Phenotypic Association of Multi-scale Architectural Traits with Canopy Volume and Yield: Moving Toward High-density Systems for Macadamia

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Abstract. The vigorous growth and large canopy size of commercial macadamia (Macadamia integrifolia, M. tetraphylla, and hybrids) cultivars generally restricts macadamia orchards to low-density planting. Little is known of the detailed interactions between plant architecture and yield components specific to macadamia. This chapter examines how dependent traits such as canopy size and yield might be determined by direct and indirect interactions between traits at different scales within the canopy. Fifteen genotypes (n = 3) were phenotyped in two growing seasons for architectural and reproductive traits, around the age of their transition from juvenility to maturity. Genotypes varied in canopy volume, cumulative yield, and canopy efficiency, and partial genotypes with low canopy volume and high yield were considered potentially useful for future high-density orchard systems. There was high variability in architectural, floral, and yield traits at multiple scales. Direct and indirect effects of architectural traits on the variability of yield and tree size were quantified using path coefficient analysis. Canopy volume was subject to positive direct effects from trunk cross-sectional area (TCA; 0.72), lateral branching (0.24), and branch unit (BU) length (0.24). Other traits showed significant indirect effects with canopy volume via TCA, such as branch cross-sectional area (BCA; 0.43), BU length (0.40), lateral branching (0.35), and internode length (0.32). Branch angle had a significant indirect negative effect on capacity volume via BU length (−0.11). Nut number had the strongest direct effect on yield (0.97), and this relationship was significantly indirectly influenced by raceme number (0.47), raceme length (0.50), nut number per raceme (0.33), canopy volume (0.37), and branch angle (0.35). In these relatively young trees, early yield was directly and positively influenced by canopy volume (0.12), presumably due to increased early light interception, which suggests that early canopy vigor contributes to early yield. This study suggests that yield and canopy size are determined by complex phenotypic interactions between architectural traits at different scales. Therefore, preplanting (i.e., scion and rootstock selections) and postplanting (i.e., pruning and training) manipulations that specifically manage architectural traits such as shoot length, branching, branch angle, raceme length, and nuts per raceme may result in the creation of efficient macadamia canopies.

Orchard planting systems for apple have been developed according to high standards in recent years. During the past 60–70 years, planting density has increased from 100 trees/ha to sometimes 10,000 trees/ha in an attempt to increase orchard productivity and profitability (Robinson, 2003, 2011). The success of intensive systems depends on balancing the management of tree architecture and yield. Early yields are mainly under the influence of the number of trees per hectare and of tree training on light interception (Loreti et al., 1976; Robinson, 1996). For temperate crops such as apple, the use of pruning, detailed training, and rootstocks to control tree size has allowed a reduction in tree spacing and has led to increased flowering points per hectare, resulting in improvements in early productivity (Robinson, 2004). Increased maximum yield and improvements in fruit quality have also been made possible by focusing on structural architecture, using rootstock and scion selection, and detailed training and pruning to increase efficiency of the conversion of solar radiation to fruit production in intensive systems (Costes et al., 2006; Smart and Robinson, 1991). Intensive orchard systems with developed cultivars and advanced management techniques (e.g., pruning, limb training, trellising) can maintain high light interception, balance flowering and vigor, provide efficient harvesting, reduce production costs, and improve the consistency of fruit quality (Palmer, 2007).

