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# Oil yield and composition of young *Santalum yasi* in Fiji and Tonga

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**ABSTRACT**

*Santalum yasi*, a sandalwood native to Fiji and Tonga, is a tree crop of significant economic potential for these countries. Development of a plantation industry underpinned by a breeding program is a high priority for industry development. Gathering information on heartwood development, oil yield and oil composition is a critical step for the domestication and tree breeding of the species. Oil yield and composition were determined for 86 *Santalum* core samples using gas chromatography and combined gas chromatography/mass spectrometry. Most (67) cores were from the lower boles of individual trees of *S. yasi*, with smaller samples of *S. album* and *S. album* × *S. yasi*, both of which are also commonly grown in Fiji and Tonga, and *S. austrocaledonicum* was included for comparison. Although the ages of the trees were unknown, they are likely to have been between 10 and 20 years. Relationships among traits, including solvent-extracted oil yield, oil composition, lower bole diameters under and over bark, and heartwood diameter, were examined. Yield was highly variable (0.05–11.8%) and only weakly correlated with underbark diameter at 30 cm above ground. Oil yield and percent composition of santalol oil components were strongly positively correlated. For those trees with oil yields >1% w/w, the oil composition was generally favourable relative to the international standard for *S. album* oil, with large proportions of santalols, particularly *β*-santalol. The study confirms that both harvesting and selection for genetic improvement of *S. yasi* trees younger than 20 years old are likely to be suboptimal, with unreliable heartwood and oil development. Further study of heartwood and oil development, both within individual trees and among genotypes in common-garden trials with known genetics and controlled environments and hosts, is a high priority. The development of an international standard for *S. yasi*, supporting the growth of a niche market for the product, is also recommended.

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(*E,E*)-farnesol; essential oil; heartwood; sandalwood; santalol; *Santalum album*

## Introduction

*Santalum* (sandalwood) is a genus of hemiparasitic trees, many species of which produce aromatic heartwood oils. The essential oil is used for a variety of purposes, including perfumery and incense, and is extracted by steam distillation of the heartwood fraction of the lower bole and major roots and branches of mature trees, which are at least 15 years old. *Santalum album* L. (Indian sandalwood) has a high oil yield and is traditionally regarded as having the most desirable oil profile. It is mainly composed of *α*- and *β*-santalols (ISO 2002). *Santalum yasi* Seem., endemic to Fiji, Tonga and Niue, also has a high oil yield and similar profile (Thomson et al. 2018). *Santalum yasi* heartwood and oils are frequently traded commercially as Indian sandalwood because the oils of the two species are difficult to distinguish. *Santalum austrocaledonicum* Vieill., which is native to Vanuatu and New Caledonia, has a more variable yield and profile, but some trees produce oils that are also similar to *S. album* (Page et al. 2010). All these species have been overexploited in the wild and are now considered threatened. All three species are being cultivated, however, with extensive plantations of *S. album* in Australia and parts of Asia and of *S. austrocaledonicum* in Vanuatu and New Caledonia, and numerous smallholdings of *S. yasi* in Fiji and Tonga.

*Santalum yasi* has been selected for domestication in Fiji and Tonga (Bush et al. 2020) because it has the potential to make a significant economic contribution to these countries (Thomson 2020; Thomson et al. 2020). The species is reputed to grow more slowly than both *S. album* and the hybrid *S. album* × *S. yasi*, both of which are also commonly planted in Fiji and Tonga, although data that confirm this are lacking. Thomson et al. 2020 argue that it makes sense for Fijian and Tongan industry to focus on *S. yasi* and develop a market niche for its product that is differentiated from *S. album*, large volumes of which are becoming available from plantations in Australia and elsewhere. Heartwood oil yield and oil quality are key selection traits for the species, with the established point of the international standard for *S. album* oil established by the International Organization for Standardization (ISO 2002). For progress to be made through selection and breeding, more information on the development and genetic variation of these traits is required. Given that common-garden progeny trials are yet to be established, information must be gathered from wild and cultivated trees.

There is a general tendency in both Fiji and Tonga to cut trees as soon as they are perceived to have merchantable heartwood, as evidenced by the size classes of available trees surveyed and measured in Fiji and Tonga in 2015 (Bush et al. 2016). This often results in trees of around 15 years of age being harvested. Consequently, few trees older than 20 years are available for measurement. Making early selections for heartwood and oil traits would be highly advantageous for tree breeding because the genetic gain per unit time will be increased. Examination of whether young-aged trees have

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adequately developed heartwood and oil profiles is a priority, therefore, both for advising growers on when to harvest and for assessing an appropriate age for the selection of breeding material.

