

Geographical variation in *Canarium indicum* (Burseraceae) nut characteristics across Vanuatu

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Abstract

Tropical forests in the Pacific region contain many tree species that bear edible nuts (kernels). *Canarium indicum* (canarium) is an overstorey tree indigenous to Melanesia that produces commercially valuable kernels due to their pleasant taste and high oil content. This study characterises natural variation in fruit, nut-in-shell (NIS) and kernels of *C. indicum* across eight islands in Vanuatu. Significant tree-to-tree variation in fruit, NIS and kernel characteristics as well as kernel recovery (kernel:NIS) was found. This variation was largely due to tree-to-tree differences and little of this variation could be attributed to location. There were significant linear correlations among fruit, NIS and kernel traits, including kernel mass with fruit mass (R^2 0.57) and kernel mass with NIS mass (R^2 0.56). Therefore, trees suitable for cultivation may be screened based on fruit and nut characters before making final selections based on kernel mass. Trees sampled over two fruiting seasons showed that kernel mass and kernel number varied significantly between years for 63.6% and 25.9% of the trees respectively. However, those trees that produced larger kernels in the first year of sampling, tended to also produce relatively larger kernels in subsequent years by rank. These results have important implications for further domestication of the species for planting in commercial agroforestry systems.

Introduction

Oceania is a region with many traditionally important edible nuts (Leakey et al. 2012). *Canarium indicum* (Burseraceae; canarium) is a tropical tree that produces highly nutritious edible nuts (kernels) that are an important local food resource (Thomson and Evans 2006). The species is indigenous to lowland rainforest of eastern Indonesia, Papua New Guinea (PNG), Vanuatu and Solomon Islands (Evans 1996). The development of *C. indicum* as a high value cash crop for edible kernels and oil extraction has been a focus of donor agency efforts in the Pacific for over two decades (Bunt and Leakey 2008; Evans 1996; Nevenimo et al. 2007; Wallace et al. 2012; Wallace et al. 2016; Wallace et al. 2021). Canarium kernels are commercially attractive due to their relatively large size, pleasant flavour and because they have a shell that is amenable to mechanical cracking. The nut-in-shell (NIS) are also robust and resistant to biological attack making them suitable for rudimentary storage facilities and transport once they have been dried (Bunt and Leakey 2008; Evans 1996; Nevenimo et al. 2008; Thomson and Evans 2006). Other *Canarium* spp. grow in the region, however their kernels are less palatable (*C. harveyi*) or smaller in size and are less widespread (*C. solomonense*) (Evans 1996). *C. vulgare* (kenari nut) in Indonesia (Lim 2012; Mailoa and Tulalessy 2021) and *C. ovatum* (pili nut) in the Philippines (Coronel 1996a; Coronel 1996b; Pham and Dumandan 2015) are commercialised for their edible kernels. The focus of this study, *C. indicum* produces highly desirable kernels that have existing domestic markets and potential for export (Wallace et al. 2021).

The fruit of *C. indicum* comprises of an outer skin (exocarp) and a fleshy mesocarp covering the nut-in-shell (NIS). The hard shell (endocarp) encloses the edible kernel that is covered by a brown-coloured, papery testa (Evans 1999a). The trees are mainly grown for their edible kernels, however, *C. indicum* is described as having multiple uses, highlighting its importance in Melanesian society (Evans 1999b).

Canarium is a food security crop that is relied upon to supplement staple crops, and particularly useful after extreme climatic events (Addinsall et al. 2016). The kernels have a high oil content (around 67 to 75%) that can be extracted and used for cooking and cosmetics (Bai et al. 2017; Djarkasi et al. 2011; Leakey et al. 2008). The fruit mesocarp can be used as fertiliser or animal feed (Evans 1996; Sam et al. 2002). Canarium trees are often used in multilayered agroforestry systems such as an overstorey crop for cocoa (Bai et al. 2017). Traditional use of its timber includes house construction, canoe fabrication, handicraft creation and use as fuel wood (Evans 1999a; Harrison and Karim 2016). In some areas, trees are traditionally important in commemorative plantings and the marking of boundaries (Evans 1999a). Further details on the status and use of *C. indicum* in Melanesia are given by Bourke (1996) for PNG; Henderson and Hancock 1988 and Evans (1991 and 1999a) for Solomon Islands; Evans (1999b), Wheatley (1992), Walter and Sam (1996) for Vanuatu.

Archaeological plant remains found throughout the species distribution support the view that *C. indicum* is the oldest domesticated tree species in the region (Bourke and Harwood 2009; Kirch 1989; Matthews and Gosden 1997; Yen 1996). Local people have selected, transplanted and tended to trees around coastal villages (Thomson and Evans 2006). Considerable variation exists in *C. indicum* fruit and nut properties between trees (Leakey et al. 2008; Randall et al. 2016). Trees are recognised as varying in nut shell and kernel colour, nut-in-shell (NIS) and kernel size, shape and mass, kernel recovery (kernel:NIS), thickness and the ease of cracking the shell, testa thickness and mass, as well as the number of kernels per shell and oil content (Leakey et al. 2008; Nevenimo et al. 2008; Randall et al. 2016; Siwatibau et al. 1998; Walton et al. 2016). Tree selection and domestication programs that select for traits with economic importance can greatly increase production and may be pivotal to commercial success (Nichols and Vanclay 2012). Thus far, donor-funded projects with an aim to commercialise the industry have focussed on market access, post-harvest processing systems and kernel nutrition (Wallace et al. 2012; Wallace et al. 2016; Wallace et al. 2021), while few studies have considered variation in fruit and nut morphology across its natural distribution.

There have been past attempts to characterise variations in canarium fruit and nut morphology in Vanuatu. The French research and development agency, ORSTOM, surveyed indigenous fruit and nuts in Vanuatu for the Department of Agriculture between 1991 and 1993. The study documented fruit, NIS and kernel size from 63 *C. indicum* trees across the Vanuatu archipelago (Walter and Sam 1993; Walter and Sam 1996). However, to our knowledge, the results of this study have not been published. The French agronomic research organisation, CIRAD, collected and planted seed from the ORSTOM collection following a workshop on South Pacific Indigenous Nuts in 1994 (Stevens et al. 1996). Unfortunately, all the seedlings and most of the information on the CIRAD collection have been lost (Evans 1999b). Following this, a Technical Report was prepared as part of the South Pacific Regional Initiative on Genetic Resources (SPRIG). Data were recorded from a relatively small number of trees (n = 24) that were targeted as a result of their superior nut morphotypes previously identified by the ORSTOM study (Evans 1999b). Thus, the tree selection was not random. Here we present the first research to characterise tree-to-tree variation in naturally occurring trees in Vanuatu, which will be used to select superior genotypes for propagation.

In the present study we aimed to enhance the availability of improved quality canarium seed through evaluation of the variation in fruit, nut and kernel characteristics of natural resources through systematic assessment. Specifically, we asked: 1) What is the proportion of variation held between fruits between individual trees, geographical subpopulations and islands? 2) Are any fruit and nut characteristics correlated with kernel-in-testa mass? 3) Are there variations in the number of single-, double- and triple-kernel fruits between trees? 4) Do trees that bear relatively large single-kernels also bear relatively large double-kernels? 5) Are morphological characteristics of nuts within trees consistent between years?