Macadamia integrifolia, Macadamia tetraphylla, and hybrids are subtropical evergreen trees native to coastal southern Queensland and northern New South Wales, Australia. Vegetative growth is vigorous and quickly forms a dense canopy. Trees are traditionally planted at low density and can grow as tall as 20 m at maturity (Nagao et al., 1992), which is several times the height of modern apple orchard systems. In mature orchards, the tall and dense canopy can lead to reduced spray efficiency, and shading can result in soil erosion and unproductive areas in the lower canopy (Huett, 2004). Nonetheless, macadamia can maintain its yield in high levels of shading of up to 94% light interception (McFadyen et al., 2004), possibly due to long-distance assimilate transport from irradiated parts of the canopy (Trueman and Turnbull, 1994). Yield reduction begins at canopy volumes greater than 43,500 m³/ha⁻¹ (McFadyen et al., 2004); eventually, a proportion of older orchards consists of an unproductive inner canopy due to low light levels. Current management techniques mainly rely on biomass removal using mechanical hedging, which is intended to maintain machinery access rather than canopy efficiency (McFadyen et al., 2011). Hedging may negatively affect yield by removing fruiting age wood (Olesen et al., 2011; Wilkie et al., 2009), stimulating competitive vegetative growth (Wilkie et al., 2010), and lowering the photosynthetic potential of newly exposed shade leaves (Huett, 2004). Selective limb removal has been shown to increase and to have no effect on or to decrease yield compared with unpruned trees (McFadyen et al., 2013; Olesen et al., 2011). The reduction in yield is related to the amount of biomass removed, which is probably related, at least partly, to reduced light interception (Olesen et al., 2011).

Controlled vigor, early flowering, high partitioning of resources to productive processes, and high yield per hectare are key attributes of intensive temperate orchards that will benefit future macadamia orchards. However, crowding, shading, and the refinement of advanced training and pruning techniques remain obstacles to subtropical crops such as macadamia and avocado (McFadyen et al., 2004, 2013; Menzel and Le Lagadec, 2014). The discovery and incorporation of less vigorous scion cultivars and dwarfing rootstocks may be the best effective means of controlling vigor and increasing canopy efficiency for macadamia; however, there is currently limited research regarding such cultivars and little understanding of canopy architecture specific to macadamia (Huett, 2004; Nagao et al., 1992). The training of...
limb angles toward the horizontal can reduce vigor and increase flowering of apple and pear (Han et al., 2007; Lauri and Lespinasse, 2001; Sherif, 2013), and increased branching can improve early flowering of mango due to availability of terminal shoots (Oosthuyse and Jacobs, 1995), although similar relationships are unclear for macadamia. Therefore, it is necessary to improve our understanding of the architecture and interactions between vegetative and reproductive growth specific to macadamia.

This study documented the diversity and development of macadamia canopy architecture and reproduction across genotypes to associate multiscale traits with canopy size and yield and to assess which traits are most valuable for high-density orchards. This study has provided initial understanding of interactions between architectural traits to stimulate improvements in canopy management techniques and trait selections for breeding to develop efficient high-density macadamia orchards.

Materials and Methods

Location and materials. Macadamia trees were sampled from a breeding trial planted in Nov. 2011 at Maroochy Research Facility, Queensland, Australia (lat. 26°38′39.8″S, long. 152°56′14.2″E, elevation 59 m). The following 15 genotypes of Macadamia integrifolia, M. tetraphylla, and hybrids were selected to encompass a range of growth habits: ‘A38’, ‘A4’, ‘A538’, ‘B93’, ‘B109’, B115’, ‘B94’, ‘B25’, ‘B46’, ‘B63’, ‘B80’, ‘B87’, ‘Daddow’, ‘Fuji’, and ‘Renown’. The trial was located within an orchard of 859 cutting-grown and seedling-grown trees planted with 4 m between rows and 1 m between trees within rows (≈2500 trees/ha). For this study, three clonal replicates each were selected from 15 cutting-grown genotypes, comprising a total of 45 data trees. Each clonal replicate was surrounded by neighboring trees of different genotypes. Trees were measured over two growing seasons (2015–16 and 2016–17) representing the fourth and fifth years since field planting.