There are many published reports of sandalwood oil yield, with percentages ranging from near zero to the low tens. Most studies have only examined a small number of trees. Tree age, sampling position in the tree and method of sampling, extraction and chemical analysis are also likely to have a bearing on results, making comparisons among studies difficult. Oil-yield estimates are consequently variable, even within a single species. For example, the best-studied species, *S. album*, has recorded yields between about 1.5% and as high as 9% (Ral 1990; Shankaranarayana et al. 1998; Jones et al. 2006; Subasinghe et al. 2013; Bisht et al. 2019), bearing in mind that different extraction (e.g. steam distillation, solvent extraction with different solvents) and assay methods (gas chromatography – GC, liquid chromatography, near infrared reflectance – NIR) can give different relative yields of oil constituents (Piggott et al. 1997). The commercial yield of *S. album* obtained by steam distillation of ground bulk heartwood is typically 60 kg $t^{-1}$ (6%), according to Ral (1990), although this estimate may have declined since the 1990s due to the increasing scarcity of high-quality heartwood. The average yield from 264 samples of *S. austrocaledonicum* (Page et al. 2010), the largest study of the oil properties of any sandalwood species to date, was reported as 2.2% (range 0.1–8%), using solvent extracts. A recent study of 126 *Santalum macgregorii* F. Muell. cores (Page, Jeffrey et al. 2020), also using solvent extraction, found yields of less than 1% for all samples.

Commercially acceptable Indian sandalwood (*S. album*) should have an *α*-santalol component accounting for 41–55% of total oil and *β*-santalol accounting for 16–24% (ISO 2002), implying that trees must have at least 57% total santalol content to be commercially acceptable. *Santalum austrocaledonicum* from New Caledonia is similar to *S. album* in composition (Braun et al. 2005). This also applies to *S. austrocaledonicum* from parts of Vanuatu, although there is marked variation within and among island provenances there (Page et al. 2010). As the key *α*- and *β*-santalol components tend to be lower than in *S. album* and other components are significant, a draft standard for *S. austrocaledonicum* oil has been proposed (Dowell 2020), with ranges for seven components including *α*-santalol (38–45%) and *β*-santalol (12–17%). Yan et al. (2020) investigated the use of NIR techniques for characterising the oils of various sandalwood species. Over five samples of *S. yasi*, the ranges of *α*- and *β*-santalol were 39–47% and 19–31%, respectively. Doran et al. (2005), reporting on the largest sample of *S. yasi* studied to date (solvent-extracted cores from 21 trees, mostly <20 years old), found that, of the 17 trees with measurable santalols, *α*-santalol averaged 43% (range 16–57%) and *β*-santalol averaged 24% (10–34%).

The objective of the study reported here was to examine the amount and quality of heartwood oils in *Santalum* trees estimated to be between 10 and 20 years old. Trees around 15 years old are often harvested, although this is generally considered to be too young. The main focus of the study was on *S. yasi*, but a small number of samples of other taxa were also included. In terms of oil quality, the main interest was in the santalol components, which are the components of prime commercial importance.

## Methods

A total of 82 trees were sampled in the field in Tonga (Tongatapu, ʻEua and Vavau) and Fiji (Viti Levu and Vanua Levu), and four *S. austrocaledonicum* were sampled in Vanuatu (two each from Espiritu Santo and Erromango) (Table 1). The samples included both wild accessions and cultivated trees. Most of the trees in Fiji and Tonga had been included in an inventory conducted in 2015 and their taxonomic identity confirmed using morphological and DNA markers (Bush et al. 2016).

