (seed/flowering problems, insect and disease resistance), abiotic (wind damage and fire), and infrastructure (staffing, funding, etc.).

Problems with seed production and flowering were investigated by Gallegos (1983). He concluded that optimal flowering and seed production occurred between 9-27° latitude (north or south), higher elevation sites within this latitude range had reduced flowering but that high elevation sites closer to the equator were more favourable for the production of viable seed. Slee (1977) also reports problems of needleless shoots and dieback often associated with abnormal flowering at low latitudes. Organisations such as SAFCOL (South Africa) have recently invested considerable resources in the development of seed production facilities at

lower latitudes (Mozambique) in an attempt to overcome seed production problems (Neville Wessells, *pers. comm*. 1996).

Nevertheless, from the experience with *P. caribaea* in Australia the situation is probably not as simple as that outlined by Gallegos (1983). For example: male and female flowering of var. *hondurensis* is asynchronous in the Northern Territory at latitude 12° S, seed production is very good at Cardwell (lat. 18°S), is poorer (though acceptable) at Byfield (lat. 23° S), but almost non-existent at latitude 26°S. Further, the varieties of *P. caribaea* and provenances within var. *hondurensis* exhibit differences in flowering and seed production: var. *caribaea* has a long delay following grafting until the on-set of flowering (over 5 years), and the coastal provenances of var. *hondurensis* also appear to be less precocious than the upland sources. These delays in the on-set of flowering have caused considerable problems in the implementation of the multiple population breeding strategy outlined by Kanowski and Nikles (1988), such that the generation interval for coastal sources will be considerably longer than the upland sources. Therefore, it is unlikely that the recently infused coastal material will "catch-up" to the more advance breeding population based on Belize Mountain Pine Ridge material.

Insect and disease problems seem to be principally restricted to south-east Asia. The main approach to solving this problem has to been to switch from the faster growing but more susceptible var. *hondurensis* to varieties *bahamensis* and *caribaea.* As Baylis and Barnes (1989) point out, if the tip moth of south-east Asia should spread further, then these two varieties could assume a much greater importance world-wide. The history of the often eventual international spread of insect pests means that all growers of *P. caribaea* should be aware of the potential risks, and perhaps invest some resources into the breeding and testing of *bahamensis* and *caribaea.* For example, Queensland has just established a 14 ha planting of var. *bahamensis* for gene conservation purposes, even though this variety *per se* is currently of no commercial interest in Queensland.

Wind-damage and fire have import consequences for breeding. Although, it has been possible to make good progress in the genetic improvement of wind-firmness in var. *hondurensis,* if progeny tests and clone banks are repeatedly damaged by fire and wind, it becomes increasingly difficult to maintain an effective breeding program (e.g. Fiji and New Caledonia, Table 3). Also, because all breeding facilities must be replicated to ensure that genetic resources are not lost in the event of severe wind-damage or fire, there are considerable additional costs imposed on the breeding program. Costs are associated with both the duplication of facilities and the opportunity cost associated with foregoing other (perhaps more productive) activities.

Infrastructure problems seem to be increasing as we move into the 20th century, as demonstrated in Table 3. Breeders are often faced with the need to accomplish more work with less resources. This continued squeeze on resources has important consequences for the improvement of *P. caribaea.* As described earlier, a wealth of genetic resources has been accumulated world-wide from the natural stands of *P. caribaea.* Many of the natural populations from which this material was derived have now been destroyed, greatly depleted since the original germplasm was exported, or likely to be threatened in the future. Further,

Table 1: Primary *ex situ* distribution of *P. caribaea* Mor. throughout the world. Information derived from survey results where indicated; otherwise, based on other information available to the authors.