Multiscale measurements. Whole tree scale measurements were recorded for canopy dimensions, yield, nut number, and nut weight. Canopy volume was estimated by calculating the basic ellipsoid volume (Thorne et al., 2002) using $V = \frac{4}{3} \pi abc$, where $a$, $b$, and $c$ represent measurements of height (minus skirting height), along-row width, and between-row width, respectively. Trunk cross-sectional area (TCA) was measured 15 cm from the ground. Yield per tree ($y$) was measured as the nut-in-shell weight (NIS, weight of the kernel and shell together) of all the nuts per tree at 1% moisture content, and the average nut weight was derived from this weight divided by the number of nuts per tree. Canopy efficiency was expressed as the cumulative NIS yield per canopy volume at the second harvest.

The branch unit (BU) is the total branch structure originating from a single trunk axillary bud, including the first-order axis and all successive branching orders. Two BUs were subsampled from opposite-facing portions of the bottom half of each canopy for measurements of BU length, number of second-order branches, and racecme count per BU. Estimates of the average racecme length and racecme diameter were made from three randomly selected racemes per BU. During the 2016–17 season, nut measurements were also obtained on the BU scale to specifically relate yield to previously detailed architectural measurements. The branch cross-sectional area (BCA) was estimated from the base of the two subsample primary branches.

Within the first-order axis of each BU, a single growth unit (GU) was observed per year, whereby the second-most recent flush (to ensure bud maturity in all trees) from the apical bud of the first-order axis was sampled for measurements of GU length, node number per GU, and individual internode lengths. Statistical analysis. Unbalanced analysis of variance (ANOVA) was performed to determine significant differences between genotypes for all traits. Path coefficient analysis was used to analyze the standardized phenotypic means of measurements as outlined by Akintunde (2012). Path analysis has been used for other crops to understand the complex interactions that underlie traits such as yield (Dewey and Lu, 1959; dos Santos Dias et al., 2017; Gravois and Helms, 1992; Güler et al., 2001).

To identify the direct effects on canopy volume and yield, traits showing significant correlation ($P < 0.05$) with the dependent variable (yield or canopy volume) were standardized and entered into a multiple regression model. Due to the multi-scaled nature of the traits and in order to select the most suitable traits for direct influences in the path analysis, only those standardized partial regression coefficients (also called direct path coefficients) that significantly contributed to the multiple regression model represent the weighted direct effects of independent traits on the dependent variable. To identify indirect influences on canopy volume and yield, all measured traits were included in the path analysis. Indirect effect weights were calculated for each trait by multiplying the direct path coefficient of trait $X_1$ and independent variable $Y$ with the correlation coefficient among traits $X_1$ and $X_2$, and repeating this for all traits that significantly correlate with $X_1$. This process was then repeated with the path coefficient of $X_0$ and $Y$ and all traits that significantly correlated with $X_0$. Relationships that were not physiologically possible were not considered. Multiple linear regressions and ANOVA were calculated using GenStat (VSN International, 2015), and indirect effects were calculated using Microsoft Excel (Redmond, WA).

Results

Phenotypic diversity of 15 macadamia genotypes. There was considerable genotype variability in canopy volume, TCA, the amount of branching, BU angle, BCA, and length of shoots on different architectural scales (Table 1). In 2015, ‘Renown’, ‘A4’, and ‘B87’ flowered heavily, whereas other genotypes remained juvenile or flowered lightly. In 2016, all genotypes flowered to some extent (data not shown). Reproductive traits such as racecme number per BU, racecme length, and nut number per racecme also displayed variability (Table 1). ANOVA revealed significant differences among genotypes for canopy volume ($P = 0.034$) and cumulative NIS yield per tree ($P = 0.018$; data not shown). Variability in cumulative yield and canopy volume among genotypes is illustrated in Fig. 1.

Phenotypic correlations. Phenotypic correlations between the measured architectural traits are presented in Table 2. Several architectural traits correlated strongly with canopy volume, particularly TCA ($r = 0.82$; $P < 0.001$), BU length ($r = 0.52$; $P < 0.001$), internode length ($r = 0.47$; $P < 0.001$), and lateral branching ($r = 0.49$; $P < 0.001$). The BU angle correlated negatively with all scales of branch length, but it had no significant relationship with canopy volume ($r = 0.24$, not significant). Several architectural and reproductive traits were correlated with cumulative yield, particularly TCA ($r = 0.45$; $P < 0.001$), BU angle ($r = 0.43$; $P < 0.001$), and all racecme and nut traits except nut number per racecme ($r = 0.26$, not significant).

