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RESEARCH ARTICLE

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

Elektra Grant · Paul Macdonell · Joseph Tungon · Michael Tabi · May David · Sammy Kaku · Tony Page

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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, by rank order, those trees that produced larger kernels in the first year of sampling, tended to also produce relatively larger kernels in the subsequent year. The implications of these results for the further domestication of the species for planting in commercial agroforestry systems is explored.

Keywords Indigenous nuts · Commercialisation · Tree selection · Agroforestry tree products · Domestication · Non-timber forest products

Introduction

Oceania is a region with many traditionally important edible nuts (Elevitch 2006; Walter and Sam 2002). *Canarium indicum* (Burseraceae; canarium) is a tropical tree indigenous to lowland rainforest of eastern Indonesia, Papua New Guinea (PNG), Vanuatu and Solomon Islands (Evans 1996). The species produces highly nutritious edible nuts (kernels) that are an important local food resource (Thomson and Evans 2006). The development of *C. indicum* as a high value cash crop for edible kernels and oil extraction has been a focus of the Governments and people of Melanesia, and has been supported by donor agencies in the Pacific for over two decades (Bunt and Leakey 2008; Evans 1996; Nevenimo et al. 2007; Wallace et al. 2012b; Wallace et al. 2016a; Wallace

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E. Grant · P. Macdonell · T. Page (✉)
Tropical Forests and People Research Centre, University of the Sunshine Coast, 90 Sippy Downs Drive, Sippy Downs, QLD, Australia
e-mail: tpage@usc.edu.au

J. Tungon · M. Tabi · M. David · S. Kaku
Department of Forestry, Port Vila, Vanuatu

et al. 2021). Canarium kernels are a commercially attractive food product 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. solomonese)* (Evans 1996). *C. vulgare* (kenari nut) in Indonesia (Lim 2012; Mailoa and Tulalessy 2021) and *C. ovatum* (pili nut) in the Philippines (Coronel 1996a, b; Pham and Dumandan 2015) are commercialised for their edible kernels. The focus of this study, *C. indicum*, has existing domestic markets and potential for export (Wallace et al. 2021).

Canarium 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 (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). There are several other traditional and medicinal uses of canarium trees including timber (Evans 1999a; Harrison and Karim 2016) and topical application of oil as an anti-inflammatory (Leakey et al. 2008; Orwa et al. 2009; Sanderson and Sherman 2004). Further details on the status and use of *C. indicum* in Melanesia are given by Bourke (1996) and Bai et al. (2017) for PNG; Henderson and Hancock (1988) and Evans (1991, 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 cultivated tree species in the region (Bourke and Harwood 2009; Kirch 1989; Matthews and Gosden 1997; Yen 1996). 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), nut thickness and the ease of cracking the shell, testa thickness and mass, as well as the number of kernels per shell and kernel 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, work towards the development of the canarium industry in PNG, Vanuatu and Solomon Islands has focussed on market access, post-harvest processing systems and kernel nutrition (Wallace et al. 2012b; Wallace et al. 2016a; 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 fruit, NIS and kernel size from 63 *C. indicum* trees from across the Vanuatu archipelago (Walter and Sam 1993, 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 this study, we aim to identify trees with superior qualities for tree selection and improvement programs for *C. indicum*. Ultimately, so that small-holder farmers participating in the canarium nut extractive economy will benefit from the development of cultivars suited to traditional forms of production and contemporary consumers. We evaluate the variation in fruit, nut and kernel characteristics of natural canarium resources through systematic assessment. Specifically, we asked: (1) What is the variation in fruit and nut characteristics held 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 to almost 3000 mm. Mean annual temperature ranges from 24.9 °C (south Malekula) to 25.8 °C (south Santo). Most canarium were found below 200 m altitude along the coastal fringe, water courses, undulating terrain and amongst gardens (detailed site description can be found in Supplementary Information 1).

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; Table 1). 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.

Fruits that were completely purple in colour were considered mature (Walton et al. 2016). Mature fruits were collected (n = 50) 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 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 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, NIS and kernel dimensions (length and width at widest point); fruit mass (excluding fruit collected from Santo and SW Malekula); NIS, kernel and testa fresh mass (at ~ 30% field moisture). These data were used to calculate pulp mass, pulp thickness, shell mass, and kernel recovery (K:NIS; [wet kernel mass/ wet NIS mass] × 100). The number of kernels per shell was also recorded.

