6.3 BREEDING BEHAVIOUR OF THREE SANDALWOOD SPECIES (SANTALUM ALBUM, *S. austrocaledonicum* and *S. lanceolatum*)

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Abstract

This study demonstrates that no reproductive barriers exist between three tropical sandalwood species (Santalum album, *S. austrocaledonicum* and *S. lanceolatum*) suggesting they have low genetic divergence between them. The high level of cross-compatibility between these three species increases the germplasm available for breeding programmes to develop cultivars suitable for commercial production. Each species could potentially contribute characters to a breeding programme, with the superior oil qualities of *S. album*, the early heartwood formation in *S. austrocaledonicum* and the straight form and fire tolerance of *S. lanceolatum*.

The production of hybrids between these species under natural conditions has conservation implications. Recent introductions of *S. album* in the southern part of Cape York means they can now hybridise with natural populations of *S. lanceolatum*. In Queensland it is unclear whether such hybrid progeny would have an advantage in these quite arid environments to persist beyond 1 or 2 generations. The planted resource of *S. album* occurs as one planting on a single property, in which monitoring of the surrounding areas could easily detect any issues with uncontrolled introgression between *S. album* and natural populations of *S. lanceolatum*.

In Vanuatu where *S. album* has also been recently introduced, spontaneous hybridisation between it and *S. austrocaledonicum* is also likely. In contrast with Queensland, there is little control over planting of *S. album* and many plantations have been established over Efate and are continuing in other islands. It is likely that hybrids between *S. album* and *S. austrocaledonicum* in Vanuatu are going to be competitive with pure forms of Vanuatu sandalwood, as has been demonstrated in Fiji hybrids between *S. album* and *S. yasi*. While it is recognised that *S. album* generally produces heartwood oil of superior quality in the marketplace, the source and therefore the quality of the Vanuatu *S. album* introductions is unclear. The introduction of *S. album* also represents a concern for the future identity of Vanuatu Sandalwood, which currently occupies an international market niche. It is looking increasingly likely that New Caledonia will emerge as a refuge for pure forms of *S. austrocaledonicum*.

Introduction

Santalum (sandalwood) is a genus of hemi-parasitic tree species occurring throughout south and southeast Asia, Australia and the Pacific. The heartwood of several species produces valuable aromatic oil widely used in perfumery, medicines and incense. Throughout the world, sandalwood products are being sourced from declining natural stands and the international price for natural sandalwood products continues to increase. Therefore significant opportunity exists to establish commercial sandalwood agroforests, to reduce pressure on wild stands, improve consistency of product supply and increase economic outcomes for smallholder farmers.

The development of sandalwood species as significant agroforestry crops will depend on the development of forms suited to commercial production, with high growth rates yielding high volumes of heartwood containing concentrated oils with high levels of Đ- and Đ-santalol. The implementation of a successful breeding programme for any sandalwood species will depend upon knowledge of its breeding system and its cross-compatibility with related species that are a source for potentially useful characters. Given also the continued exploitation of many sandalwood species a knowledge of their breeding systems will assist those developing strategies aimed at conserving current wild populations and establishing new plantings within their natural distributions. Information on the breeding system and patterns of gene flow are important for planning germplasm collection, designing and managing seed orchards and for maintaining genetic diversity in breeding populations. This study includes information published in Tamla et al. (2011), with additional data related to *S. album* and *S. austrocaledoni-cum*, and updated on the original presentation to the Vila workshop. The objectives of the present study were to determine levels of (i) self- and (ii) cross-compatibility within Santalum lanceolatum, *S. album* and *S. austrocaledonicum* and (iii) cross-compatibility between these three sandalwood species.

Materials & Methods

Controlled pollination

Grafted clones of *S. lanceolatum*, *S. album* and *S. austrocaledonicum* were grown in 300mm-diameter pots in a soil-less potting medium in an insect-proof greenhouse with drip irrigation. Flowers were emasculated during anthesis using pointed forceps. The anthers removed during this process were either placed in small plastic vials and placed in a desiccator with silica gel or used immediately for pollination. All pollinations were made using pollen collected during the day (i.e. pollen was not stored and used on subsequent days). Pollinations were carried out by applying the pollen-shedding anther to the stigma until pollen grains had adhered to the stigma. Individual inflorescences were pollinated with a single pollen source and each was tagged with details of pollen donor.