Methods

Site description

The survey area included eight islands north of Efate Island (latitudinal range 15.2–16.9°S) (Fig. 1). Mean annual rainfall ranges from 2500 mm in the south (Tonga) to almost 3000mm in the north (Pentecost and Santo). Mean annual temperature ranges from 24.9°C (south Malekula) to 25.8°C (south Santo). Canarium were found along the coastal fringe, water courses, undulating terrain and amongst gardens. They occurred on all directional aspects. Most trees (70%) occurred on gentle slopes (0–3°) with 25% on moderate slopes (4–10°) and 5% on steep slopes (11–23°). The altitude ranged from 10 to 434 meters above sea level (masl) with 82% occurring below 200m and 7% above 300m. The geology was primarily reef derived carbonate, but some with basaltic-andesite volcanic igneous rock. Soil textures ranged from clay loam (58%), loam (25%), sandy loam (15%) to sandy clay loam (2%). Soil pH ranged from 6.0 to 8.5 with 7% of trees occurring in acidic (6.0-6.5) soils, 25% slightly acidic (6.5-7.0), 34% neutral (7.0), 17% slightly basic (7.0-7.5), 10% basic (7.5-8.0) and 7% strongly basic (8.0-8.5). The Islands of Ambrym, Paama, and Tonga had a pH range of 7.0 or less and Epi's soil pH range was 7.0 or above. Soil colour was always dark ranging from brown to black. A reddish-brown colour was apparent at most tree locations on Malo and Santo, and black soil was prominent on Ambrym and Paama. Overall, 68% of trees occurred on brown soil, 14% on reddish brown and 18% on blackish soil.

Fruit sampling strategy

Canarium indicum is widely distributed across the northern islands of Vanuatu. Sampling locations were based on important source areas for the canarium market. In total, 256 trees were sampled from eight of the northern islands (Fig. 1). Of these trees, 82 were sampled in 2017 from two islands, Santo (east n = 25; south n = 5) and south-west Malekula (n = 52). The remaining 174 trees were sampled in 2018 across seven islands, north Malekula (n = 47); Epi (Epi1, n = 18; Epi2, n = 12); Pentecost (central, n = 13; south-west, n = 32); Malo (n = 10); Ambrym (n = 20); Tonga (n = 12) and; Paama (n = 10). The locations and the number of trees sampled within islands were based on the size of the island, accessibility of the canarium trees and the number of mature fruits in the crown of the tree at the time of sampling. For example, 99 trees (over two years) were included from Malekula which is a large Island with putatively high morphological diversity (Walter 1994), whereas less trees were sampled from smaller Islands such as Paama and Malo.

Mature fruits (n = 50) were collected from each tree by either stoning, climbing, using a bamboo pole, or a throwing rope. Fruits were placed in a plastic mesh bag and transported back to a central location for processing. A random sample of 25 fruits from each tree were selected and their morphological traits characterised (total n = 6400).

Characterisation of fruits, nuts and kernels

The tree-to-tree morphological variation of *C. indicum* fruit, nut-in-shell (NIS) and kernel was completed by measuring the following on each of the fruit collected: fruit dimensions (length and width at widest point) and fruit mass (excluding fruit collected from Santo and SW Malekula); NIS dimensions (length and width at widest point) and fresh mass (at ~ 30% field moisture); kernel descriptors including dimensions (length, width, thickness), fresh kernel mass and testa mass. These data were used to calculate pulp mass, pulp thickness, shell mass, kernel recovery (K:NIS; [wet kernel mass/ wet NIS mass] x 100). The number of kernels per shell was also recorded as NIS can contain either a single kernel, double kernel, or triple kernel, and an individual kernel is sometimes a twin kernel (two kernels with individual testas within a single locule).

Subjective assessments of the fruits were recorded for ease of cracking the NIS (1 = very easy to crack with developed fracture lines on the shell to 4 = very hard to crack; n = 102 trees). The ease of testa removal was also rated on a scale of 1 to 4. Observations of fruit and nut characteristics were also recorded during the data collection process.

Comparison of fruit, nut and kernel traits between years

To test for stability of morphological characteristics of fruit, NIS and kernels within trees, 25 fruits from selected trees that were assessed for fruit and nut morphological traits in 2017 or 2018 were resampled in 2019 (n = 81 trees). Fruit mass, individual kernel-in-testa fresh mass and the number of kernels per shell was recorded for each fruit sampled. Fruits from a subsample of these trees (n = 28) were recorded for kernel length, width and thickness.

Statistical analysis

The sample population refers to the combined data from all trees across all islands. These trees were then geographically grouped together into subpopulations according to the island they were located. The larger islands of Santo, Malekula, Epi and Pentecost were separated into two regions each to allow for distance-based comparison of morphological traits within island. Therefore, 12 sub-populations were sampled and analysed (Fig. 1).

Characterisation of fruits nuts and kernels

A nested random effects model was fitted to determine differences in kernel fresh mass between trees. Two separate analyses were conducted. The first used trees that produced more than 80% single-kernel

fruits (20–25 kernels per tree). Therefore, trees with a higher propensity for double- or triple-kernel fruits were excluded and only the kernel mass of single-kernel fruits was used in the analysis. Individual trees ($n = 152$) and subpopulation ($n = 12$) were included as random effects (package: 'lme4'; (Bates et al. 2015)). The second analysis included double-kernel fruits only where the combined kernel mass per fruit was used in the analysis. Only trees with more than eight observations per tree were included. Again, individual trees ($n = 77$) and subpopulation ($n = 12$) were included as random effects (package: 'lme4'; (Bates et al. 2015)). For each analysis, the intraclass correlation was calculated to determine how much variation in kernel mass is accounted for by each random effect (package: 'sjstats'; (Leakey et al. 2008; Lüdtke 2021)). The most parsimonious model was chosen and the island from which the trees were located was not included in either of the nested designs.

Kernel recovery is the proportion of nut-in-shell (NIS) that is kernel-in-testa by mass (Kernel:NIS) and was analysed using a beta regression model (package 'betareg'; (Cribari-Neto and Zeileis 2010)). Two separate analyses were conducted for single- ($n = 226$ trees) and double-kernel ($n = 77$ trees) fruits. Trees with less than eight observations in an individual analysis were excluded, therefore the sample size ranged from 8–25 single- or double-kernel fruits per tree per year. Where differences were detected, we applied a Tukey's HSD test.

A Kendall's tau-rank correlation coefficient was calculated to determine the association in the rank order of an individual tree's mean single-kernel fresh mass and mean combined double-kernel fresh mass between trees. Trees with less than 8 observations of either single or double kernels were excluded, therefore 47 trees were included in the analysis. A Welch Two Sample t-test was performed to determine the differences in kernel characteristics: mass, length, width, and thickness between single- and double-kernel fruits. Similarly, a Wilcoxon Signed Ranks Test was used to analyse kernel recovery.

Pearson Correlations were performed ($n = 4806$) to determine relationships between the measured fruit and nut characteristics. Spearman Rank Correlations were used to assess relationships between kernel recovery and other measured traits (package 'Hmisc'; (Harrell 2021)). Characteristics included were fruit mass, fruit length, fruit width, NIS mass, NIS length, NIS width, shell mass, kernel fresh mass, KITF mass, kernel length, testa fresh mass, kernel width, kernel thickness, kernel:testa (%), kernel:NIS (%). Correlations using single kernel fruits and double kernel fruits were performed separately. For double-kernel fruits, the combined mass of the two kernels was used. All analysis were performed in R v1.4.1717.