The majority of trees were sampled by taking a 4.3 mm core at approximately 30 cm above ground using a hand-powered corer (Haglof, Sweden) and their diameter over bark (DOB) measured. Sampling at exactly this height was not always possible due to branching and/or extreme fluting, in which case the core was taken slightly lower or higher. The cores were wrapped in plastic in the field to avoid rapid desiccation, shrinkage and warpage. They were then placed in a sealed container with silica gel and transported back to a laboratory in Canberra, Australia, within ten days of collection. There, the cores were stored in a constant-temperature room (19°C) to equilibrate to air-dry condition, which was determined by accurately weighing the cores until their masses were stable. In most cases, the heartwood extent was difficult to determine visually in the cores. To assist, each core was stained with a potassium iodide/iodine solution, an indicator of starch (which is usually more prevalent in sapwood). The heartwood diameter (HD) was then measured and its extent marked on the core in pencil. Two trees were harvested destructively for reasons not related to this study and a wood disc taken at approximately 30 cm above ground level. Staining was not required to identify the heartwood in the discs. One tree had been recently harvested and its stump left in-ground: heartwood chips were taken from this tree at ground level. Estimates of total wood and heartwood areas were calculated assuming circular cross-sections using diameter under bark (DUB) and HD measured from the core. Percent heartwood (%HW) was calculated using these two estimated areas.

Heartwood samples were ground from the heartwood area of each air-dried core using a high-speed mini die grinder (Dremel, USA) and a 2.1 mm carbide end mill bit to produce 0.1 g of very fine shavings. The shavings were placed in a 2 ml GC vial fitted with a screw-fitting Teflon-coated septum. To each vial, a 1 ml aliquot of a solution containing 0.0685 g of n-hexadecane ($C_{16}H_{32}$) in 100 ml (63.5456 g) of pentane was added. This $C_{16}$ compound was selected as an internal standard because it would have a similar flame ionisation detector response to the sesquiterpene ($C_{15}$) compounds of primary interest in this study and because it elutes in the GC trace in a region that does not contain any compounds present in the *Santalum* oil. The samples were extracted for one week prior to analysis.

Table 1. Summary of 86 samples, by taxon and country of origin

| | Country | | | |
|---|---|---|---|---|
| Species | Fiji | Tonga | Vanuatu | Total |
| *Santalum yasi* | 30 | 37 | - | 67 |
| *S. album* | 2 | 6 | - | 8 |
| *S. album* × *S. yasi* | 5 | 2 | - | 7 |
| *S. austrocaledonicum* | - | - | 4 | 4 |
| Total | 37 | 45 | 4 | 86 |

GC was carried out on a GC17 gas chromatograph (Shimadzu Corporation, Kyoto). Following the protocol developed for *S. macgregorii* by Brophy et al. (2009), a WCOT BP-20 column (60 m × 0.25 mm, 0.25 µm film thickness) was programmed from 50°C to 225°C at 3°C $min^{-1}$ with helium carrier gas at 1 mL $min^{-1}$. GC integrations were performed on a SMAD electronic integrator without correction factors. Inspection of GC results indicated that a small proportion of samples had (*E,E*)-farnesol present. As (*E,E*)-farnesol elutes almost simultaneously with (*Z*)-*α*-santalol and is therefore difficult to quantify accurately using GC alone, follow-up analysis of these samples was done with gas chromatography/mass spectroscopy (GC/MS) to confirm the presence of (*E,E*)-farnesol.

A Shimadzu 2010 GC/MS operating at 70 eV ionisation energy was used. The GC column was a BP-5 (30 m x 0.25 mm x 0.25 µm) programmed from 35°C to 250°C at 5°C $min^{-1}$ with helium as the carrier gas, the injector temperature was 250°C. Mass spectra were recorded in electron impact mode at 70 eV, scanning the 41–450 m/z range. Interface and source temperatures were 250°C and 220°C, respectively, with 1 scan $s^{-1}$ cycle time.

Oil yield (w/w) was calculated by comparing the sum of peak areas of all oil components with that of the peak area of the known mass of hexadecane standard and the known mass of ground wood sample.

Compound identities were made by comparing them with known retention times and mass spectra. The main focus of the study was (*Z*)-*α*- and (*Z*)-*β*-santalol. Minor compounds such as *α*-santalene, (*Z*)-*α*-santalal, (*Z*)-*β*-santalal, (*E*)-*epi*-*β*-santalal and (*E*)-*β*-santalol were detected in some samples, but these are not reported here as they constituted only very minor oil components; where total santalols are reported hereafter we refer to the sum of (*Z*)-*α*-santalol and (*Z*)-*β*-santalol components. We noted significant levels of (*E,E*)-farnesol, (*Z*)-lanceol and (*Z*)-nuciferol in some samples.

Linear regression models among variables were implemented with the FIT directive in Genstat 18 (VSN International, Hemel Hempstead, UK). Comparisons among samples from different countries and taxa were made using the Genstat REML directive, with Country and Taxon fitted as fixed effects.