Tracts associated with canopy volume. The multiple regression model suggested direct effects of architectural traits on canopy volume ($R^2 = 0.74$; $P < 0.001$) (Fig. 2A; Supplemental Table 2). The direct path coefficients that significantly contributed to the multiple regression were from TCA (0.72), BU length (0.24), and lateral branching on the second-order axes (0.24). The direct association between BCA and canopy volume was negative (–0.33). The relationship between TCA and canopy volume had significant indirect contributions.
from BU length (0.40), internode length (0.32), and lateral branching (0.35), as well as from BCA (0.43). The significant indirect contributions to canopy volume through the effect of BU length came from GU length (0.11) and nodes per GU (0.09), whereas branch angle (toward horizontal) had a negative indirect effect on canopy volume (−0.11).

**traits associated with yield.** A second multiple regression model directly associated particular architectural and reproductive traits to yield ($R^2 = 0.97; P < 0.001$) (Fig. 2B; Supplemental Table 3). The total number of nuts per tree had the strongest direct effect on yield (0.97). Canopy volume and raceme length also had equal positive direct effects on yield (0.81). The number of nuts per BU had a negative direct effect on yield per tree (−0.13).

The relationship between the nut number per tree and yield had significant indirect contributions from nut number per BU (0.69), average nut weight (0.41), nut number per raceme (0.33), raceme number per BU (0.47), raceme length (0.50), and raceme diameter (0.42). Architectural traits such as TCA (0.41), branch angle (0.35), and canopy volume (0.42) also indirectly contributed to the effect of nut number on yield. The effect of canopy volume on yield had an indirect contribution from TCA (0.10), and small but significant contributions from BCA, BU length, internode length, and lateral branching.

**Discussion**

Plants are generally considered to regulate and modify vegetative architecture at a modular level (Kawamura, 2010), that is, plant architecture on one scale is determined by architecture on a lower scale. Path analysis extends the multiple regression analysis and provides a method of estimating the relationships between multiple traits as direct effects on the complex dependent variable and indirect contributions to those direct relationships (Akintunde, 2012; Garson, 2013). In the current study, a range of architectural traits on lower scales were shown to contribute to variability in the complex traits of canopy volume and yield. Exploitation of the diversity in these architectural characteristics may suggest approaches for improvements in canopy efficiency. The implications of these results in terms of architectural characteristics of the macadamia canopy for improved productivity and adaptation to high-density plantings are discussed.

**Understanding variability in macadamia canopy volume.** Multiple regression showed a very strong interaction between TCA and canopy volume for macadamia. TCA is also a complex trait that is often used as an indicator of tree growth (Westwood and Roberts, 1970). Rather than eliminating TCA from the analysis, indirect contributions to the TCA–canopy volume relationship were observed for further insight regarding the role of independent traits. BU length, internode length, lateral branching, and BCA all had strong positive indirect associations with the canopy volume–TCA relationship, most likely by increasing canopy dimensions by shoot extension and the number of hydraulic vessels in the primary branches and trunk.

The branch length (on the BU scale) also directly influenced canopy volume, and length on the GU scale and node number per GU provided small significant indirect influences on that relationship. GU number (the number of separate flushing events) per branch axis also may have had a very strong influence on BU length and canopy volume, although in this study it was not possible to accurately measure flushed in retrospect. The relationship between BU length and canopy volume was negatively influenced by branch angle, suggesting that the branch angle may indirectly reduce canopy volume by shortening the BU length, which could be due to a reduction in the apical dominance of branches at more horizontal angles (Lauri and Lespinasse, 2001; Wilson, 2000). The branch angle correlated negatively with all
Table 2. Phenotypic correlation coefficients (r) between dependent traits (gray highlight) and architectural and yield component traits.