Comparison of fruit nut and kernel traits between years

A Student t-test was used to compare kernel-in-testa fresh (KITF) mass ($n = 60$ trees), kernel length ($n = 22$ trees) and fruit mass ($n = 37$ trees) between years for individual trees. Equal variances between years were confirmed with a Levene's Test. Double- and triple-kernel fruits were excluded from the analysis as were trees with less than eight single-kernel samples. A Mann Whitney U test was used to determine differences between the number of kernels per shell within trees ($n = 81$ trees) between years using all 25 sampled fruits from each tree for each year. A Kendall's tau- rank correlation coefficient was calculated to determine the association in the rank order of an individual tree's mean KITF mass (2017, $n = 17$; 2018, n

= 41), mean kernel length (2017, $n = 8$; 2018, $n = 12$), mean fruit mass (2017, not recorded; 2018, $n = 37$) and mean number of kernels (2017, $n = 32$; 2018, $n = 50$) between years. Two separate analyses were conducted for fruits first sampled from trees in different years (2017 and 2018). Analyses were performed using IBM SPSS v 26.

Results

Characterisation of fruits, nuts and kernels

The pulp (exocarp and mesocarp) component comprises the majority of the fruit weight (Fig. 2). Whereas the fresh NIS make up approximately one third of the overall fruit weight (Fig. 2).

The tree with the largest single kernels (tree MAL022, mean 4.63 ± 0.08 g) had kernels almost four times greater in mass than the tree with the smallest single kernels (tree SAN004, mean 1.28 ± 0.06 g) (Fig. 3). Approximately one fifth of individual trees (19.35%) possessed single kernels that had a mean fresh mass greater than 3 g. These individual trees with the largest mean kernel mass were widely spread across nine of the 12 subpopulations (Fig. 3). This suggests that this trait is not confined to discrete locations, which was confirmed in the linear mixed-model analysis.

There were significant differences in single-kernel fresh mass between trees. The linear mixed-model indicated that tree-to-tree variability mostly contributed to differences in single-kernel mass with a standard deviation of 0.526 and 95% confidence interval of 0.47 to 0.59. The subpopulation of the tree's origin had a small influence with a standard deviation of 0.149 and a 95% confidence interval of 0 to 0.30. The intraclass correlation determined that individual trees accounted for 68.3% and subpopulation accounted for 5.5% of the overall variation in single-kernel fresh mass.

There were tree-to-tree differences in the combined kernel mass of double-kernel fruits with the sampled trees bearing an average mass of as little as 1.3 ± 0.04 g (tree MAL025) and as large as 6.66 ± 0.22 g (tree MAL003). The linear mixed model analysis using double-kernel fruits revealed significant differences between trees. Tree-to-tree variability contributed the most to differences in the combined kernel mass of double-kernel fruits with a standard deviation of 1.026 and 95% confidence interval of 0.87 to 1.22. The subpopulation of the tree's origin had a small influence with a standard deviation of 0.245 and a 95% confidence interval of 0 to 0.62. The intraclass correlation determined that individual trees accounted for 71.7% and subpopulation accounted for 4.1% of the overall variation in the combined double-kernel fresh mass.

Significant positive associations were found in the rank order of single- and combined double-kernel fresh mass between trees indicating that those trees that yielded larger single kernels also had larger double kernels ($\tau_b = 0.680$, $P < 0.001$).

Single-kernels had a significantly greater mass than individual kernels extracted from double kernel fruits ($t_{(2648.6)} = 27.545$, $P < 0.001$). However, when the combined mass of kernels from double-kernel fruits was

considered, these had a significantly greater overall mass compared to single-kernels ($t_{(1731.6)} = -46.877$, $P < 0.001$). This pattern also applied to kernel dimensions where kernels from single-kernel fruits were significantly larger than kernels from double-kernel fruits for length ($t_{(2419.9)} = 2.829$, $P = 0.005$) and width ($t_{(2622.1)} = 3.4664$, $P < 0.001$). Despite these differences, most (78.7%) of the trees sampled met the kernel size specifications outlined in Wallace et al. (2021) with a length greater than 30 mm and wider than 13 mm (Fig. 4). Mean single-kernel length, and width across the sampled trees ranged from 23.7–42.2 mm and 13.9–24.3 mm respectively. Dimensions of individual kernels from double-kernel fruits ranged from 20.4–41.2 mm in length and 13.7–24.6 mm in width.

Two separate analyses determined significant differences in the kernel recovery of single-kernels ($F_{(223)} = 71.5$, $P < 0.001$) and double-kernels ($F_{(76)} = 117.8$, $P < 0.001$) between trees. Kernel recovery for single-kernel fruits ranged from a minimum 0.058, median 0.21 and maximum 0.42. A total of 119 trees achieved a kernel recovery of 0.25 (1:3; Kernel:NIS) representing 52.6% of all trees sampled. The kernel recovery for double-kernel fruits ranged from a minimum of 0.08, median of 0.26 and maximum of 0.54. Double-kernel fruits achieved a significantly greater kernel recovery overall compared to single-kernel fruits ($Z = 1047$, $P < 0.001$).

Number of kernels per nut

Variation in the proportion of double kernels within a tree was recorded (Table 1). Over half of the trees (59.4%) had less than 20% double kernel fruits, and solely double kernel fruits were recorded in four trees (1.6%).

At least one twin kernel was observed in 25% of the sampled trees. Most of these (80%) had ≤ 4 twin kernel fruits, however, 11 trees (17%) had ≤ 8 twins and two trees (3%) had more than 50% twins (Tree SAN023, $n = 20$ fruit; Tree EPI003, $n = 13$ fruit). Twin kernels occurred in both single and double kernel fruits where either one or both kernels were twins. Triple kernels, where a single kernel developed in each of the three locules, were rarely encountered (0.001%).

Subjective assessment of nut cracking and testa removal

Ease of testa removal is an important consideration for kernel processors. Testa removal was classified as easy on all trees, with only twin kernels having a minor degree of difficulty. Ease of cracking the shell and extracting the kernel varied between trees and were scored the same for all nuts within a tree. More than half (60.78%) of the 102 trees assessed produced nuts that were easy to crack and extract whole kernels. In addition, 15.69% of the assessed trees were rated very easy to crack with shells displaying clear fracture lines forming an operculum (locally known as ‘coffin-lid’ or easy-to-open shell; (Evans 1999b; Nevenimo et al. 2008)). Conversely, 10.78% were rated moderately difficult to crack and or extract whole kernels and another 12.75% of assessed trees were rated extremely difficult to crack and extract the kernel whole.

Correlations with morphological traits

Correlations were performed among the morphological traits recorded for the fruit, NIS and kernels using single kernel fruits. The results suggest that 22 out of 105 correlations were statistically significant, being greater than or equal to $r(4804) \geq .65$, $P < .001$ (Supplementary information – Table 1). The relationship between kernel-in-testa fresh (KITF) mass and other traits can help to predict the kernel mass before cracking single kernel fruits. Fruit mass ($r(4804) = 0.752$) and nut-in-shell (NIS) mass ($r(4804) = 0.733$) were the best predictors of KITF mass (Fig. 5). KITF mass had a stronger linear association each with fruit length and width ($r(4400) = 0.552$ and $r(4396) = 0.628$ respectively) compared with each NIS length and width ($r(4545) = 0.489$ and $r(4541) = 0.531$ respectively). Kernel recovery (kernel:NIS) was moderately linearly related to KITF mass ($r(4552) = 0.519$) and kernel fresh mass ($r(4597) = 0.561$) but to none of the other fruit or nut traits.