| Country | Date of Introduction (year) | Organis-ations (#) | Total Estate (ha) | Latitude Range | Longitude Range | Total Rainfall Range (mm) | Summer Rainfall Range | Days Below -2°C | Coldest Annual Temp. |
|---|---|---|---|---|---|---|---|---|---|
| Argentina[6] | 1960-1970s | 2? | ? | ≈ 25°-28° S | ≈ 57° - 58° W | 800 to 2400 | – | ? | -1.5°C? |
| Australia | 1930s | 2 | ≈58,000[‡] | 12-26°S | 132-154°E | 1,000 to 2,000 | 700 to 1,500 | nil | 5°C |
| Brazil[1] | 1950s | 4? | 300,000 | 1°N-27°S | 49-52°W | 1,000 to 1,500 | 800 to 1,200 | nil | 10°C (*c,h*) 6°C (*b*) |
| China[2] | 1961 (*c*)[†] 1973 (*b,h*) | 1 | 40,000[§] | 18°55′-24°15′N | – | 1,530 to 2,250 | – | nil | |
| Fiji[3] | 1960 | 1 | 43,000 | 16-18°S | 177.5-179° E | – | – | nil | 27°C |
| New Caledonia[4] | 1965 (*h*) 1973 (*c,b*) | 1 | 5,000 | 20°50′S-21°S | 165°E-165°10′E | 1,550 | 600 | nil | 10°C |
| South Africa[5] | 1929 | 1 | < 1,000 | 22°30′-29° S | – | 950 to 1,500 | 600 to 900 | | |
| Venezuela | 1960s | 2? | > 600,000[7] | ≈ 8° - 12° N | – | ? | ? | nil | ≈ 15°C |

*b, c,* and *h* refer to var. *bahamensis, caribaea,* and *hondurensis* respectively.
55,000 ha in Queensland and ca. 3000 in Northern Territory planted with *P. caribaea,* approximately another 17,000 ha planted with *P. caribaea* hybrids
NJ Estimated to reach 100,000 to 150,000 ha by ²010 (Zheng 1996, page 1-²0)
Jarbas Y. Shimizu, EMBRAPA-Florestas, Colombo, Brazil
[2] Wan Huoran, Chinese Academy of Forestry, China
[3] N.W. Yalimaitoga, Research & Development Manager, Fiji Pine Limited, Lautoka, Fiji
Jean-Micheal Sarrailh, Manager CIRAD-Forét, Noumea, New Caledonia
[5] Luckhoff (1964)
[6] Barrett (1991)
MARNR-SEFORVEN (1997)

Table 2: Summary of the silviculture and products of *P. caribaea* Mor. by country (where available).. Information derived from survey results where indicated; otherwise, based on other information available to the authors.

| Country | Rotation Length (yrs) | Important Diseases | Important Pests | Wood Specific Gravity | Main Products | Destination of products |
|---|---|---|---|---|---|---|
| Australia | 25 | nil | nil | 0.45 – 0.55 | Sawn timber, MDF, chip | Australia and export |
| Brazil[1] | 12 – 25 | nil | leaf cutting ants | 0.40 | Veneer, plywood, pulpwood | Brazil and export |
| China[2] | 15 – 20 | *Macrophomina, Denspora, Laplodermium* sp. | tip moth | 0.47 – 0.58 | Pulpwood, sawn timber, resin | China |
| Fiji[3] | 20 | nil | nil | 0.66 | Sawn timber, chips | Fiji and export |
| New Caledonia[4] | 25 – 30 | nil | nil | – | Treated posts, sawn timber | New Caledonia |

[2, 3, 4] Source of information the same as in Table 1.