| Trait                        | Canopy volume | Cumulative yield | Raceme number | Raceme diameter per raceme | Nut weight |
|------------------------------|---------------|------------------|---------------|---------------------------|------------|
| Canopy efficiency            | 0.03***       |                  |               |                           |            |
| TCA                         | 0.66***       | 0.47***          |               |                           |            |
| BCA                         | 0.59***       | 0.71***          |               |                           |            |
| GU length                   | -0.02**       | -0.05**          |               |                           |            |
| Nodes per GU                | -0.22**       | -0.25**          |               |                           |            |
| Internode length            | -0.01**       | -0.02**          |               |                           |            |
| Lateral branching           | -0.16**       | -0.16**          |               |                           |            |
| BU angle                    | -0.28**       | -0.28**          |               |                           |            |
| Racemes per BU              | -0.21**       | -0.21**          |               |                           |            |
| Raceme length               | -0.28**       | -0.28**          |               |                           |            |
| Nuts per raceme             | -0.20**       | -0.20**          |               |                           |            |
| Nuts per tree               | -0.17**       | -0.17**          |               |                           |            |
| Nuts per tree (B.C.A.)      | -0.14**       | -0.14**          |               |                           |            |

TCA = trunk cross-sectional area; BCA = primary branch cross-sectional area; BU = branch unit; GU = growth unit.

NS, *, **, ***Nonsignificant or significant at $P < 0.05$, $0.01$, or $0.001$, respectively.

Increased lateral (axillary) branching indirectly influenced canopy volume, possibly by allowing the vegetative parts of the canopy to spread in three dimensions, potentially increasing light interception but also possibly altering light distribution within the canopy due to increased shading. This trait is desirable in early growth to quickly fill orchard space and create a strong structure and in mature trees to generate new axillary positions for flower production (Wilkie et al., 2009). However, in mature trees, increased canopy volume from excessive branching is not desirable.

The negative direct influence of BCA on canopy volume in the path analysis coupled with a significant positive correlation coefficient for the same relationship suggests that the correlation is explained mainly by the indirect effects, following the reasoning of Akintunde (2012). In this case, the positive indirect influence of BCA on canopy volume via TCA, BU length and lateral branching (Fig. 4.4a) suggests that the overall relationship of BCA to canopy volume is a positive influence.

In terms of independent correlations, GU length and node number had significant relationships with BU length, but internode length did not (Table 2). However, we can suggest from the path analysis that internode length may have a stronger indirect influence on overall canopy volume through TCA than GU length or node number. Internode length and lateral branching are particularly likely to be under the control of basic mechanisms (i.e., growth rate of internodes) and under the genetic control of axillary bud release (Shimizu-Sato and Mori, 2001). Furthermore, lower-scale traits may be more heritable and easier to manipulate through selection than composite traits on higher architectural scales.

Understanding variability in macadamia yield. This study suggested that the basis of yield was the number of nuts produced per tree rather than the individual weight of nuts. A number of key reproductive and architectural traits indirectly influenced the association between nut number and yield, mostly branch angle, TCA, canopy volume, raceme number, and nut number per raceme (Fig. 2B).

Raceme number per BU had the strongest indirect relationship with yield through nut number per tree; in the young trees in this study, it represented precocity. BU angle was strongly correlated with raceme number per BU ($r = 0.50; P < 0.001$) and yield ($r = 0.43; P < 0.001$) (Table 2). This suggested that the indirect effect of the BU angle on yield through nut number shown by the path analysis (Fig. 2B) may be due to an increase in raceme number per BU. Additionally, negative correlations between the BU angle and node number and between the node number and racemes per BU (Table 2) suggested an
interconnection with vigor; furthermore, it has been shown in macadamia that shorter shoots are more likely to flower (Wilkie et al., 2009). As with vegetative growth, more horizontal branch angles may improve the partitioning of assimilates to floral axillary buds (Zhang et al., 2017) due to reduced apical dominance in higher branch angles, which may partly explain these relationships. More spreading canopies may also result in reduced shading and more homogenous light distribution, with a consequent effect on raceme and, therefore, nut number. It is unclear what degree of flowering is optimal for certain canopy sizes of macadamia, although there is no evidence that prolifically flowering macadamia trees have reduced yield because of internal competition for assimilates, such as is speculated for avocado (Wolstenholme, 1989).