Significant correlations were also found between fruit, nut and kernel traits of double kernel fruits (Supplementary information – Table 2). Strong linear relationships were recorded between KITF (g) with each of fruit mass ($r(708) = 0.728$) and NIS mass ($r(1437) = 0.755$). Kernel recovery was again moderately linearly related to KITF mass ($r(1437) = 0.576$) and kernel fresh mass ($r(1449) = 0.601$) but to none of the other fruit or nut traits.

Comparison between years

More than half of the trees assessed for fresh kernel-in-testa (KITF) mass (61.6%) and kernel length (63.6%) showed significant differences in these traits between years (Student t-test, $P < 0.05$). There were also significant differences in 15 of the 37 trees (40.5%) measured for fruit mass between years (Student t-test, $P < 0.05$). However, significant positive associations were found in the rank order of all calculated traits between years 2017 and 2019 (mean KITF mass, $\tau_b = 0.426$, Fig. 6; $P < 0.05$; mean kernel length, $\tau_b = 0.741$, $P < 0.05$) and also between years 2018 and 2019 (mean KITF mass, $\tau_b = 0.495$, $P < 0.01$, Fig. 6; mean kernel length, $\tau_b = 0.794$, $P < 0.01$; mean fruit mass, $\tau_b = 0.646$, $P < 0.01$).

Approximately one quarter (25.9%) of the trees reported significant differences in the number of single kernel fruits recorded within the tree between years (Mann-Whitney U test, $P < 0.05$). A significant association was found in the rank of the mean number of kernels per tree between trees recorded in year 2017 and resampled in 2019 ($\tau_b = 0.601$, $P < 0.01$) as well as between years 2018 and 2019 ($\tau_b = 0.379$, $P < 0.01$).

Discussion

With significant tree-to-tree variation evident in economically important traits including kernel mass and kernel recovery, *Canarium indium* is a suitable candidate tree species for improvement through domestication. This result is particularly important given it is the focus of commercialisation efforts to benefit stakeholders along its value chain (Carias et al. in press). Improvement must be based on individual tree selection rather than provenance-based domestication, because little of the variation was attributed to sampling location. There were significant linear correlations among fruit, nut-in-shell (NIS)

and kernel traits, particularly between kernel mass and fruit mass and between kernel mass and NIS mass. This means that when screening for trees with large kernel mass, they can first be selected on fruit and NIS mass before undertaking further detailed assessments. Trees were found to primarily have single-kernel fruits. Double kernel fruits were relatively common and triple kernel fruits were rare. Twin kernels occurred in both single and double kernel fruits. More than half of the trees that were sampled over two fruiting seasons varied significantly between years in mean kernel mass (63.6%), and one quarter (25.9%) of trees varied significantly in kernel number. However, trees that produced larger kernels in the first year of sampling, tended to maintain their rank among the trees and produced relatively larger kernels in the second year of sampling. The results from this study have important implications for further domestication of the species to make selections that are desirable for planting in commercial agroforestry systems. Small-holder farmers participating in the canarium nut extractive economy will also benefit when superior germplasm is disseminated for new plantings.

Characterisation of fruits, nuts and kernels

This study confirmed that tree-to-tree differences in fruit, nut-in-shell (NIS) and kernel dimensions and mass as well as kernel recovery (kernel:NIS) were highly significant. Little of this variation was attributed to the subpopulation level. This suggests that there has been no effective isolation between subpopulations due to anthropogenic seed movement between islands, and human selection has not occurred more strongly in any given location. This is consistent with studies of canarium trees in other locations in Vanuatu (Evans 1999b), Papua New Guinea (Nevenimo et al. 2007; Leaky et al. 2008) and Solomon Islands. Randall et al. (2016) found that variation in economic traits for canarium nut production is high and continuous, and significant tree-to-tree variations exist with no significant differences between populations.

The large variation in the kernel morphology of *C. indicum* provides the opportunity to select and breed trees with desirable traits for commercial production. Higher market prices for edible nuts can be achieved for larger and less damaged kernel with a kernel recovery above 0.25 (1:3 Kernel:NIS) (Adeigbe et al. 2016; Leakey et al. 2008). Kernel mass is an important trait to the industry because larger kernels generally require fewer relative inputs from both producer and processor. We found that trees with the largest mean single kernels were almost four times greater in mass than the smallest single kernels (4.63 vs 1.28 g), which is very similar to previous studies (1–4 g) (Evans 1999b; Leakey et al. 2008; Randall et al. 2016). Almost 20% of the trees met the threshold (> 3 g kernel mass) considered for improvement in kernel quality and uniformity (Leaky et al. 2008).

Significant differences in fruit mass occurred in approximately 40% of the trees measured between years. Variation between years in kernel traits such as mass, kernel recovery, and kernel number is not uncommon and has been reported in other nut crops such as hazelnuts (Bostan and Günay 2009; Cristofori et al. 2008). Importantly in our study, those trees that produced larger kernels in the first year of sampling, tended to maintain their rank amongst the trees and again produced larger kernels when

measured in a subsequent season. This gives confidence that the trees selected in any given season will continue to produce larger kernels compared to other trees in the population across other seasons.

Kernel recovery is of interest for processors seeking to maximise return for effort and is an important selection criterion for other commercialised nuts (Arzani et al. 2008). Just over half (52.6%) of the trees sampled in our study had a kernel recovery of at least 0.25. This means that tree selections based on this attribute can increase efficiency in terms of transport mass per unit of kernel recovered. This is particularly important for canarium since shell mass comprises over one quarter of the total fruit mass.

Correlations of fruit components

Correlating kernel mass to other traits, such as fruit and NIS mass, can help to determine kernel mass by grading fruit. Positive correlation was found between kernel-in-testa (KIT) fresh mass and both fruit mass and NIS mass ($r = 0.752$ and 0.733 respectively). Research elsewhere suggests that NIS circumference is a moderately good predictor of KIT mass (Evans, 1991). Our results conform with Evans (1999b) who found significant correlation between NIS dry mass and KIT dry mass. This means that high mass fruits and NIS typically also produce higher mass kernels. This can help in grading NIS to accurately cost the purchasing of kernels without the need to crack the NIS (Evans 1996).

These results are in contrast with a study of canarium nut characteristics in young (6 year) plantation trees in Solomon Islands, which found that trees with the heaviest average NIS mass did not produce the heaviest kernel (Randall et al. 2016). It is possible tree age may influence the relationship between NIS and kernel mass, therefore selection for kernel traits may need to occur in only mature trees. Future canarium fruit collections that aim to improve overall kernel mass should initially target trees with high fruit mass to select potential candidates for NIS and kernel trait assessment. Caution must be applied if using fruit characteristic predictors of kernel mass as it is unknown whether the NIS contains a single or double kernel.

Kernel Number

Canarium nuts most commonly contain one kernel with the other two locules remaining undeveloped (single-kernel fruit). However, many fruits contain two kernels and one undeveloped locule (double-kernel fruit), or rarely, fruits contain three kernels (triple-kernel fruit). A combination of single- and double-kernel fruits occurred in approximately 75% of trees sampled and the remaining proportion contained exclusively single kernel fruits. The proportion of single- to double-kernel varied between trees and some trees have a greater frequency of double-kernel fruits than others. Very little is known about the pollination biology of the species and whether kernel number is maternally influenced or is related to pollination levels. However, trees that produced a high proportion of double-kernel fruits in the first year of sampling tended to maintain their rank and produce an equivalent proportion of double-kernel fruits in the second year of sampling. This infers that the factors influencing this trait stayed relatively constant between years. This could be a combination of maternal genotype, resource allocation and/ or pollination

success. Further investigation is required to determine what controls this important trait and its heritability.