Table 3: Summary of current international breeding activity with *P. caribaea*. [Symbols: + , (+), ? and – refer to "yes", "possibly", "unknown", and "not applicable".]

| Organisation/ | Relative importance | | | Hybrids | Constraints to Genetic Improvement | | | | | Coop.† | Active Breeding |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Country | *hond.* | *car.* | *bah.* | of interest | Wind | Seed | Pest/ Disease | Staff | Other | Collab. | Program 1997‡ |
| Argentina-INTA | 2 | 1 | ? | + | – | + | ? | ? | ? | ? | ? |
| Australia (Qld.) | 1 | 2 | 3 | + | + | – | – | – | Funds | + | + |
| Brazil-Klabin | – | – | – | + | – | + | Ants | ? | ? | + | ? |
| Brazil-EMBRAPA[4] | 1 | 3 | 4 | + | + | + | Ants | – | Yes – not specified | + | ? |
| China[3] | 4 | 1 | 2 | + | (+) | + | + | (+) | Funds, Cold | + | (+) |
| CIRAD/Congo | 1 | – | – | (+) | – | – | ? | ? | ? | + | (+) |
| Cuba | ? | 1 | ? | (+) | + | – | ? | ? | Funds | – | (+) |
| Fiji[2] | 1 | ? | – | + | + | – | – | + | Fire | + | (+) |
| India | 1 | – | – | (+) | ? | ? | ? | ? | ? | ? | ? |
| New Caledonia[1] | 1 | – | – | + | + | + | – | + | Small program | + | (+) |
| South Africa | 1 | – | ? | + | – | + | – | (+) | Wood quality (density, resin) | + | (+) |
| Venezuela | 1 | – | – | + | – | + | ? | ? | ? | + | ? |

[1, 2, 3, 4] Source of information the same as in Table 1.

† Involved in a cooperative breeding program or inter-agency collaborative projects

‡ Based solely on a subjective assessment by the authors who define "active breeding" as undertaking recurrent selection or hybrid breeding, not just establishment of one-off seed sources.

Table 3: Summary of current international breeding activity with *P. caribaea.* [Symbols: + , (+), ? and — refer to "yes", "possibly", "unknown", and "not applicable".]

| Organisation/ | Relative importance | | | Hybrids | Constraints to Genetic Improvement | | | | | Coop.† | Active Breeding |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Country | *hond.* | *car.* | *bah.* | of interest | Wind | Seed | Pest/ Disease | Staff | Other | Collab. | Program 1997‡ |
| Argentina-INTA | 2 | 1 | ? | + | – | + | ? | ? | ? | ? | ? |
| Australia (Qld.) | 1 | 2 | 3 | + | + | – | – | – | Funds | + | + |
| Brazil-Klabin | – | – | – | + | – | + | Ants | ? | ? | + | ? |
| Brazil-EMBRAPA[4] | 1 | 3 | 4 | + | + | + | Ants | – | Yes – not specified | + | ? |
| China[3] | 4 | 1 | 2 | + | (+) | + | + | (+) | Funds, Cold | + | (+) |
| CIRAD/Congo | 1 | – | – | (+) | – | – | ? | ? | ? | + | (+) |
| Cuba | ? | 1 | ? | (+) | + | – | ? | ? | Funds | – | (+) |
| Fiji[2] | 1 | ? | – | + | + | – | – | + | Fire | + | (+) |
| India | 1 | – | – | (+) | ? | ? | ? | ? | ? | ? | ? |
| New Caledonia[1] | 1 | – | – | + | + | + | – | + | Small program | + | (+) |
| South Africa | 1 | – | ? | + | – | + | – | (+) | Wood quality (density, resin) | + | (+) |
| Venezuela | 1 | – | – | + | – | + | ? | ? | ? | + | ? |

[1, 2, 3, 4] Source of information the same as in Table I.

[I] Involved in a cooperative breeding program or inter-agency collaborative projects

Based solely on a subjective assessment by the authors who define "active breeding" as undertaking recurrent selection or hybrid breeding, not just establishment of one-off seed sources.

many of the stands and tests established in the 1970s are now nearing rotation age, therefore the breeder must face the question of whether of not she can afford not to conserve the genetic resources within the control of her organisation. Given the current economic imperatives, it seems likely that individual organisations will choose to rationalise theirgenetic resources of *P. caribaea.* The international (collective) consequences of these individual decisions could be very serious, perhaps disastrous, in the long term. Dvorak (1996) identifies a lack of resolve to work together as the greatest threat to advances in the exploration, conservation and utilisation of genetic resources.