Three genotypes of *S. album* (E5, E7 & E8) originating from two Indian seedlots, one genotype of *S. austrocaledonicum* (T1) from Vanuatu and 13 genotypes of Santalum lanceolatum (accessions 0, 1, 2, 5, 8, 10, 14, 16, 25, 27, 29, 30 and 31) from Cape York Peninsula (Queensland) were used to examine self- and intraspecific-compatibility within, and interspecific compatibility between them. Seed production was recorded across 2732 different controlled pollinations (Table 1).

TABLE 1: THE NUMBER OF GENOTYPE COMBINATIONS (UNIQUE 'POLLINATIONS') AND TREATED/POLLINATED FLOWERS FOR SEVEN DIFFERENT POLLINATION TYPES.

Pollination Type	Genotype Combinations	Flowers 'Treated'
S. album self-pollinated	4	332
S. album intraspecific	4	279
S. lanceolatum self-pollinated	10	234
S. lanceolatum intraspecific	13	241
S. austrocaledonicum self	1	16
S. album x *S. austrocaledonicum* (reciprocal)	4	144
S. album x *S. lanceolatum* (reciprocal)	28	1250
S. lanceolatum x *S. austrocaledonicum* (reciprocal)	5	236
Total	**69**	**2732**

Pollinations were carried out on three separate flowering events during September 2007, December 2007 and February 2008. Flowers were left on the plants for approximately 8-10 weeks from pollination to fruit harvest. Fruits from each pollination category were collected, the flesh was removed and the seed air-dried before storing in a sealed plastic containers at 4°C.

Germination of seed resulting from controlled pollination was undertaken in a seed raising mix with a 1:1 ratio of medium grade perlite and vermiculite. Seeds were placed under 50% shade and were watered through an automatic irrigation system for 15 minutes per day. Seeds were considered germinated after they had been pricked into pots and survived for a period of 3 months.

Differences in the (i) proportion of pollinated flowers developing into seed and seedlings between pollination types (i.e. unpollinated, self-pollinated, intraspecific out-cross pollinated etc.) and (ii) the proportion of unique pollinations developing seed and seedlings were evaluated using an equality test of two binomial proportions (Ott and Longnecker 2001) calculated by:

$$z = \frac{(\hat{\pi}_1 - \hat{\pi}_2)}{\sqrt{\dfrac{\hat{\pi}_1(1 - \hat{\pi}_1)}{n_1} + \dfrac{\hat{\pi}_2(1 - \hat{\pi}_2)}{n_2}}}$$

The two binomial populations are denoted by $\hat{\pi}_1 = \dfrac{y_1}{n_1}$ and $\hat{\pi}_2 = \dfrac{y_2}{n_2}$ where by and where y_1 seeds / seedlings are recorded for the random sample of n_1 pollinations from population 1, and y_2 seeds/seedlings are recorded for the random sample of n_2 pollinations from population 2. The null hypothesis was rejected where the absolute value of the statistic z was greater than $z_{0.05} = 1.645$.

This statistical approach was used because, although a sufficient number of pollinations per pollination type were performed, in some cases a low number of replicates or genotype combinations did not permit evaluation by two-way ANOVA

Results

Unpollinated flowers
No signs of fruit development were observed in any of the unpollinated flowers in this experiment. Flowers of all species in this treatment were shed towards the end of their expected 'life' (*S. album* 7-9 days, *S. austrocaledonicum* 24-48 hours and *S. lanceolatum* 12-24 hours). No floral-tube abscission, indicating fruit development, was observed and no seeds were set from any flowers of this treatment.