The mass, length, and width of the kernels was found to be significantly lower in individual kernels from double-kernel fruits compared with single-kernel fruits, but the combined kernel mass of the double kernels was on average higher. Kernel recovery was also significantly higher in double-kernel NIS compared to single-kernel NIS. In an NIS buying model, this makes double-kernel fruits overall more efficient to transport and crack per unit of kernel. However, double-kernel fruits are generally less preferred by large-scale commercial processors because of their smaller individual kernel mass and greater difficulty in removing two whole kernels from the shell (Wallace et al. 2021).

Some NIS contain twins where two individual kernels with separate testas are present within a single locule. Twins occurred in both single- and double-kernel NIS, and in the latter either one or both kernels were twins. This appeared to randomly occur within trees as only occasionally one or two NIS contained twin kernels, although some trees had a greater propensity for twin kernels. The presence of two ovules within each of the three locules indicates that twin kernels are biologically possible in all trees. It is unclear if twin kernels are related to pollination levels when fertilisation of both ovules within a locule occurs, and if so, if maternal barriers may preclude this from occurring more frequently. Twin kernels are undesirable for processors due to the small kernel size and additional testa removal time required (Wallace et al. 2021).

Testa removal and nut cracking

Ease of testa removal is an important consideration for processors as it is a labour intensive process (Wallace et al. 2021). The testa was removed from fresh kernels in this study, and almost always liberated in one piece without breaking. Testa removal was classified as easy on single and double kernels from all trees, with only twin kernels having a limited degree of difficulty. Testa removal was performed on fresh kernels and does not reflect the potential resistance once the NIS or KIT has been dried. Drying NIS or KIT results in the testa shrinking and adhering to the kernel thereby making it more difficult to remove (Wallace et al., 2010).

Ease of cracking the NIS remained consistent within a tree and most (60.78%) trees had NIS that were easy to crack and extract whole kernels. Whole kernels are preferred by the market and kernels must be whole to conform to premium-graded nuts (Wallace et al. 2021; Walton and Wallace 2005). Around 16% of trees produced NIS that formed a 'coffin-lid' and were rated very-easy to crack. Such nuts can be considered desirable among resource owners that consume the kernels immediately or sell them fresh in local markets (Nevenimo et al. 2008). However, this is an undesirable trait when storing the NIS as they can open during storage and cause premature spoiling of the kernel (Evans 1999b). Very-easy to crack kernels also had a greater propensity for 'water kernels' where a clear liquid was found inside the intact testa.

Ease of cracking the NIS is an important trait that needs to be considered in conjunction with other selection criteria. For example, in this study, Tree MAL022 had the greatest kernel mass (4.63 g) of all the trees surveyed yet most of the NIS had a very-easy to crack 'coffin-lid' form rendering them unsuitable for long-term storage. Moreover, although the 'coffin-lid' was removed easily, the kernel was retained in the shell and difficult to extract whole, often resulting in a damaged kernel. Another tentatively elite tree that met the strict selection criteria (MAL038) was also difficult to extract whole kernels due to the way the shell broke during cracking. This can possibly be ameliorated by mechanical cracking and would be acceptable with an NIS buying model, but not a KIT buying model, where manual cracking by producers is likely to produce a high proportion of kernel pieces.

Selection and improvement

Natural populations of canarium trees have sufficient phenotypic variation to permit more intense selection and propagation of commercially desirable traits (Evans 1999b; Leakey et al. 2008). Amongst the traits of interest that identify superior canarium mother trees are kernel mass, high kernel recovery (kernel:NIS) and fruit traits such as an easy to crack shell and easy to extract kernel (Bunt and Leakey 2008; Leakey et al. 2008; Randall et al. 2016), which were investigated in this study.

The productivity of a canarium planting may depend on the seed sourced for its establishment. It is important to identify superior mother trees as the seed source to use in selection (progeny) trials. At least two kernel traits, kernel mass and kernel recovery, have been recommended when selecting superior trees (Leakey et al. 2008). Large kernels with a mean fresh mass of greater than 3 g are generally preferred by processors and considered to improve the economic viability of entities along the value chain (Leakey et al. 2008). In our study around 20% of trees produced kernels with a mean mass of 3 g or more. Further research is required to determine if a trade-off exists between kernel size and fruit set and prolonged fruit development like in other nut crops such as cashews (Adeigbe et al. 2016; Aliyu and Awopetu 2011).

Kernel recovery is an important consideration for kernel processors, though, it should not be considered in isolation from other desirable fruit characteristics to select mother trees. Moreover, these two traits, kernel mass and kernel recovery, alone may not capture market requirements. For example, the largest kernel tree in our study (4.63 g) were mostly a very-easy to crack operculum form ('coffin-lid') which are unsuitable for long term storage as NIS. However, as we are employing a seed-based improvement program due to the difficulties of asexual multiplication, this tree was still selected as it is unknown if coffin-lid NIS is a heritable trait.

Commercial nut industries rely on consistent and high yielding cultivars (Walton and Wallace 2011). When considering artificial selection requirements of trees with a higher propensity of single-kernel fruits (i.e., 20 or more of the 25 fruits sampled per tree were single kernels), a mean kernel mass greater than 3 g, a mean kernel length of > 30 mm, a mean kernel width > 13 mm, a kernel recovery ≥ 0.25 and without a 'coffin-lid' form, very few ($n = 5$) of the 256 trees surveyed met these standards. This either suggests that the search for trees meeting these selection criteria should continue, since founding a tree improvement program on five trees is unwise, or the selection criteria are too strict in the Vanuatu context

and should be relaxed. Whilst some confidence is given by trees maintaining their superior ranking in terms of relative kernel mass, year-to-year variability in fruit and nut characteristics was demonstrated and it is necessary to undergo field trials to determine the stability of commercially important traits.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

Tony Page, Paul Macdonell, Joseph Tungon and Michael Tabi contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Elektra Grant and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Table

Table 1: Number of trees from 256 *Canarium indicum* trees sampled and their percent range of double kernels present from 25 fruits sampled per tree. Therefore, 1-20% means that five or less sampled fruits contained double-kernels and the remainder were single-kernel fruits.

Percent double kernels	Number of trees (%)
0	62 (24.2)
1-20%	90 (35.2)
21-40%	43 (16.8)
41-60%	26 (10.2)
61-80%	19 (7.4)
81-100%	16 (6.2)