## Results

Trees ranged in size from 70 mm to 260 mm DOB. Core samples ranged in size from less than 50 mm to greater than 200 mm DUB (Fig. 1). The regression relationship between DOB and DUB was highly significant ($P < 0.001$) but only moderately strong ($r^2 = 0.43$) due to stem eccentricity and the fluting of many trees.

The linear relationship is given by

$$DUB = 0.46(DOB) + 30.7 \qquad \text{(Eq. 1)}$$

Given that the number of data points of *S. album, S. album* × *S. yasi* and *S. austrocaledonicum* are low (Table 1), fitting separate relationships for each taxon was not appropriate.

Ideally, each tree would have been cored through its longest axis and/or through two perpendicular axes to estimate ellipsis, but this was not possible in many cases due to tight access caused by nearby host trees, low branching and the reluctance of owners to cause additional damage to trees associated with double coring. There was a significant positive regression relationship between DUB and HD ($P < 0.001$), with $r^2 = 0.41$. Staining of cores helped determine the heartwood–sapwood boundary, but this boundary was still difficult to distinguish in some cases due to the presence of starch throughout the sap and heartwood, as has also been found in *S. album* (Jones et al. 2006).

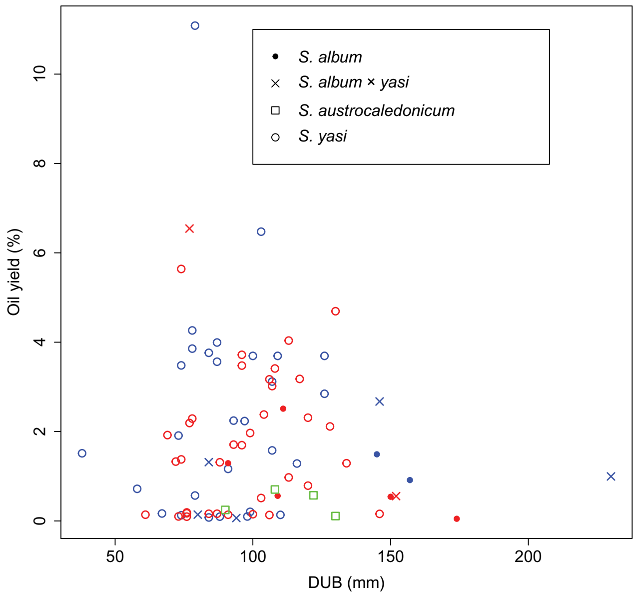


**Figure 1.** Relationship between tree size (diameter under bark (DUB) of the sample core or disc) and oil yield (percent of wood air-dry weight) in *Santalum album*, *S. austrocaledonicum*, *S. album* × *S. yasi* and *S. yasi*. Red, blue and green symbols denote trees from Tonga, Fiji and Vanuatu, respectively

Oil yield varied considerably among trees, from 0.05% to 11.8%, although, as seen in Figure 1, there was no significant relationship with tree size. Peaks corresponding with (*Z*)-*α*- and (*Z*)-*β*-santalol as well as (*E,E*)-farnesol and other minor compounds were clear in many of the samples (Fig. 2).

There were significant differences in HD and %HW among countries (Table 2). For both traits, the differences were attributable to the sample of four *S. austrocaledonicum* samples from Vanuatu, which had more heartwood in absolute terms and as a proportion than the mixed taxa from Fiji and Tonga. There was also a difference among countries in the three santalol traits, again because the Vanuatu samples had a markedly lower santalol content than the mixed taxa from the other countries. There was no significant difference in oil yield among the three countries.

There were significant differences among taxa in DUB, HD and %HW but no significant differences in oil yield (Table 3). There was a significant difference for each of the santalol traits, which was attributable to the very low santalol content of the four *S. austrocaledonicum* samples. *Santalum yasi* had a significantly lower HD than *S. album*, but the difference between *S. yasi* and the hybrid was not significant. The varying sample sizes and probable different age distributions of treatments should be borne in mind when considering differences among them.

There was no significant relationship between either DOB or DUB and heartwood oil yield ($P > 0.6$), nor was there a relationship between HD and oil yield ($P = 0.2$). There were strong, positive, pairwise relationships between total santalol, *α*-santalol, *β*-santalol and oil yield – that is, trees with a greater oil yield tended to have a higher proportion of the desirable santalol components (Fig. 3).