Subjective assessments of the fruits were recorded for ease of cracking the NIS using the traditional method of cracking the shell with two stones (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 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 and kernel-in-testa fresh mass as well as the number of kernels per shell was recorded. Kernel dimensions were also recorded from a subsample of these trees (n = 28).

Statistical analysis

Trees were 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

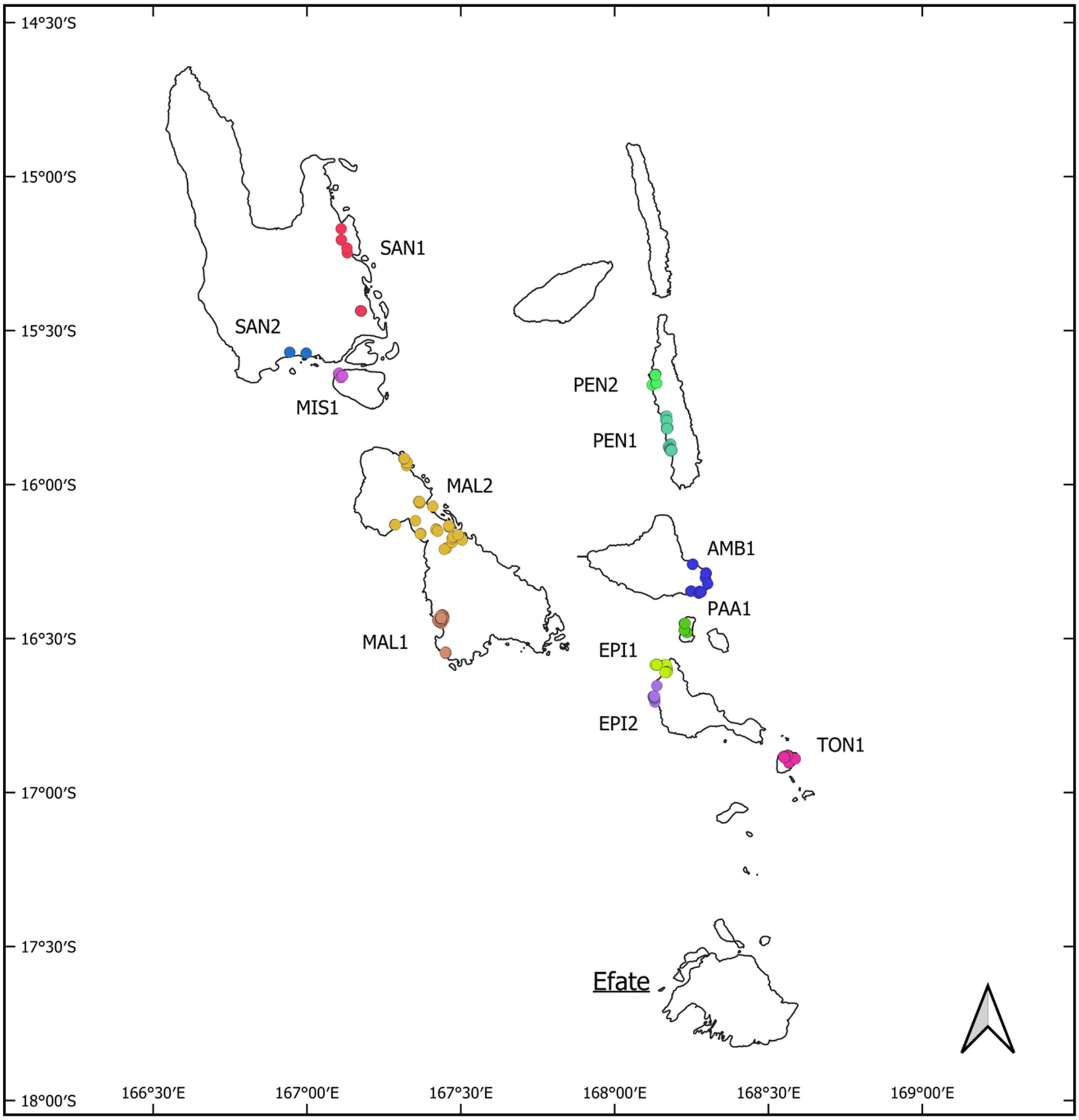


Fig. 1 Location of trees characterised from eight islands in Vanuatu: Santo (SAN1 red; SAN2 blue), Malo (MIS1 light purple), Malekula (MAL1 orange; MAL2 yellow), Pentecost (PEN1 aqua; PEN2 lime green), Ambrym (AMB1 dark blue), Paama (PAA1 green), Epi (EPI1 green; EPI2 purple) and Tongoa (TON1 magenta). Individual sites of the sub-populations are represented by colour coded dots and described in parenthesis

within island. Therefore, 12 sub-populations were sampled and analysed (Fig. 1).