## HYBRIDISATION

The commercial deployment of *P. caribaea* in some environments is limited by a number of factors including: susceptibility to wind-damage, tip moth attack, concerns about wood properties, poor tolerance of periodic water-logging, and low frost tolerance. Hybridisation offers the potential to expand the potential area over which *P. caribaea* and its derivatives may be successfully deployed, through broaden adaptability, complementary combination of economically important traits, and the potential to breed for improved hybrid performance.

Potential gains through operational deployment of hybrids: *P. caribaea* produces fertile intra-specific hybrids between provenances and varieties and inter-specific hybrids with *P. elliottii, P. oocarpa* and *P. tecunumanii* as well as some other species (Slee 1971, Nikles 1989, Nikles 1991, Nikles 1995). Inter-provenance hybrids in var. *hondurensis* may provide the opportunity to rapidly infuse the greater wind-firmness of the coastal and island sources into the more advanced upland sources. In a test in south Queensland, an inter-provenance hybrid (Belize Mountain Pine Ridge by Coastal provenances, MPR x COA) grew at least as fast as crosses amongst the MPR provenance to four years of age, but suffered less wind damage (Figure 2). Likewise, the three varieties of *P. caribaea* display a number of complementary traits that might be combined advantageously through the use of inter-variety hybrids (Nikles 1995).

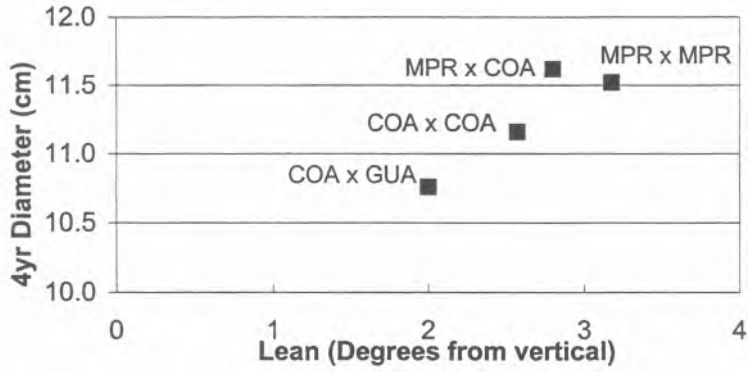


Figure 2: Wind-firmness (as measured by tree lean following strong winds) of *P. caribaea* var. *hondurensis* inter-provenance hybrids on a poorly-drained site in south-east Queensland (lat. 26° S). COA, GUA and MPR refer to coastal, Guanaja and Belize Mountain Pine Ridge provenances.

Hybrids between var. *hondurensis* and var. *caribaea* are showing considerable promise in central Queensland coastal lowlands, exhibiting very good stem straightness, fine (and flat)

branching, combined with growth rates comparable to var. *hondurensis* (Figure 3). This hybrid has also demonstrated improved wind-firmness compared to var. *hondurensis*, and hence has considerable potential in the low elevation tropics where wind-damage is a problem (e.g. Fiji, New Caledonia, northern Australia, and areas of southern China). Similarly, hybrids between var. *hondurensis* and the other two varieties are likely to combine the good growth rates of var. *hondurensis* with the resistance to tip moth. However, the insect resistance of the hybrids would need to be evaluated prior to operational deployment since Huber et al. (1997, page 14) report that *P. taeda* x *P. elliottii* hybrids inherit the susceptibility of *P. taeda* to tip moth attack, rather than the resistance of slash pine.