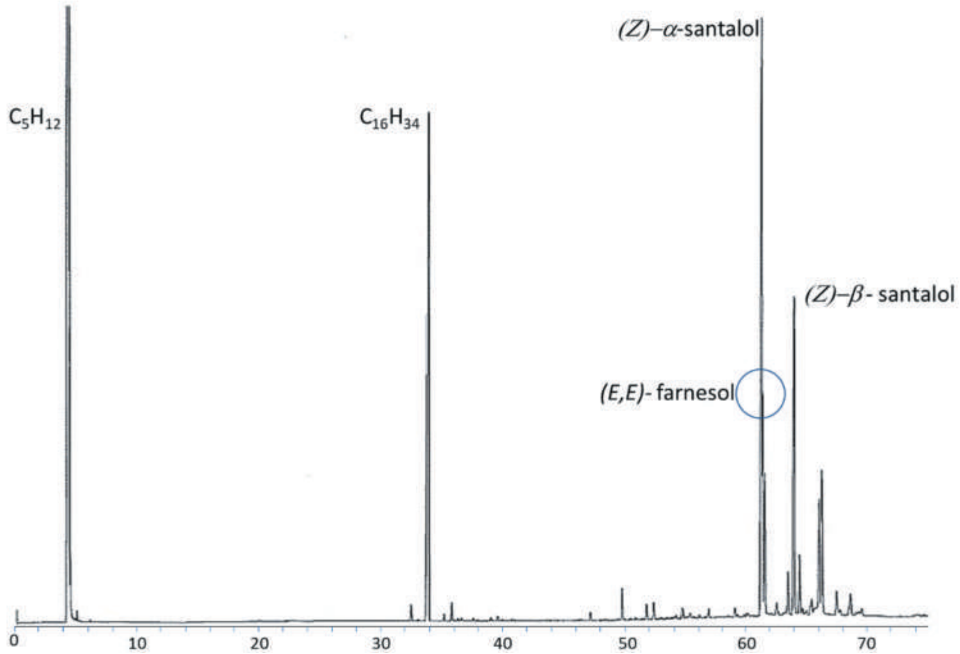


Figure 2. Example of *Santalum yasi* sample from 'Eua, Tonga, showing (L-R) a truncated peak for the pentane solvent and significant peaks for the hexadecane internal standard, *α*-santalol, (*E,E*)-farnesol (top of peak circled) and *β*-santalol. The latter three compounds corresponded to 28%, 16% and 9% of total oils in this sample, respectively

Table 2. Summary of adjusted trait means by country with average standard errors of difference (SED) among treatments and probability from F-test that the means are equal. Differences among pairs of country means (within traits) can be considered significant if they are greater than twice the SED

| Trait | Fiji | Tonga | Vanuatu | Av. SED | F probability |
|---|---|---|---|---|---|
| DUB (mm) | 98.5 | 101.3 | 112.5 | 12.24 | 0.640 |
| HD (mm) | 40.4 | 49.7 | 71.0 | 9.75 | 0.022 |
| %HW | 19% | 26% | 44% | 6% | 0.003 |
| Oil yield | 2.2 | 1.8 | 0.4 | 0.8 | 0.180 |
| Total santalol | 45.7 | 51.9 | 7.8 | 9.4 | 0.001 |
| *α*-santalol | 29.1 | 31.8 | 4.5 | 6.4 | 0.003 |
| *β*-santalol | 16.5 | 20.1 | 3.3 | 3.3 | <0.001 |

DUB = diameter under bark; HD = heartwood diameter; %HW = percent heartwood.

For those *S. yasi* trees (65% of samples) with an oil yield of >1%, total santalols averaged 62%, *α*-santalol averaged 39% and *β*-santalol 23% (Table 4). None of the four *S. austrocaledonicum* samples met the standard for either santalol compound. Small sample sizes of the other taxa precluded meaningful statistical comparison, although the four samples of *S. album* with >1% oil yield had higher *α*-santalol and similar *β*-santalol relative to *S. yasi*, while the three *S. album* × S. *yasi* specimens were very similar to *S. yasi*.

A total of 29 trees had oils that met the minimum *S. album* standard for both santalols, and an additional 19 met the *β*-santalol standard but did not meet the *α*-santalol standard: all but four of these trees had greater than 57% total santalols (i.e. the overall santalol content of the oil would meet the ISO standard for *S. album* if *β*-santalol were allowed to substitute for *α*-santalol). A large proportion of *S. yasi* trees (36% of all samples) had *β*-santalol proportions that exceeded the maximum prescribed for *S. album*, an occurrence also observed in one *S. album* sample and two hybrids.