Tree-to-tree differences in kernel mass

A nested random effects model was fitted to determine differences in kernel fresh mass between trees. Two separate analyses were conducted. The first used

Table 1 The number of trees sampled from different subpopulations from eight islands in Vanuatu

Island	Subpopulation	Number of trees	Year
Santo	SAN1	25	2017
	SAN2	5	
Malekula	MAL1	52	
	MAL2	47	2018
Epi	EPI1	18	
	EPI2	12	
Pentecost	PEN1	13	
	PEN2	32	
Malo	MIS1	10	
Ambrym	AMB1	20	
Tongoa	TON1	12	
Paama	PAA1	10	

trees that produced more than 80% single-kernel fruits (20–25 kernels per tree; n = 152 trees) and the kernel mass of single-kernel fruits only was used in the analysis. The second analysis included double-kernel fruits only (> 8 double-kernel fruits per tree; n = 77 trees), and used the combined kernel mass per fruit. For both analysis individual trees and subpopulation were included as random effects (package: 'Ime4'; Bates et al. 2015) and the intraclass correlation was calculated to determine how much variation in kernel mass is accounted for by each random effect (package: 'sjstats'; Lüdecke 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.

Tree-to-tree differences in kernel recovery

Kernel recovery (the proportion of nut-in-shell (NIS) that is kernel-in-testa by mass (Kernel:NIS)) 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 (n = 8–25). Where differences were detected, we applied a Tukey's HSD test.

Differences in single- and double-kernel attributes

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 (n = 47 trees). 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.

Relationships between fruit and nut characteristics

Pearson Correlations were performed (n = 4806) to determine relationships between the measured fruit and nut characteristics: 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. Spearman Rank Correlations were used to assess relationships between kernel recovery and the other measured traits (package 'Hmisc'; Harrell 2021). Correlations using single- 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. 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.

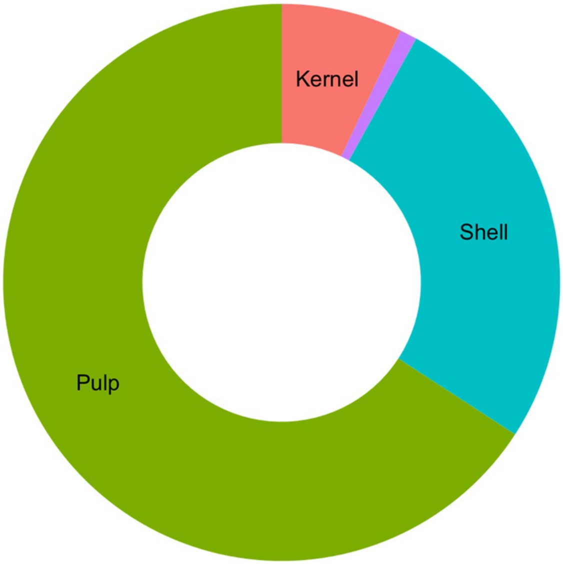


Fig. 2 Percentage mass of the different components that make up a Canarium fruit (n = 6,400 fruit); pulp (65.8%), shell (26.1%), kernel (7.0%) and testa (1.0%)

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, indicating that tree-to-tree variability made a substantial contribution to the differences in single-kernel mass (Table 2). 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

Fig. 3 Mean single-kernel fresh mass for individual Canarium indicum trees (n = 152 trees; 20–25 kernels per tree)