Raceme length had a direct influence on yield and a strong indirect influence through nut number. Raceme number and length were well-correlated \((r = 0.55; P < 0.001)\) (Table 2), which may suggest a common gene expression mechanism that influences both axillary release (raceme number) and resource allocation to racemes (raceme length) (Toft et al., 2018). This mechanism could possibly continue to allow more assimilates to be directed toward racemes for improved nut production, retention, and yield. Raceme length was also correlated with branch angle \((r = 0.40; P < 0.01)\) (Table 2), which may also be related to a reduction in apical dominance and an increase in resource allocation to inflorescences. The significant negative correlations of GU length and node number with raceme length (Table 2) suggest this idea, suggesting that apical vegetative vigor may inhibit axillary raceme development.

The positive direct and indirect relationships between canopy volume and yield are likely the result of increased overall light interception on early flower and fruit production (Jackson, 1980). In this study, trees were young and the canopies were still relatively small. Increasing early light interception is important for early yield per hectare at high densities, and increased canopy volume and light interception are beneficial to yield, until \(\approx 94\%\) light interception for macadamia (McFadyen et al., 2004). Therefore, shading may be less problematic in high-density plantings of macadamia compared with apple. The relationships between traits described in this study are relevant to early growth and are unlikely to reflect relationships in dense mature canopies; however, further continuous studies are required.

Identification of potential genotypes and architectural management for high-density macadamia plantings. In terms of canopy size, our analysis suggested that a reduction in internode length, BU length, and branching might be effective mechanisms for reducing canopy volume. Vigor on the BU scale may be decreased by decreasing the length on the GU scale or node number. Selection for more horizontal branch angles may be useful for reducing branch length and vigor (Table 2; Fig. 2A) while also physically spreading the canopy to allow better light distribution. These beneficial architectural characteristics may be identified in genotypes or modified by breeding or postplanting manipulation, for example, by pruning, limb bending, or growth regulators. The reduction in tree size by scion and rootstock selection would greatly reduce the future cost of postplanting pruning and training in high-density orchards.

Variations in tree size between genotypes are promising for high-density macadamia; however, the measurement of the canopy volume does not take into account the canopy shape. The two smallest trees displayed a low canopy volume for different reasons; ‘B63’ was short with a rounded canopy, whereas the canopy of ‘B80’ was tall and narrow. The
Supplemental Table 1). Canopy efficiency and vegetative growth was assumed to vary similar to that of 'A4' (canopies. For example, 'B87' achieved a yield of 2138 g; its yield is twice that of the 'A4', found to be most suitable for high-density planting. This tree would perform well at higher planting densities, this tree would perform well despite 'B80' having a canopy volume nearly 2009; Stephenson and Gallagher, 2000), although several canopy shapes are currently used in orchards. Further details of canopy shape will need to be specifically addressed for high-density macadamia, and knowledge of the modular and genetic determinations of such characteristics across cultivars will only become more valuable as macadamia orchards become intensified.

The ratio of resource partitioning to yield and vegetative growth was assumed to vary dramatically between genotypes based on the measurements of canopy efficiency (Table 1; Supplemental Table 1). Canopy efficiency (g m⁻³) was calculated to distinguish genotypes based on the ratio of canopy size to yield (Supplemental Table 1). Canopy efficiency ranged from 242 g m⁻³ for 'Renown' to 10 g m⁻³ for 'B94'. 'Renown' has a large canopy volume (22.5 m³) and the greatest cumulative yield (2138 g); its yield is twice that of the 'A4', which is similar in size. Due to the high cumulative yield of 'Renown', the canopy efficiency was the highest value despite the large canopy size, suggesting that at traditional planting density, this tree would perform well in terms of yield per hectare. However, the majority of trees displaying a high canopy efficiency value were those with the smallest canopies. For example, 'B87' achieved a yield similar to that of 'A4' (~1000 g) while producing approximately half the canopy volume (12 m² and 23 m², respectively).