Self pollination in *S. album*, *S. austrocaledonicum* and *S. lanceolatum*
The percentage of self-pollinated *S. lanceolatum* flowers developing into seed (1.3%) was significantly (P < 0.05) lower than for all other pollination types except that of self-pollinated *S. album* (3.1%). Seeds were produced following self pollination in 50% of *S. album* and 20% of *S. lanceolatum* genotypes tested. The percentage of self-pollinated *S. lanceolatum* flowers that developed into seedlings (0.7%) however, was not significantly different from intraspecific crosses among *S. album* (0.6%) and *S. lanceolatum* (1.8%) genotypes. No seedlings were recorded from self-pollinated *S. album* flowers. A comparatively higher level of self-pollinated flowers developed into seed (12.5%) and seedlings (6.25%) for *S. austrocaledonicum* when compared with self-pollinated *S. album* and *S. lanceolatum* flowers (Figure 1).
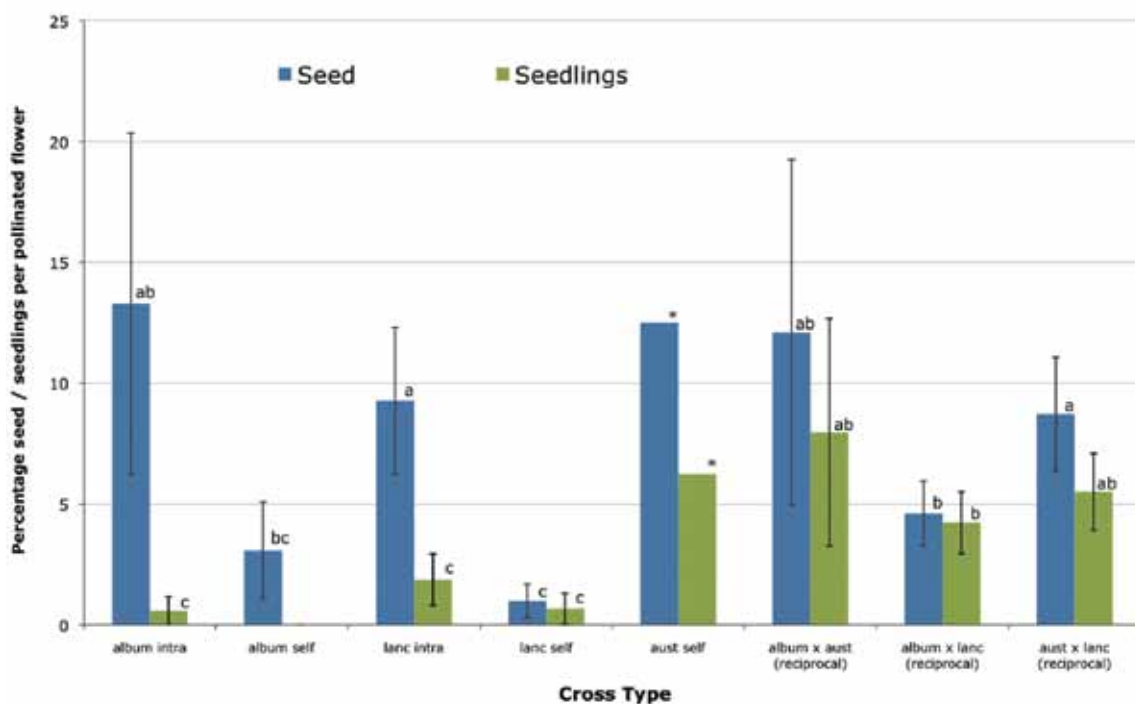

Figure 1: Number of seed and seedlings per pollinated flower for self and intraspecific pollinations in *S. album* ('album self' and 'album intra' respectively) and *S. lanceolatum* ('lanc self' and 'lanc intra' respectively), self pollination in *S. austrocaledonicum* ('aust self') and reciprocal interspecific pollinations between these three species ('album x aust', 'album x lanc', 'aust x lanc'). Vertical bars represent standard errors. Cross types sharing lower case letters are not significantly (P < 0.05) different within either the seed or seedling response variable.
* Calculation of standard error and significance values not possible because of low sample size.

Intraspecific pollination within *S. album* and *S. lanceolatum*

Of the 241 intraspecific crosses made between *S. lanceolatum* genotypes only 9.0% and 1.8% of pollinations resulted in the production of seed and seedlings, respectively. For those crosses representing greater than 10 pollinations the seed set ranged from 0% in 3 different genotype combinations (averaging 16 pollination for each) to 14.2% in crosses between accessions 16 (♀) and 29(♂) (totalling 14 pollinations).