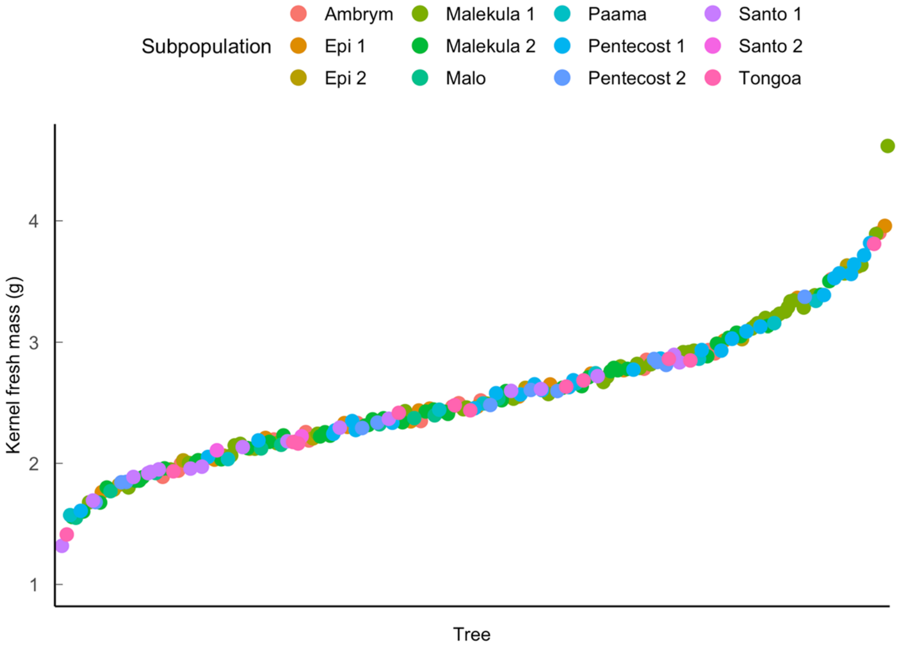


Table 2 Summarised results of the linear mixed-model analyses to determine significant differences in single- and double-kernel fresh mass and the subpopulation of tree origin between trees

	SD[1]	95% CI[2]
Single kernels		
Kernel mass	0.526	0.47–0.59
Subpopulation	0.149	0 to 0.30
Double kernels		
Combined kernel mass	1.026	0.87–1.22
Subpopulation	0.245	0–0.62

[1] standard deviation

[2] 95% confidence interval

Table 3 Range of the mean of single-kernel and individual kernels from double-kernel fruits for length, and width dimensions across individual trees

	Mean single-kernel length (mm)	Mean single-kernel width (mm)
Single kernels	23.7–42.2	13.9–24.3
Double kernels	20.4–41.2	13.7–24.6

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 (Table 2). 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 (Table 3) 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).

Variation in the kernel recovery of individual trees was recorded (Table 4). There were significant differences in the kernel recovery between

Table 4 Kernel recovery range for single-kernel and double-kernel fruits

	Minimum	Median	Maximum
Single kernels	0.058	0.21	0.42
Double kernels	0.08	0.26	0.54

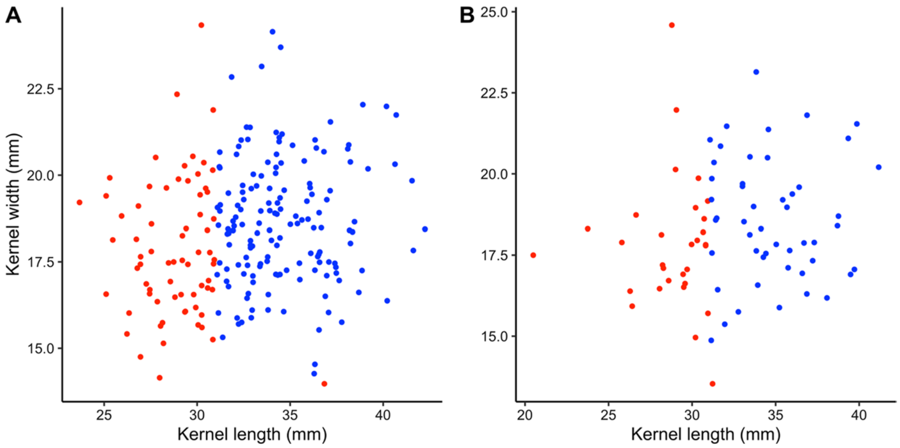


Fig. 4 Mean kernel length and width for **A** single-kernel fruits and **B** double-kernel fruits. Data points represent different trees. Blue coloured data points met the specifications of a Premium-A grade as defined by Wallace et al. (2021) with kernel size measuring greater than 30 mm long and 13 mm wide. Red coloured data points do not meet premium grade specifications (< 30 mm × < 13 mm)

trees (single-kernels, $F_{(223)} = 71.5$, $P < 0.001$; double-kernels, $F_{(76)} = 117.8$, $P < 0.001$). A total of 119 trees achieved a kernel recovery of 0.25 (1:3; Kernel:NIS) representing 52.6% of all trees sampled. 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

Nut-in-shell (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). Variation in the proportion of double kernels within a tree was recorded (Table 5). 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%).