The same canopy efficiency of 137 g m⁻³ was calculated for both 'B80' and 'A4', despite 'B80' having a canopy volume nearly five-times smaller than that of 'A4'. Genotypes such as 'B80' have the potential to be planted at higher planting densities than genotypes like 'A4', potentially allowing an increase in yield per hectare. However, the tree with the lowest vigor, 'B63' (Fig. 1), displayed a very dwarfed canopy, which may have led to low light interception, and subsequent carbon source limitations may have been responsible for the low yield per tree in this genotype. Optimal tree size for intensified orchards will depend on the planting density; in the case of smaller genotypes like 'feathering' to increase early light interception and increase in yield per hectare. However, the number of nuts per raceme was significantly correlated with raceme number per BU, raceme length, and raceme diameter (Table 2), suggesting that increased branching (and, therefore, increased local light interception) may increase carbohydrates available for racemes and available axillary positions. Increased branching may be a useful trait for improving flowering in macadamia, although balance between early light interception and ongoing canopy size may be necessary due to strong positive direct and indirect effects on canopy volume (Fig. 2A), indicating that canopy shape will also have an important role in efficient orchard design. Additionally, branching did not affect the overall canopy efficiency (Table 2) because both yield and canopy volume were increased by branching.

BU and branch angles are likely to be key traits for the selection of high-density genotypes. The analyses suggested that high BU angles may be beneficial to canopy efficiency (Table 2) and promote branching and axillary bud release for raceme production. This relationship between branch angle and canopy efficiency may also suggest that limb bending could be beneficial for intensified macadamia orchards.

Internode length was the most promising lower-scale candidate for mediation of canopy volume, and it seems to be a key candidate trait when selecting genotypes suitable for orchard intensification. Node number per GU was more closely related to flowering and yield, and manipulation of this trait may also be useful for intensification, although neither node number nor internode length showed a relationship with overall canopy efficiency in this analysis.

All reproductive traits except nuts per raceme correlated strongly with overall canopy efficiency. However, the number of nuts per raceme was significantly correlated with the number of nuts per BU and the number of nuts per tree, which were both correlated with yield. The lack of a strong relationship with nuts per raceme may be due to the yield of these young trees during the first years of their cropping being strongly limited by raceme production. In mature trees, nut number per raceme appeared to be strongly affected by competition for resources between racemes, with more nuts per raceme in raceme-limiting situations and less nuts per raceme when the tree has sufficient racemes (Wilkie et al., 2009).

Within these genotypes, those with small canopy volume and high canopy efficiency may be viable in high-density plantings because they should maintain optimal light distribution over a long period of time. Of the genotypes observed in this study, the most appropriate trees suggested for high-density planting are 'B80', 'B25', 'Fuji', and 'B87'. It seems reasonable to suggest that yield per hectare could be increased in future macadamia orchards by using these genotypes (or genotypes with similar traits) in high-density plantings. Further studies are required to determine how these genotypes would perform in single-cultivar plantings at high density.

Conclusions

This study illustrated a high level of diversity in architectural and reproductive traits and presented evidence of less vigorous, high-yield trees suitable for intensification from a relatively small sample of macadamia genotypes.

The results of this study suggest that variation in canopy volume and yield may be determined by a combination of key architectural traits. Modification focused on key lower-scale architectural traits through management and breeding may successfully alter complex traits. This study suggested that preplanting (i.e., scion and rootstock selections) and postplanting (i.e., pruning and training) manipulations that specifically increase branch angle, raceme number, raceme length, and nuts per raceme and that decrease internode length, BU length, TCA, and excessive branching could lead to the development of macadamia trees with higher canopy efficiency that are better suited for intensification.