Figures

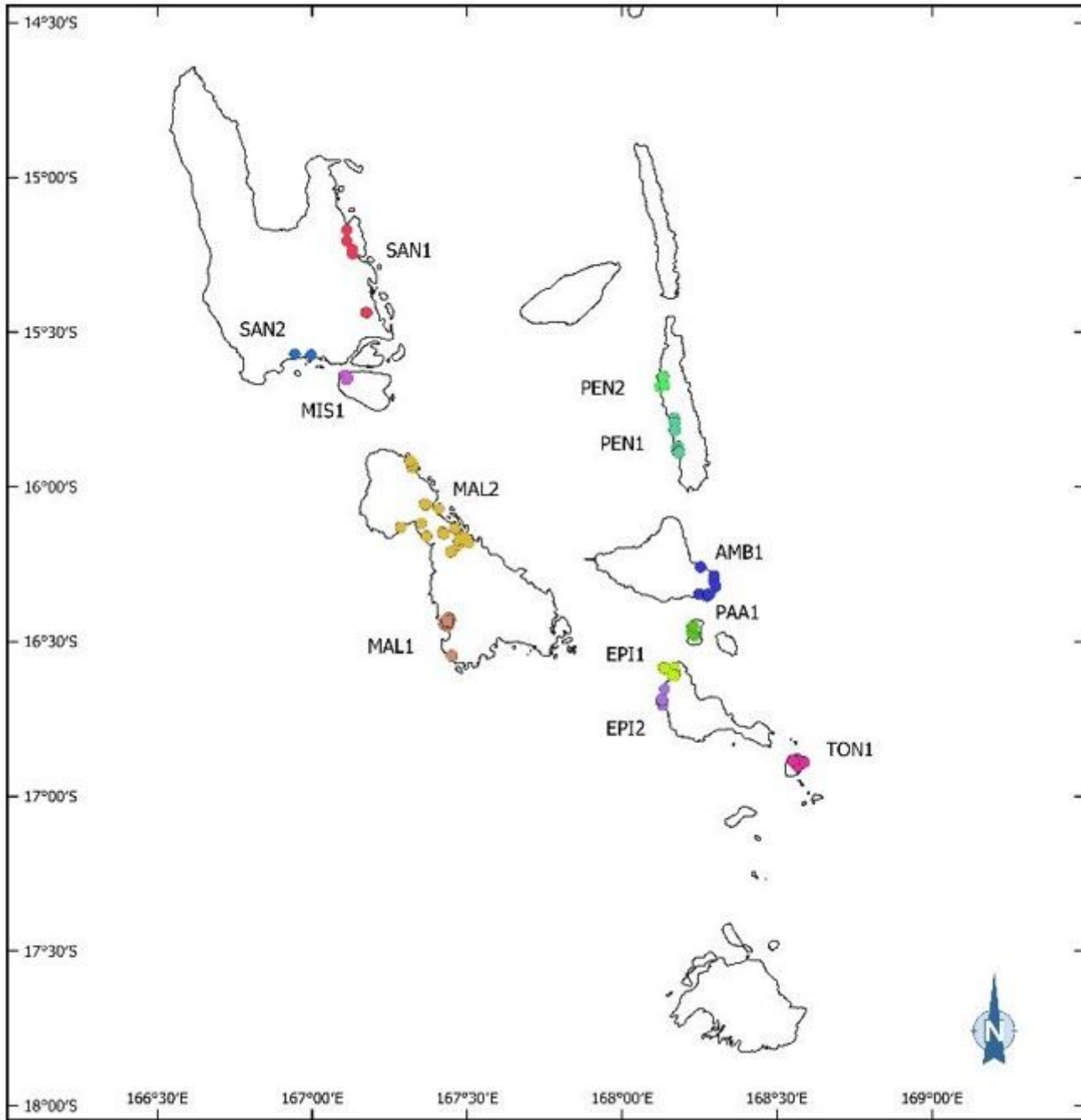


Figure 1

Location of trees characterised from eight islands. Santo, Pentecost, Malekula and Epi were divided into two sub-population each

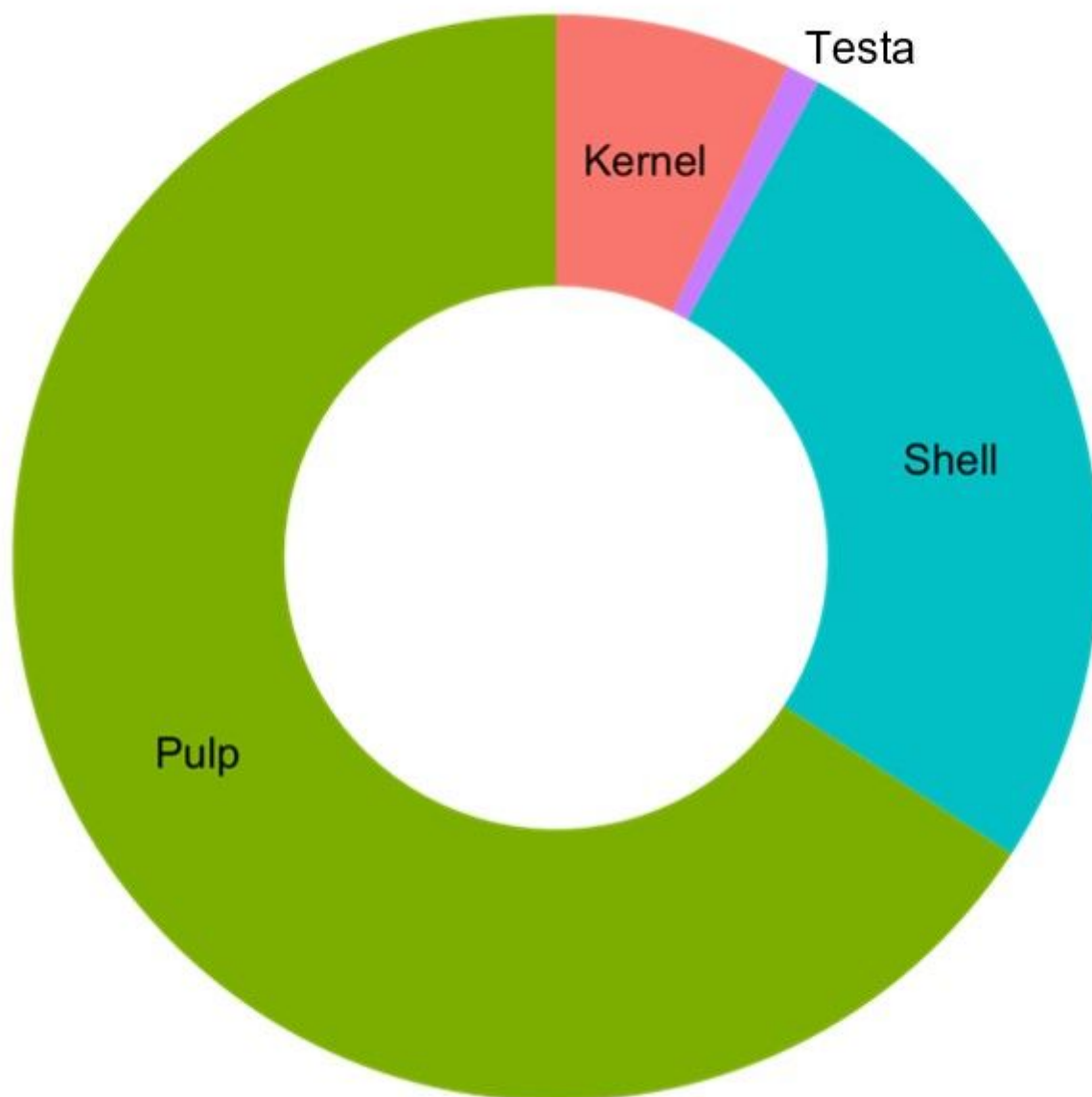


Figure 2

Percentage mass of the different components that make up a Canarium fruit (n= 6,400 fruit); pulp (65.8%), shell (26.1%), kernel (7.0%) and testa (1.0%)