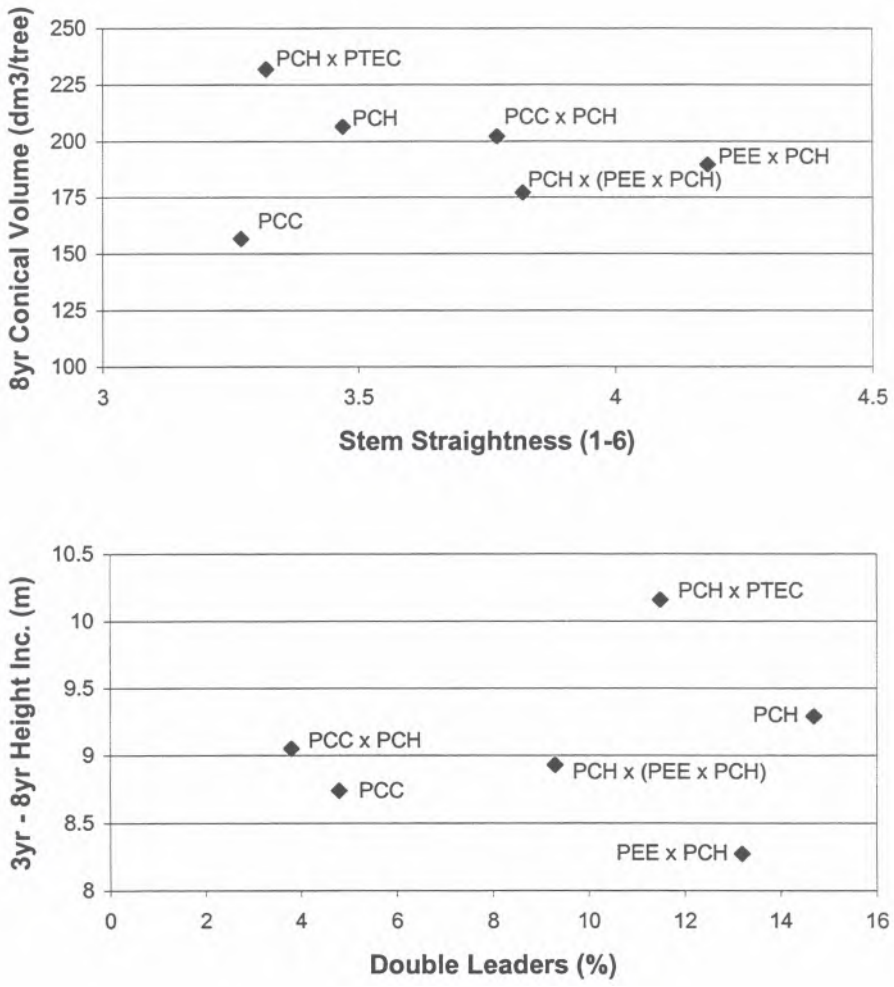


Figure 3: Volume and stem straightness, and percentage of double leaders verses tree height of *P. caribaea* var. *hondurensis* (Poi), var. *caribaea* (Pcc), inter-variety hybrids, and PCH x *P. tecunumanii* hybrids at 8 years of age on a well-drained in central Queensland (lat 23° S).

Inter-specific hybrids, particularly the slash x var. *hondurensis* hybrids, are performing well in Argentina, Australia, Brazil, China, South Africa and the United States (Kikuti et al. 1996, Nikles 1991, Nikies 1995, Nikies 1996, Powell and Nikles 1996, Rockwood et al. 1991, Rockwood and Nikies 1996, White et al. 1996). The $F_1$, $F_2$ and backcross hybrids are

showing improved growth rates and branch quality compared to slash pine, and improved wind-firmness, stem straightness and wood density when compared to *P. caribaea* (Refer to Figure 4, for an example from south-east Queensland). The backcross to slash pine is likely to find application on particularly poorly drained sites, or sites subject to frosts.