Table 5 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)

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.

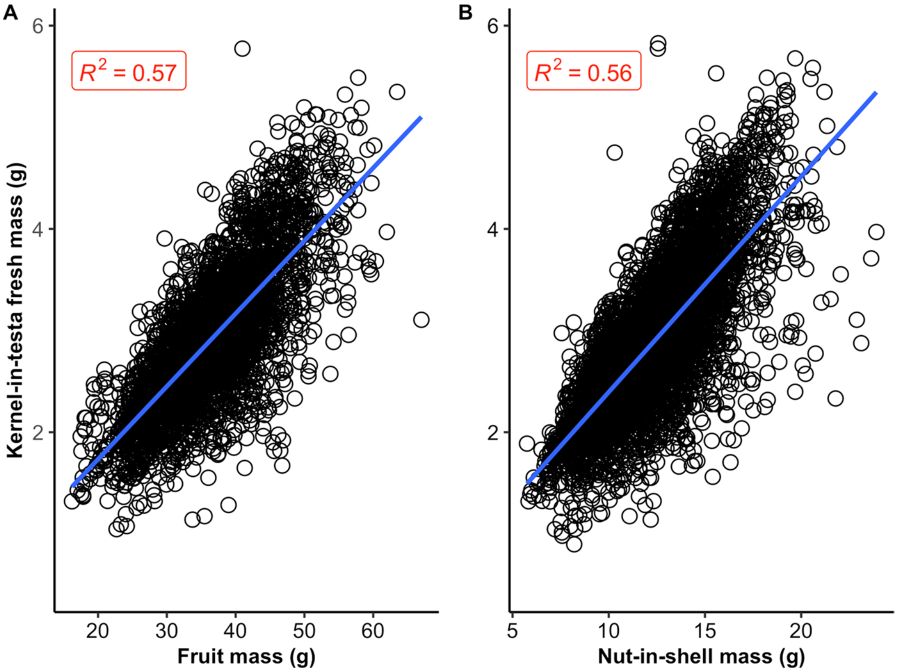
Correlations with morphological traits

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 $r(4804) \geq 0.65$, $P < 0.001$ (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 (Table 6). Fruit mass and nut-in-shell (NIS) mass were the best predictors of KITF mass (Fig. 5). KITF mass had a stronger linear association each with fruit length and width compared with each NIS length and width. Kernel recovery (kernel:NIS) was moderately linearly related to KITF mass but to none of the other fruit or nut traits.

Table 6 The relationship between kernel-in-testa fresh (KITF) mass (g) and other traits: Fruit mass (g); nut-in-shell (NIS) mass (g); Fruit length (mm); Fruit width (mm); NIS length (mm); NIS width (mm); and Kernel recovery (kernel:NIS) for single- and double-kernel fruits

	Fruit mass	NIS mass	Fruit length	Fruit width	NIS length	NIS width	Kernel recovery
Single kernels	$r(4804) = 0.752$)	$r(4804) = 0.733$)	$r(4400) = 0.552$	$r(4396) = 0.628$	$r(4545) = 0.489$	$r(4541) = 0.531$	$r(4552) = 0.519$
Double kernels	$r(708) = 0.728$	$r(1437) = 0.755$	$r(708) = 0.497$	$r(708) = 0.539$	$r(1437) = 0.425$	$r(1437) = 0.508$	$r(1437) = 0.576$)

Fig. 5 Scatterplot of Canarium indicum fruit mass (**A**) and nut-in-shell mass (**B**) with kernel-in-testa fresh mass (n = 4806)



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 and NIS mass (Table 6). Kernel recovery was again moderately linearly related to KITF mass 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

Significant tree-to-tree variation exists in economically important and food security related traits in natural populations of canarium. Currently the canarium market in Vanuatu is small and aimed toward tourists, 'suitcase' exports and re-establishing traditional diets for growing urban populations (Bunt and Leakey 2008; Wallace et al. 2016b). With the progressive erosion of traditional agricultural practices and traditional diets in Vanuatu (Rantes et al. 2022), the domestication of canarium can potentially address agro-ecological and human diversity aspirations (Krug et al. 2023). The industry has potential to grow and the results of our study are particularly important given the interest in Indonesia and the Pacific in commercialising kernel product from this tree species (Carias et al. 2023; Sundari et al. 2021; Wallace et al. 2022).