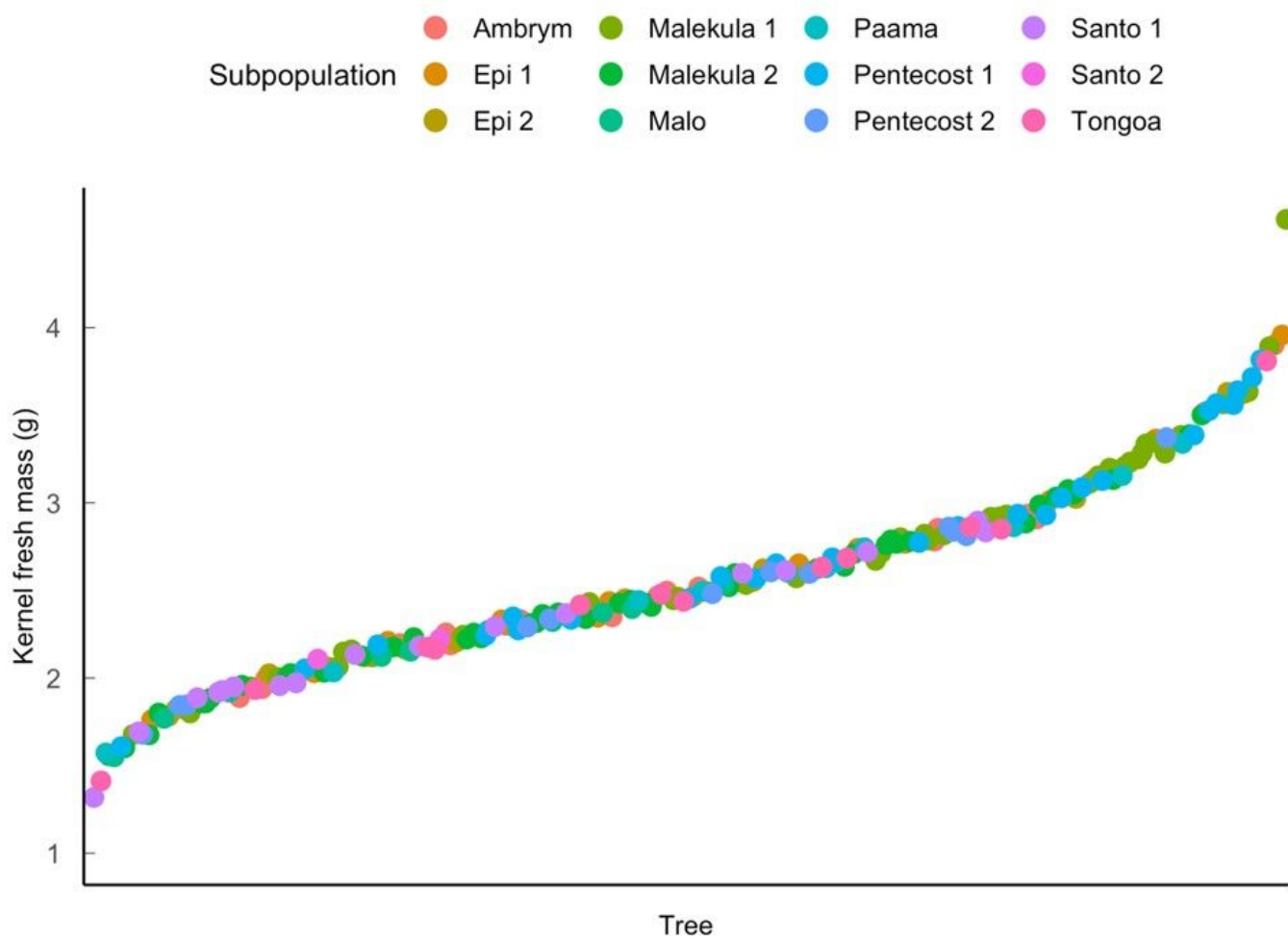


Figure 3

Mean single-kernel fresh mass for individual *Canarium indicum* trees (n = 152 trees; 20-25 kernels per tree)

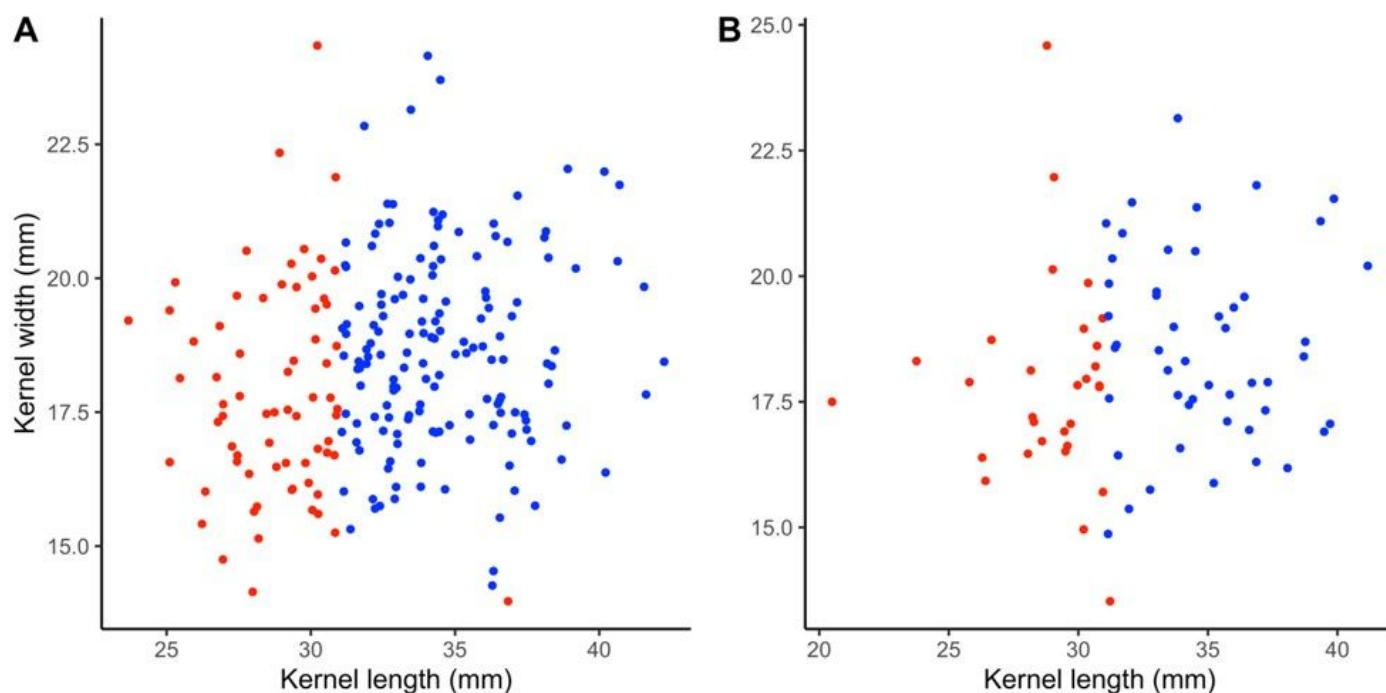


Figure 4

Mean kernel length and width for (A) single-kernel fruits and (B) double-kernel fruits. Data points represent different trees. Blue coloured data points met the specifications of a Premium-A grade as defined by Wallace et al. (2021) with kernel size measuring greater than 30 mm long and 13 mm wide. Red coloured data points do not meet premium grade specifications (<30 mm x <13 mm)