A similar difference in seed production compared with seedlings was recorded for intraspecific crosses within *S. album*, where 13.2% of flowers developed seed but only 0.6% of flowers pollinated resulted in successfully growing seedlings. Variation within of the four genotype combinations with greater than 10 pollinations the seed set ranged from 3% ('E8' x 'E5' totalling 56 pollinations) to 56% ('E5' x 'E8' totalling 50 pollinations) indicating that some genotypes might have a greater compatibility in one direction of a reciprocal cross.

Within *S. lanceolatum* only accession number 25 was used in over 50 intraspecific cross-pollinations each as a pistillate and pollen parent with at least 3 different genotypes. The mean percentage of seed set per pollination in this accession was not significantly different between pistillate (4.8%) and pollen (5.4%) parent. No other accession had a sufficient number of pollinations or was crossed with at least 3 different genotypes to permit such evaluation of differences in fecundity between its use as either a 'female' or 'male' parent for intraspecific crosses.

Interspecific pollination between *S. album*, *S. austrocaledonicum* and *S. lanceolatum*

S. album x *S. lanceolatum*

Variation among the interspecific crosses between *S. lanceolatum* (♂) and *S. album* (♀) was found in the percentage of seed set per pollinated flower, ranging from 0–23% and from 0-16% in its reciprocal crosses (*S. album* (♂) and *S. lanceolatum* (♀) for those crosses with greater than 10 pollinations. Interestingly 38% of the seeds that developed from the former interspecific cross type resulted in 2 seedlings following germination. In crosses involving *S. album* (♂) and *S. lanceolatum* (♀) the percentage of seed producing 2 seedlings was 7.5%. No other cross type in this study had seed that produced 2 seedlings.

A significantly ($P < 0.05$) greater number of seeds per pollinated flower were found following intraspecific pollination among *S. lanceolatum* genotypes (9.0%) compared with reciprocal interspecific crosses between *S. album* and *S. lanceolatum* (4.6%). However the number of seedlings per pollinated flower was significantly ($P < 0.05$) greater among reciprocal crosses between *S. album* and *S. lanceolatum* (4.2%) compared with *S. lanceolatum* intraspecific pollinations (1.8%).

S. lanceolatum x *S. austrocaledonicum*

In the present experiment only one genotype of *S. austrocaledonicum* (T1) flowered during the period of controlled pollinations. The flowering of this genotype coincided only with the flowering of five genotypes of *S. lanceolatum* (accessions 2, 5, 14, 16, and 29). Therefore in the evaluation of the compatibility between *S. austrocaledonicum* and *S. lanceolatum* only reciprocal crosses between T1 with each of accessions 2, 5, 14, 16, and 29 were possible.

Variation among the crosses between *S. lanceolatum* (♂) and *S. austrocaledonicum* (♀) was found in the percentage seed set per pollinated flower, ranging from 4–23% and from 0-18% in the reciprocal cross (*S. austrocaledonicum* (♂) and *S. lanceolatum* (♀). No significant differences in the number of seed per pollinated flower were found between *S. lanceolatum* intraspecific crosses and each of the reciprocal interspecific crosses between *S. austrocaledonicum* and *S. lanceolatum*. Number of seedlings per pollinated flower for *S. austrocaledonicum* (♂) x *S. lanceolatum* (♀) cross was significantly ($P < 0.05$) greater than both self- and intraspecific crosses within *S. lanceolatum*. The reciprocal interspecific cross (*S. lanceolatum* (♂) and *S. austrocaledonicum* (♀) however, was not found to differ from these self- and intraspecific crosses.

S. album x *S. austrocaledonicum*

Interspecific compatibility was also found between *S. album* and *S. austrocaledonicum* with a substantial percentage of flowers producing seed (12.1%) and seedlings (8.0%). This result contrasts with that found in intraspecific pollinations among *S. album* genotypes, where a significant ($P < 0.05$) reduction was recorded between the percentage flowers producing seed (13.3%) and seedlings (0.6%).

Discussion and Conclusions

Unpollinated flowers

In this study, no fruit or seeds were set following isolation of flowers and restricting pollination of all three species in this study. This result suggests that these species do not possess a capacity for the development of parthenocarpic fruit or clonal seed. This result is similar to that found in *S. album* in China, where no seeds were found in flowers isolated from open pollination by bags (Ma et al. 2006).