Hybrids between *P. caribaea* and *P. oocarpa/P. tecunumanii* can be produced more easily than hybrids between *P. caribaea* and slash pine (Nikles 1989). Further Nikles (1989) reports that hybrids between *P. caribaea* and *P. tecunumanii* were superior in growth to both parental species across a range of sites in northern Australia and Fiji. Although these hybrids have demonstrated good growth potential (refer Figure 3), they are still susceptible to stem breakage on some sites. Therefore, the operational deployment of this hybrid will probably be restricted to sites that are not affected by strong winds, such as in eastern Venezuela.

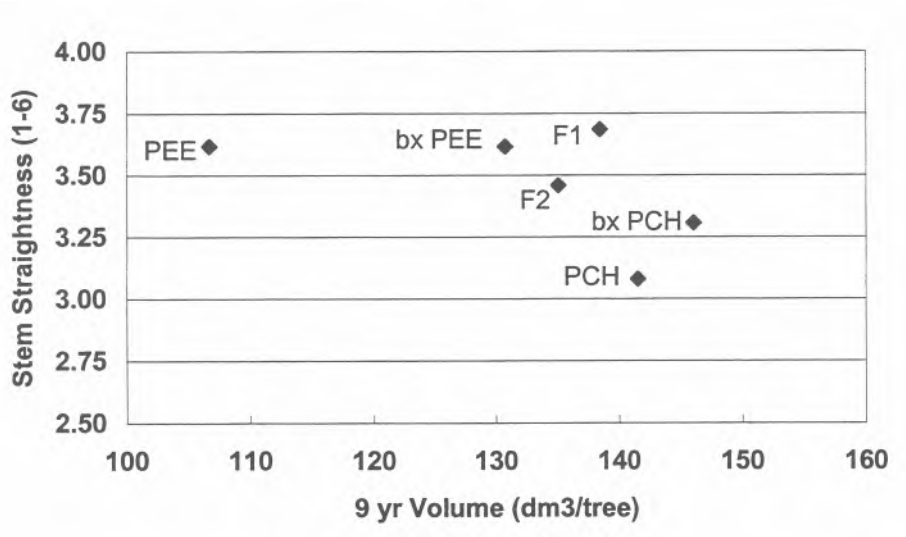


Figure 4: Volume and stem straightness (1-6, 6 good) at 9 years of age on a well-drained site in south-east Queensland (lat. 26°S) for slash pine (PEE), *P. caribaea* var. *hondurensis* (PCH) and their $F_1$, $F_2$ and backcross (bx PEE, bx PCH) hybrids.

Application of hybridisation to breeding: Hybridisation offers the opportunity to infuse genes of interest into existing breeding populations, and to obtain hybrid vigour. Most advanced breeding populations of *P. caribaea* are based on upland sources. Consequently, separate populations can be maintained for conservation purposed, but rather than maintain separate breeding programs of upland, coastal and island sources of var. *hondurensis (e.g.* Kanowski and Nikles 1988), the best coastal and island material can also be intercrossed with the best upland material. Selections in the off-spring of these crosses then carried forward into subsequent generations. If pollen from the coastal sources is used, the 'new' genes from coastal/island sources can be rapidly infused into the main breeding population at a relatively low cost.

The use of composite intra- and inter-specific hybrids to infuse favourable genes into advanced populations of var. *hondurensis* offers a number of advantages. For example:
• Only one breeding population is required, and overall breeding costs are reduced.

- Seed production problems in the first generation are over come. Seed set of the slash x var. *hondurensis* hybrid improves from approximately 20 seeds per cone in the F1 generation to over 80 seeds per cone in the $F_2$. Thus, the production of large quantities of seed for operational use can be much easier.
- Favourable genes are likely to be incorporated into operational plantations much more rapidly, particularly if one population is at a considerably earlier stage of genetic improvement.