In addition to the santalol oil components, we detected significant other minor and major compounds. The potentially allergenic (*E,E*)-farnesol compound that is often a significant component of *Santalum spicatum* (R.Br.) A. DC. oil (Moniodis et al. 2017) was often a minor component in those samples where it was identified, ranging between 5.5% and 15.8% of the total oil composition in six *S. yasi* samples and recording 2% in one *S. album* sample. This compound may constitute a smaller component of other samples, although estimation of small proportions of (*E,E*)-farnesol would have been unreliable due to the very similar retention time to *α*-santalol, as is usual for polar GC columns (Baldovini et al. 2011). Major oil components of the four *S. austrocaledonicum* samples included (*Z*)-lanceol and (*Z*)-nuciferol.

## Discussion

This study examined the heartwood content and oil yield of young-aged *S. yasi* from Fiji and Tonga, as well as some samples of *S. album, S. album* × *S. yasi* and *S. austrocaledonicum*. Although the oil yield and composition of a significant

Table 3. Summary of adjusted trait means by taxon with average standard errors of difference (SED) among treatments and probability from F-test that the means are equal. Differences among pairs of taxon means (within traits) can be considered significant if they are greater than twice the SED

| Trait | *Santalum yasi* | *S. album* | *S. album* × *S. yasi* | *S. austrocaledonicum* | Av. SED | F probability |
|---|---|---|---|---|---|---|
| DUB (mm) | 93.9 | 133.9 | 123.3 | 112.5 | 13.28 | <0.001 |
| HD (mm) | 43.03 | 65.86 | 47.71 | 71.00 | 11.68 | 0.014 |
| %HW | 23% | 28% | 13% | 44% | 8% | 0.015 |
| Oil yield | 2.0 | 1.3 | 1.8 | 0.4 | 0.9 | 0.300 |
| Total santalol | 48.6 | 58.1 | 43.0 | 7.8 | 11.3 | 0.003 |
| *α*-santalol | 30.1 | 37.6 | 27.3 | 4.5 | 7.6 | 0.005 |
| *β*-santalol | 18.5 | 20.6 | 15.8 | 3.3 | 4.3 | 0.003 |

DUB = diameter under bark; HD = heartwood diameter; %HW = percent heartwood.

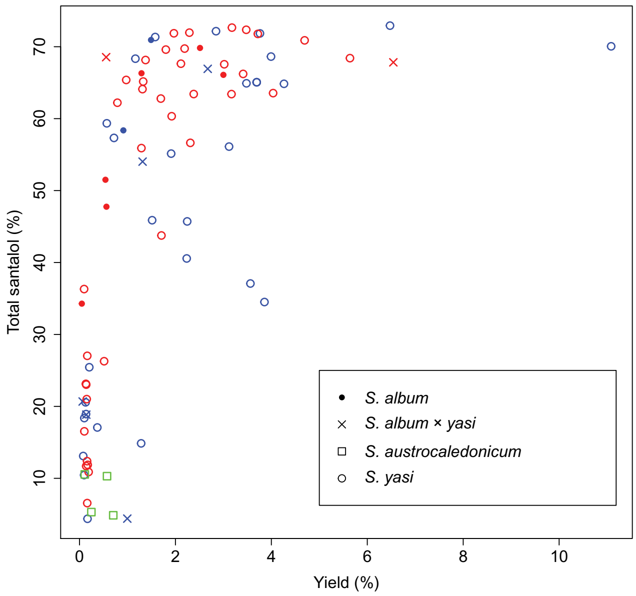


Figure 3. Relationship between oil yield (% of air-dry wood mass) and total santalol in *Santalum album*, *S. austrocaledonicum*, *S. album* × *S. yasi* and *S. yasi*. Red, blue and green symbols denote trees from Tonga, Fiji and Vanuatu, respectively