Self compatibility in Santalum

The mean seed set per pollinated flower in both *S. album* and *S. lanceolatum* was significantly greater following outcross- compared with self-pollination. This result indicates a possible self-incompatibility mechanism(s) operating in these species. Rugkhla et al. (1997) proposed that both pre- and post- fertilisation self-incompatibility mechanisms were operating in *S. album* and S. spicatum. This study however, found that putative self-incompatibility mechanism(s) in these species, may either be incomplete, or subject to genetic variation between accessions, given that seed set was affected following self pollination in 50% and 20% of genotypes tested for *S. album* and *S. lanceolatum* respectively. Two self-pollination derived seeds in *S. lanceolatum* were successfully germinated and have continued to grow for a period of 2 years without indication of any deleterious effects of inbreeding. In contrast none of the self-pollinated seed in *S. album* successfully germinated to produce a seedling.

The percentage of self-pollinated flowers that produced seed and seedlings for *S. austrocaledonicum* was substantially greater than that of *S. album* and *S. lanceolatum*. Given that the measures in *S. austrocaledonicum* are based on only one genotype, this result cannot be generalised across the species since often the degree of self-compatibility can vary between genotypes. It does however suggest that individual trees of *S. austrocaledonicum* can be self compatible, which supports anecdotal reports of isolated trees producing good quantities of seed.

These results are similar to those found by Muir et al. (2007) for S. spicatum, where one family showed a high level of inbreeding, which was contradictory to the high mean outcrossing rate (95.2%). These authors proposed that flowering of this family was non-synchronous with many other families, resulting in higher inbreeding. This flexibility in breeding strategy would be of advantage in continental Australian species dispersing and colonizing many islands in south-east Asia and Pacific (Harbaugh and Baldwin 2007). In *Santalum album* Ma et al. (2006) reported 24% of flowers with geitonogamous (same plant and different flower) self-pollination set seed. While the results of this present study are indicative of the incomplete nature of self-incompatibility in these three species of Santalum further work is required to determine the extent of genetic variation in this trait.

In this study all cross types (self-, intraspecific and interspecific) were carried out on a given individual ramet. Therefore it is possible that the reduced selfing rate recorded in this study could be due to competitive interactions between flowers with 'outcross' and those with 'self' pollen and preferential maternal resource allocation to those most competitive. It would be of interest to evaluate the percentage seed set between these three cross types, where each type is restricted to an individual ramet of a given genotype. This would remove any interaction effects that may have been operating in the present study.

Intraspecific pollinations

The mean level of seed set per pollinated flower varied between the intraspecific crosses within *S. album* (13.3%) and *S. lanceolatum* (9.0%). No intraspecific pollinations were possible for *S. austrocaledonicum* in this study, since only one genotype flowered during the experimental period and therefore we are not able to make comparisons of intraspecific pollination success between each of the three species. The rates of seed set in intraspecific pollinations in this present study are similar to those found in other studies of reproductive biology in Santalum. For instance fruit set (and thus seed set, given a fruit is generally single seeded) from open pollinated *S. album* trees was less than 2-3% in China (Ma et al. 2006) and 5.2% in India (Sindhu Veerendra and Anantha Padmanabha 1996). Rugkhla et al. (1997) reported a final fruit set of 1.3% in controlled intraspecific outcross pollination of S. spicatum in Western Australia. These authors also found a 10% fruit set in controlled outcrosses of *S. album*, which was similar to the 9.4% found by Kulkarni and Muniyamma (1998) in India. While Ma et al. (2006) found that 2-3% of open pollinated *S. album* flowers set seed, this was increased to 14% during artificial outcross pollinations. The results of this and other studies suggest that while improved seed set may be achieved using controlled pollination, several Santalum species produce an abundance of flowers but less than 10% of these typically develop into viable seed.

The significantly greater (i) number of seeds set per intraspecific outcross and (ii) percentage of unique intraspecific pollinations (genotype combinations) developing seed compared with self-pollinated flowers suggests a putative self-incompatibility mechanism. However the low germination rate (40%) for intraspecific outcross derived seed resulted in no significant difference in the number of seedlings between intraspecific and self-pollinated flowers. Further replication of this work is likely to reveal the exact nature of the low germination rate among 'intraspecific seeds'.