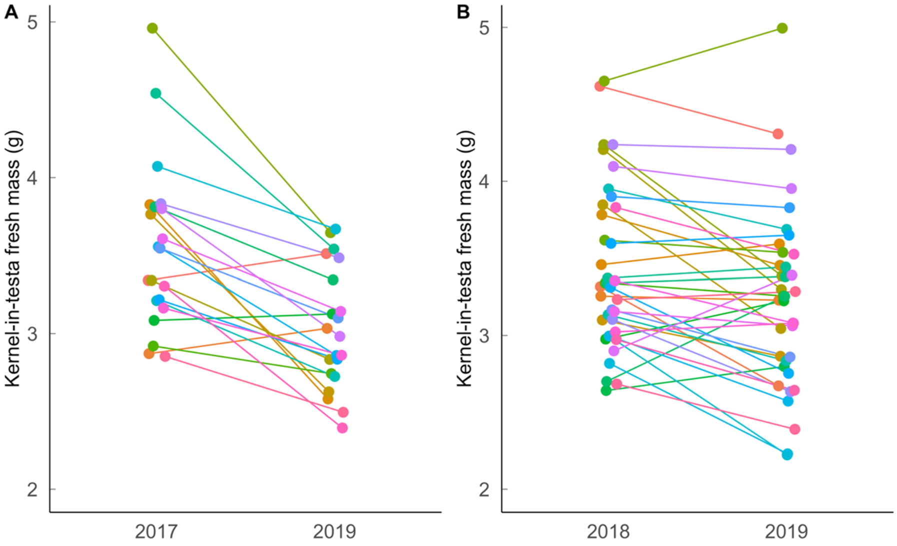


Fig. 6 Differences in mean kernel fresh mass for within individual trees between sampling years. Different coloured points represent individual trees. The rank order of the mean kernel mass of trees were significantly associated between years 2017 and 2019 ($P > 0.01$, $r = 0.426$) and between years 2018 and 2019 ($P < 0.01$, $r = 0.495$)

The results from this study have important implications for further domestication of the species to make selections that are desirable for planting in agroforestry systems. Small-holder farmers participating in the canarium nut extractive economy can also benefit from being involved in the process of domestication through capacity building in efficient methods of selection and clonal capture (Leakey 2017).

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). Improvement must be based on individual tree selection rather than provenance-based domestication because little of the variation within traits was attributed to sampling location. 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). Therefore, the traits of interest that identify superior canarium mother trees are kernel mass, high kernel recovery, nut-in-shell (NIS) traits such as an easy to crack shell and easy to extract kernel as well as number of kernels per fruit (Bunt and Leakey 2008; Leakey et al. 2008; Randall et al. 2016), which were investigated in this study.

Kernel mass is an important trait to the industry. Large kernels with a fresh mass of greater than 3 g are considered to improve the economic viability of entities along the value chain because larger kernels generally require fewer relative inputs from both producer and processor (Leakey et al. 2008). In our study, only around 20% of trees produced kernels with a mean mass of 3 g or more. More than half of the trees (63.6%) that were sampled over two fruiting seasons varied significantly in mean kernel mass between years. 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. 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 selectable traits. Further research is also required to determine if a trade-off exists between kernel size and fruit set and prolonged fruit development in canarium, as recorded in other nut crops such as cashews (Adeigbe et al. 2016; Aliyu and Awopetu 2011).

Kernel mass and kernel recovery are important considerations for producers and processors, though, alone may not capture market requirements. These traits should not be considered in isolation from other desirable fruit characteristics to select mother trees. 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 recommend a dual seed- and clonal-based improvement program, due to the current knowledge gaps in routine methods of asexual multiplication, this tree was still selected as it is unknown if coffin-lid NIS is a heritable trait.

When considering artificial selection requirements of trees including: a high proportion of single-kernel fruits (i.e., 20 or more of the 25 fruits sampled per tree were single-kernel fruits), 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.