Table 4. Summary of heartwood and oil characters for number (*n*) of trees with >1% oil yield w/w and tally of samples that meet and/or exceed the International Organization for Standardization *Santalum album* standards (*α*-santalol 41–55%; *β*-santalol 16–24%) (ISO 2002)

| Trait | *Santalum yasi* | *S. album* | *S. album* × *S. yasi* | *S. austrocaledonicum* |
|---|---|---|---|---|
| *n* trees | *67* | *8* | *7* | *4* |
| *n* trees (oil >1%) | 43 | 4 | 3 | 0 |
| *α*-santalol | 38.8 | 46.4 | 40.2 | - |
| *β*-santalol | 23.0 | 21.9 | 22.8 | - |
| Total santalols | 61.8 | 68.3 | 62.9 | - |
| *n* meeting ISO minima | 22 | 4 | 3 | - |
| *n* [*α*-santalol >41%] | 23 | 4 | 3 | - |
| *n* [*β*-santalol >16%] | 41 | 7 | 4 | - |
| *n* [*β*-santalol >24%] | 24 | 1 | 2 | - |

proportion of *S. yasi* samples confirms that the species has considerable promise in terms of its oil yield and chemical profile, our results indicate that the harvesting of small-sized trees will result in variable heartwood oil yields and quality and therefore unreliable and suboptimal returns. A further implication is that selection for breeding programs should be delayed until the trees are older and larger, unless it can be shown that non-destructive sampling from lower in the bole gives results that will be reflective of mature oil yield and composition.

The finding that *S. yasi* trees with DUB between 100 mm and 150 mm have highly variable oil yields and chemical profiles has significant implications for both commercial harvesting and making early selections for the breeding program. Our sample includes trees that range between commercially acceptable, having good yields of oil with high santalol content, and commercially unacceptable. Applying Equation 1, these are trees that have a basal DOB between 150 mm and 210 mm. They are likely to be at ages between 12 and 20 years, assuming a growth rate of approximately 10 mm per year, which is the growth rate recorded for a wider sample of 200+ trees, including those studied here, inventoried in Fiji and Tonga (Bush et al. 2020). Very similar growth rates have been recorded for other Pacific sandalwood species, including *Santalum insulare* Bertero ex A.DC. and *S. austrocaledonicum* (Butaud 2012; Page et al. 2012).

The development of significant oil-yielding heartwood varied markedly among our samples, even among trees of approximately the same diameter, supporting the conclusion of Doran et al. (2005) that the age of initiation of oil-bearing heartwood varies considerably in sandalwood species, including *S. yasi*, *S. album* and their hybrid. Jones et al. (2006) also found that *S. album* oil yield from 15-year-old plantations was highly variable. Figure 1 shows that several trees from all studied taxa had oil yields below 2%, with many below 1%, and the average value across all trees was 1.9%. Conversely, numerous *S. yasi* and a single hybrid tree with a DUB of less than 100 mm had oil yields above 4%, which is well within the acceptable range for mature *S. album*. Our average was similar to the content of *S. austrocaledonicum* oils, which averaged 2.2% across 264 samples (Page et al. 2010). We therefore contend that the present result may reflect immaturity rather than trees that will not develop an acceptable yield at a later age.

It is possible that some of the sampled trees have already developed acceptable oil yields at close to ground level and/or in the upper root system. It is also the case that *S. album* and *S. yasi* (and assuming intermediate heritability of this trait, their hybrid) typically have santalols as major oil constituents. We think it likely that those samples that lack santalols and which are invariably from smaller trees (Fig. 3) are also likely to develop an oil profile that is richer in santalols as they mature. The development of heartwood, oil yield and oil profile is known to vary throughout an individual tree, usually with earlier and better development of heartwood and oils towards the base (e.g. Doran et al. 2005; Subasinghe et al. 2013; Page, Doran et al. 2020). It would be useful, therefore, to determine whether sampling at a very low point in the bole, just above, at, or below ground level, would give a more reliable estimate of yield and oil profile for the purpose of selection for breeding.

Our results for trees that had oil yields above about 1% were largely in agreement with those of Doran et al. (2005), who studied 21 samples of *S. yasi*, ten of *S. album* and eight of *S. album* × *S. yasi*. We concur that *S. yasi* between 10 and 20 years of age cannot be relied on to have produced mature heartwood, characterised by essential oil yields >1% and rich in santalols at around 30 cm above ground level. Our results also lend support to their observation that *S. yasi* tends to have a high proportion of *β*-santalol relative to the *S. album* standard. Although only 31% of our *S. yasi* samples met the ISO standard for *S. album*, 60% met the minimum *β*-santalol standard and 35% exceeded the allowable maximum. There is no intrinsic reason why a *β*-santalol-rich oil would be commercially undesirable. In fact, high *β*-santalol content may be highly desirable for perfumery applications, being described as more potent than *α*-santalol and responsible for many of the distinctive aromas associated with sandalwood products (see review in Baldovini et al. 2011). It may therefore be advantageous to *S. yasi* growers if a dedicated standard was created, as is being done for *S. austrocaledonicum* (Dowell 2020). This would assist in creating a differentiated market niche for the product, which in turn would increase profitability, potentially increase planting rates, and thereby increase returns to smallholders and aid species conservation.