## FUTURE CHALLENGES

A significant future role of *P. caribaea* in plantation forestry seems assured, both as a pure species (e.g. Venezuela) and as a parent of hybrids (e.g. Australia). Nevertheless, the future conservation status of its genetic resources is not as certain. Successive waves of introductions (especially of var. *hondurensis)* to many countries over a fairly long period, facilitated by the separate comprehensive collection and wide-spread distribution of seed by OFI and CAMCORE especially, have resulted in the *ex situ* assembly of a very large sample of the genetic resources of *P. caribaea.* The world-wide distribution of germplasm *ex situ* through a broad range of geographic regions (Table 4), has now resulted in the formation of what are effectively multiple populations, and the development of locally adapted land races. This is particularly true for var. *hondurensis.*

These regional gene pools are potentially of great significance for the long-term genetic conservation of this species, especially since *in situ* conservation seems unlikely to be a reliable long-term option, and because different adaptations are likely to have developed *ex situ.* If maintained, these *ex situ* genetic resources are likely to act as huge reservoirs of genetic variability. Currently, the genetic resources of this species are controlled by a range of government and private organisations with varying resources, and differing levels of interest in the continued conservation of *P. caribaea's* genetic resources. Clearly, there is a need for a coordinated approach to the genetic conservation of genetic resources of this (and other widely disseminated) species.

We suggest that the following steps are necessary:

1. Documentation of the genetic resources currently held *ex situ,* perhaps using a similar system to that being tested by DANIDA/FAO (Hansen 1996). In some cases the documentation is fairly recent and accurate (e.g. CAMCORE, Queensland). This work could perhaps be sponsored by the International Plant Genetic Resources Institute (IPGRI, previously IBPGR).
2. Description of the genetic resources held in conservation stands, seed orchards and clones banks.
3. Development of a cooperative/collaborative approach to the world-wide conservation of the significant, viable holdings within each region.
4. Coordinated analyses of later-age data from the various international provenance and family-in-provenance trials of *P. caribaea,* in a similar manner to those on var. *hondurensis* by Crockford et al. (1990) and recently completed by CAMCORE (Gary Hodge, *pers. comm.* 1997) for var. *hondurensis* and *P. tecunumanii* (CAMCORE 1996).

5. Form a voluntary organisation to help coordinate this work; perhaps a separate IURFO working group dealing with *P. caribaea* would be an appropriate forum.

Table 4: The broad geographic distribution of significant *ex situ* gene pools of *P. caribaea,* and special adaptations likely to have been developed within local land races.

| Geographic Region | Countries/Organisations Holding Significant Genetic Resources | Main Source of Germplasm | Variety, Provenances† | Special Adaptations Expected |
|---|---|---|---|---|
| Caribbean | Jamaica, Puerto Rico | OFI | *h* | Tolerance to high pH, wind-firmness |
| Central-eastern Brazil | CCGMT | Seed merchants, OFI | *h, b, c* | Local climatic – edaphic conditions |
| Eastern Venezuela | PROFORCA | Seed merchants, CAMCORE | *h* (Poptun) | Low rainfall, deep sands in tropics |
| Equatorial Brazil | Jari Florestal | Nicaragua | *h* (Coastal, Guanaja) | Humid tropics environment |
| S.E. Africa | SAFCOL | OFI, CAMCORE | *h* (+ *b, c*) | Local climatic – edaphic conditions |
| S. Brazil – N. Argentina | EMBRAPA – INTA | OFI, CAMCORE | *h, c* | Cold hardiness |
| S.E. China | CAF | Cuba, OFI | *c*, (+ *b*) | Pest and wind tolerance |
| S.E. India | Mysore Paper Mills | OFI, Australia | *h* | Local climatic – edaphic conditions |
| S.W. Pacific | Australia, Fiji, New Caledonia | OFI, CIRAD | *h* (+ *c, b*) | Wind-firmness, tolerance of poor soils and drainage (Aust.) |
| Thailand | RFD | OFI | *h* | Local climatic – edaphic conditions |
| W. Africa | Congo, Nigeria | OFI, CIRAD | *h* | Local climatic – edaphic conditions |

*b, c, h* refer to the *bahamensis, caribaea* and *hondurensis* varieties of *P. caribaea.*

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