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. Minimal variation attributed to the subpopulation level 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 (Leakey et al. 2008; Nevenimo et al. 2007) and Solomon Islands (Randall et al. 2016). Continuous variation and little population differences was also found for other traditionally consumed nut tree species in the Pacific such as *Barringtonia procera* (Cutnut) and *Inocarpus fagifer* (Tahitian chestnut) (Pauku et al. 2010).

The large variation in the kernel morphology of *C. indicum* provides the opportunity to select and breed trees with desirable traits for commercial production. 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 (Leakey 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.

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 is particularly important for canarium since shell mass comprises over one quarter of the total fruit mass and tree selections based on this attribute can increase efficiency in terms of transport mass per unit of kernel recovered.

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). Our results conform with Evans (1999b) who found significant correlation between NIS dry mass and KIT dry mass in *Canarium indicum*. A similar positive relationship between fruit and nut mass was reported for the edible nut species *Sclerocarya birrea* subsp. *caffra* (Marula) in South Africa and Namibia (Leakey 2005). In canarium, this result 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), although such grading would depend on the development of a mechanised approach to sorting.

These results are in contrast with a study of canarium nut characteristics in young (6 yr) 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. In *Sclerocarya birrea* subsp. *caffra* (Marula) the number of kernels contained in each fruit varied between trees and was putatively influenced by pollination success (Leakey et al. 2005). Very little is known about the pollination biology of canarium 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).

Testa removal and nut cracking

Testa removal is an important consideration for processors as it is a labour-intensive process (Wallace et al. 2021). We found no difference in the ease of testa removal between trees. 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.

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. This attribute can be 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. This is because some tentatively elite trees had shells that broke in a way that made it difficult to extract whole kernels. The problem of difficult to crack NIS can possibly be ameliorated by mechanical cracking with an NIS buying model (Wallace et al. 2012a). Shell characteristics and efficiency of nut cracking and kernel extraction has been identified as a desirable trait for other agroforestry species *Irvingia gabonensis* (Atangana et al. 2002; Awono et al. 2009) and *Ricinodendron heudelotii* (Mbosso et al. 2015) in Cameroon. Similarly, for canarium, mechanical cracking has been identified as being important efficiency measure for expanding the scale of the industry in PNG (Wallace et al. 2012a) and Vanuatu (Carias et al. 2023). However, ease of cracking is still an important consideration in regions that adopt a KIT buying model (Wallace et al. 2012a), where manual cracking by producers is likely to produce a high proportion of kernel pieces.

Canarium domestication

Canarium has been cultivated by people in Melanesia for thousands of years with several domesticated forms with desirable kernel characteristics being incorporated from both cultivated and wild-harvested species (Matthews and Gosden 1997; Nevenimo et al. 2007; Thomson and Evans 2006; Weeks 2009). Efforts to further domesticate *Canarium indicum* can help to meet the contemporary needs of farmers and the expectations of consumers (Nevenimo et al. 2008). Appropriate options for more systematic domestication of the species will depend upon the resources available to support the process.

Two broad approaches have been developed by the authors for the further domestication of *Canarium indicum* in Vanuatu (Macdonell and Page 2022). These approaches were developed to align with various access to resources and based on the assumption that the species was primarily outcrossing. Typically tree crop species have tended to be propagated clonally to avoid genetic segregation associated with sexual reproduction, eliminate or reduce periods of juvenility and deploy desirable and highly heterozygous genotypes into cultivation (Leakey et al. 1994; McKey et al. 2010). Given that vegetative propagation efforts have so far been unsuccessful in canarium, the first approach, with a more conservative application of resources, centres around establishing progeny trials from seed collected from candidate plus trees and selecting the best trees to serve as seed orchards. The second approach encompasses a similar progeny trial, but also addresses knowledge gaps on reproductive biology and cloning methods, to clonally multiply candidate plus trees from cultivated populations and trial resources. While the selection criteria included kernel mass, kernel yield and early onset of reproductive maturity (Macdonell and Page 2022), additional traits such as mass and yield consistency between years, kernel oil content, nutrition, and medicinal properties, as well as nut physical parameters for mechanical processing can also be considered. Combining multiple traits into future cultivars can benefit from the development of an ideotype (Leakey and Page 2006) to inform the process of selection and maximise the harvest index for market-driven traits in *Canarium indicum*.

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

Declarations

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

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