Interspecific crosses between *S. album, S. austrocaledonicum* and *S. lanceolatum*
Despite total geographic isolation and significant morphological divergence between the three species of this study, no reproductive barrier appears to exist between them. We demonstrated equivalent or greater seedling production in all three reciprocal interspecific pollinations compared with the two intraspecific crosses. Seed producing two seedlings were found in crosses between *S. album* (♂) and *S. lanceolatum* (♀), and although this is not unusual, the level (7.5% of seed) was elevated compared with all other crosses in this study and with *S. album* intraspecific crosses in controlled crosses in China where the frequency was 2.5% (Ma et al. 2006).

The results of this study reflect similar findings with spontaneous hybridisations between *S. album* and *S. yasi* in Fiji, with no apparent reproductive barrier or hybrid breakdown (Bulai and Nataniela 2005; Doran et al. 2005). Bulai (2007) further reported that open pollinated hybrids between *S. album* and *S. yasi* are now being produced in clonal seed orchards, and these hybrids appear to have higher vigour, wider environmental tolerances and are less dependant on forming host associations. Rugkhla et al. (1997) found that no seeds developed after 1930 reciprocal controlled pollinations between *S. album* and S. spicatum, and reported that strong incompatibility mechanisms operated between pollen and style, and possibly in the developing zygote.

Doran and Brophy (2005) proposed that interspecific hybrids may provide the opportunity to improve the planted form of sandalwood particularly given the good vigour of F1 hybrids between *S. album* and *S. yasi* observed in Fiji. Hybridisation between *S. album*, *S. austrocaledonicum* and *S. lanceolatum* may be used to incorporate important characters from each of these species into a cultivar for use in commercial plantations. Combining characters such as high heartwood oil concentration and quality (% α - and β-santalol) from *S. album*, precocious heartwood development from *S. austrocaledonicum* and straight form and fire tolerance from *S. lanceolatum* in cultivars may be possible provided additive genetic effects predominate in the characters of interest.

The high level of cross-compatibility between these three species indicates the likelihood that they are not widely divergent genetically and chromosomally (few chromosome structural differences) and thus the transfer of characters, even those under quantitative genetic control, would appear to be feasible from interspecific crosses. While the high cross-compatibility between these three species indicates the likelihood that they are not widely divergent genetically, it would be necessary to evaluate the fertility and seed production level of both their F1 hybrid and F2 progeny, because it is possible that genetic divergence between the two species may not be significantly manifest until these post-hybridisation stages.

The apparent lack of interspecific barriers between *S. lanceolatum* with each of *S. album* and *S. austrocaledonicum* also has implications for the conservation of their natural stands. Given the low relative value of *S. lanceolatum* it is unlikely that it would be introduced into areas of natural populations of *S. album* or *S. austrocaledonicum*. Commercial plantings of *S. album* have however, already been established in some areas of Queensland with existing natural populations of *S. lanceolatum*. It is likely that gene flow will occur between the *S. album* plantings and adjacent *S. lanceolatum* populations. It is unclear whether such hybrid progeny would have an advantage in these more arid environments and persist beyond 1 or 2 generations. These considerations however may need to be evaluated by those responsible for (a) management of *S. lanceolatum* wild stands and (b) improvement of *S. album* germplasm for commercial production.

The genetic purity of *S. austrocaledonicum* appears to be under threat in Vanuatu, where *S. album* has been introduced in recent years (Page et al. 2012). Given the cross compatibility between these species, this development is of concern in terms of the long-term preservation of the genetic variation in this species. While it is recognised that *S. album* generally produces oil that is of superior quality in the marketplace, the heritage and therefore the quality of the Vanuatu introductions is unclear. Page et al. (2012) also reported that heartwood production in *S. austrocaledonicum* may be more precocious compared with *S. album* and therefore producers of hybrids in the future may need to consider increasing the length of the production rotation.

The introduction of *S. album* also represents a concern for the ongoing identity of Vanuatu Sandalwood, which currently occupies an international market niche. It is therefore looking increasingly likely that pure forms of *S. austrocaledonicum* may only persist New Caledonia. There may however be opportunity to preserve the identity of Vanuatu sandalwood in isolated parts of the country including the regions of Malekula and Santo, where forms of *S. austrocaledonicum* exist that have superior oil quality (Page et al. 2010).

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