Although non-destructive and therefore desirable, a possible problem with small-volume solvent-based extractions from 4 mm core 'microsamples' (typically around 0.1 g) is the very small proportion of the tree that is sampled. The presence of microvariations, even within a small heartwood zone, could result in errant whole-tree indications of oil yield and possibly composition. Brophy et al. (2009) discounted yield determinations they had made using solvent-extracted microsamples from *S. macgregorii* wood that had aged for several years on the assumption that the volatilisation of essential oils may have led to unreliable estimates, which may be an additional issue for comparisons with other published work.

Heartwood extractives in hardwoods are known to vary radially, with the outer heartwood typically containing compounds that are more active in resistance to biodeterioration than the inner heartwood (Rudman 1966). Radial variation in sandalwood was studied by Shankaranarayana et al. (1998), who concluded that the inner heartwood typically has higher santalol yields than the zone of transition between sapwood and heartwood. This is also likely to have a bearing on the results obtained from microsamples relative to the comparatively larger samples associated with steam distillation, which would necessitate using a more homogenised radial distribution of heartwood. Doran et al. (2005) found significant variation between oil-yield estimates determined using pentane extraction (same method as this study) and hydro-distilled samples based on 50–100 g of wood in two *S. yasi* samples. From a genetic improvement perspective, it is a high priority to determine whether solvent-based microsamples from small, non-destructive cores can reliably be used to determine oil yield. If they cannot, and destructive discing is required, selection and breeding for oil-related traits will be more challenging.

Because most of the samples are of unknown age, and the samples *of S. album, S. album* × *S. yasi* and *S. austrocaledonicum* are small, comparisons among countries and taxa should be viewed with circumspection. Further, the samples are from a range of growing conditions and have a wide range of different hosts, so neither taxon-by-environment nor taxon-by-host interactions can be taken into account. Clearly, this is not ideal, but it is probably the best available sample of *S. yasi* and hybrid *S. album* × *S. yasi* that can be accessed, given that there are no suitable trials of even-aged material and planting records are generally absent or unreliable. It is possible that genetic differences in *S. yasi* exist among countries and provenances within countries; indeed, it is likely, because both Fiji and Tonga comprise numerous islands and geneflow is probably restricted between populations on different islands. Page et al. (2010) identified subpopulation-level differences in %HW in a large sample of 264 *S. austrocaledonicum* trees growing *in situ* on seven island subpopulations in Vanuatu. Page, Jeffrey et al. (2020) similarly found provenance variation in morphological, wood and oil characters among five provenances of *S. macgregorii* in Papua New Guinea. The differences in these studies may be attributable to subpopulation genetic variation, differences among the sites, or interaction between these. The establishment of common-garden trials, where tree growth and heartwood development can properly be studied, and which will also serve as conservation stands, is an objective of the breeding and conservation strategy for *S. yasi* (Bush et al. 2020) and also a high priority for other sandalwood species, including *S. austrocaledonicum* (Page, Doran et al. 2020).

## Conclusion

This study, the most comprehensive published to date on *S. yasi* heartwood and oil yields, has confirmed earlier assertions that young-aged trees (less than 20 years old) are unlikely to have developed commercially acceptable heartwood beyond the upper roots and around ground level. We therefore strongly recommend delaying harvest until trees reach the age of 20 years. This does not bode well for making early sections for breeding: investigation of whether sampling at near-ground level, where heartwood may have more reliably developed in smaller-sized trees, is recommended. Trees that had developed acceptable oil yields (lower threshold of 1% w/w) tended to have acceptable overall santalol proportions relative to the ISO standard for *S. album*, although in many cases the proportion of $\beta$-santalol met the acceptable threshold while the proportion of $\alpha$-santalol did not. A high proportion of *S. yasi* trees exceeded the maximum allowable $\beta$-santalol limit. Given that $\beta$-santalol is a commercially desirable oil fraction, it may be prudent to develop a specific standard for *S. yasi* that will allow the development of a market niche for the product.


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