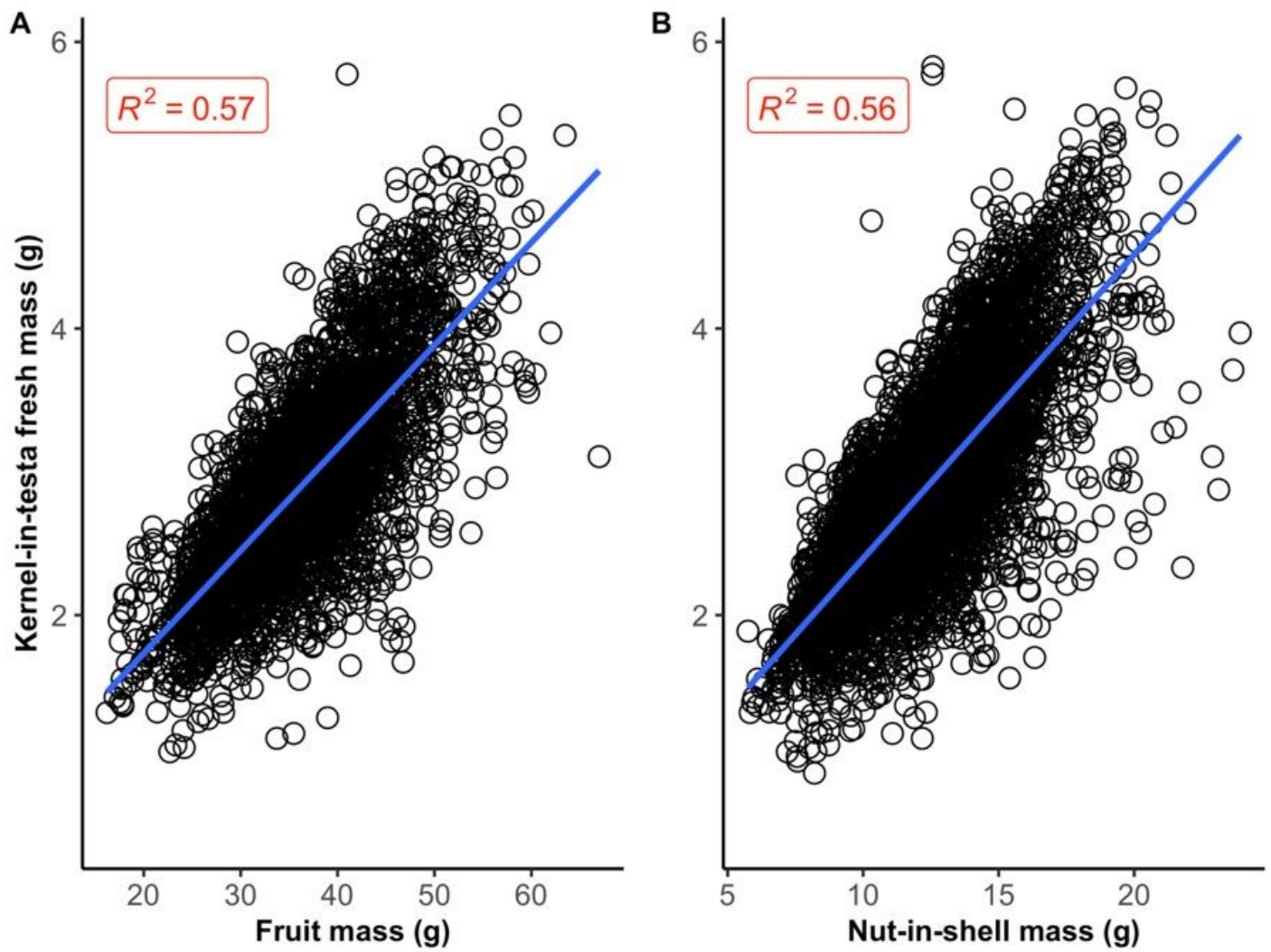


Figure 5

Scatterplot of *Canarium indicum* fruit mass (A) and nut-in-shell mass (B) with kernel-in-testa fresh mass (n = 4806)

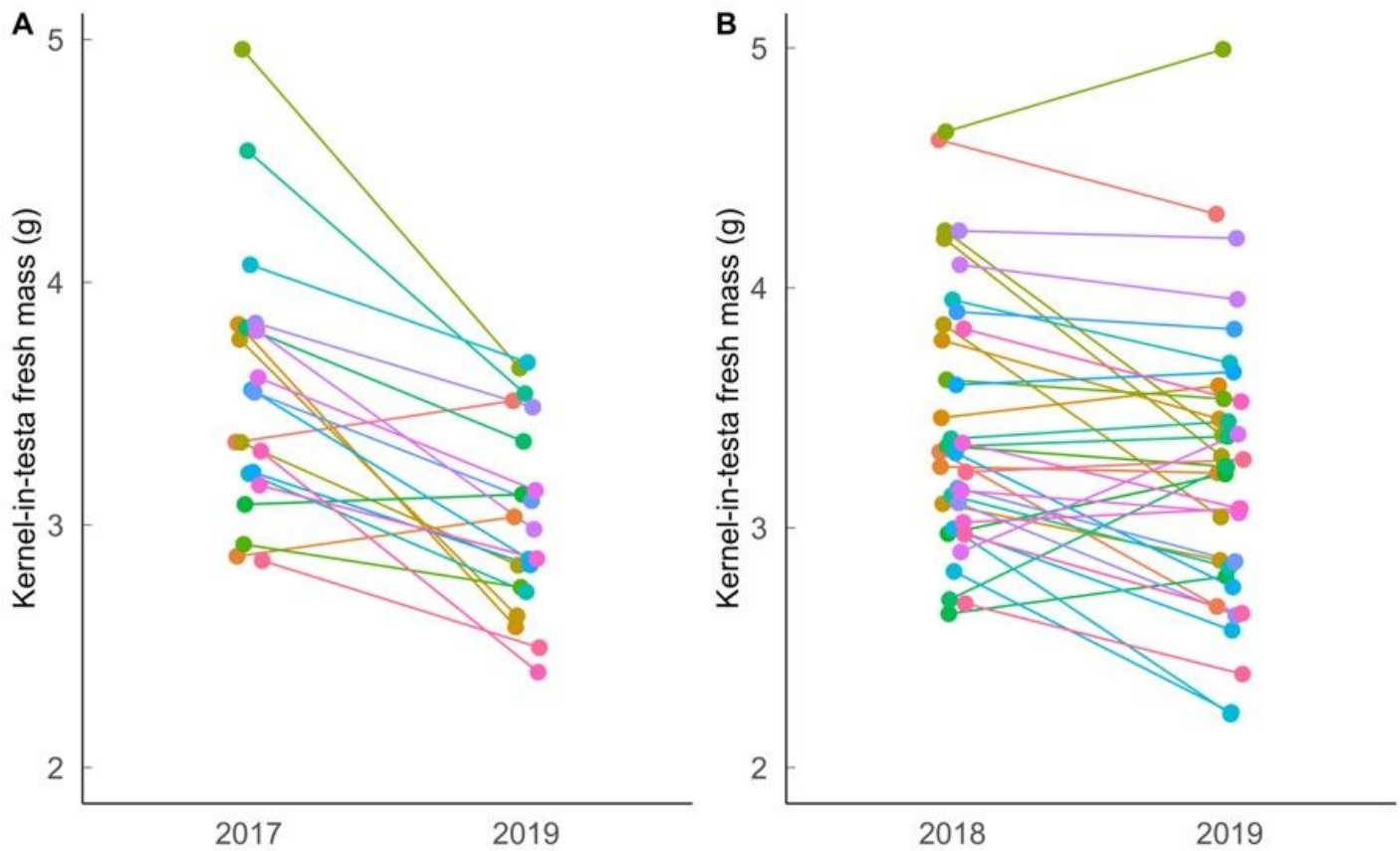


Figure 6

Differences in mean kernel fresh mass for within individual trees between sampling years. Different coloured points represent individual trees. The rank order of the mean kernel mass of trees were significantly associated between years 2017 and 2019 ($P > 0.01$, $r = 0.426$) and between years 2018 and 2019 ($P < 0.01$, $r = 0.495$)