Although intensification of macadamia orchards aims to increase early light interception and provide early returns, it is also important to optimize light distribution within the mature canopy and maintain the balance between vigor and nut production. This study has provided information to aid the understanding of how genotypic selection and management techniques may be used to alter specific architectural traits, thereby adding to the development of future high-density macadamia plantings.

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| Genotype | Canopy efficiency | Canopy volume | Yield | TCA | BCA | BU length | GU length | Nodes per GU | Internode length | Lateral branch | BU angle | Racemes per BU | Raceme length | Raceme diameter | Nuts per raceme | Nuts per BU | Nuts per tree | Nut weight |
|----------|------------------|--------------|-------|-----|-----|-----------|-----------|-------------|-----------------|----------------|-----------|--------------|--------------|----------------|----------------|--------------|--------------|-------------|
| A38      | 86               | 12           | 784   | 30  | 5.7 | 237       | 18        | 5           | 35              | 8              | 27        | 6            | 5            | 1.13           | 0.2           | 6            | 107          | 5.1         |
| A4       | 137              | 23           | 1088  | 39  | 8.2 | 266       | 21        | 5           | 42              | 15             | 45        | 81           | 29           | 3.60           | 0.8           | 36           | 141          | 8.0         |
| A538     | 86               | 16           | 1003  | 47  | 8.3 | 194       | 18        | 5           | 39              | 12             | 32        | 12           | 12           | 4.28           | 2.1           | 26           | 154          | 6.5         |
| B93      | 47               | 20           | 134   | 37  | 8.5 | 254       | 36        | 10          | 38              | 9              | 23        | 8            | 12           | 1.62           | 0.2           | 2            | 25           | 4.4         |
| B15      | 97               | 19           | 775   | 40  | 6.4 | 234       | 26        | 8           | 32              | 11             | 27        | 28           | 16           | 4.77           | 1.5           | 16           | 100          | 6.4         |
| B115     | 78               | 13           | 612   | 33  | 4.6 | 196       | 23        | 7           | 31              | 10             | 33        | 9            | 7            | 3.03           | 2.0           | 23           | 114          | 2.9         |
| B94      | 10               | 11           | 96    | 35  | 6.0 | 286       | 37        | 12          | 32              | 4              | 8         | 0            | 2            | 0.75           | 0.7           | 1            | 11           | 1.5         |
| B25      | 97               | 7            | 642   | 29  | 6.8 | 209       | 36        | 9           | 38              | 8              | 29        | 10           | 8            | 2.23           | 0.9           | 22           | 102          | 3.1         |
| B46      | 64               | 11           | 277   | 19  | 3.9 | 174       | 28        | 7           | 43              | 8              | 38        | 2            | 5            | 0.95           | 0.5           | 5            | 37           | 2.6         |
| B63      | 113              | 3            | 141   | 14  | 3.0 | 120       | 16        | 6           | 27              | 11             | 46        | 12           | 11           | 1.88           | 0.4           | 3            | 30           | 3.3         |
| B80      | 137              | 5            | 800   | 19  | 4.8 | 149       | 19        | 7           | 28              | 7              | 31        | 13           | 11           | 1.75           | 0.9           | 23           | 154          | 2.5         |
| B87      | 111              | 12           | 1051  | 38  | 3.6 | 182       | 15        | 5           | 30              | 8              | 32        | 23           | 24           | 4.12           | 2.3           | 26           | 177          | 6.0         |
| Daddow   | 30               | 20           | 229   | 34  | 6.8 | 250       | 26        | 9           | 30              | 11             | 32        | 5            | 9            | 3.22           | 2.6           | 7            | 33           | 5.4         |
| Fuji     | 152              | 7            | 421   | 14  | 5.5 | 231       | 19        | 9           | 23              | 7              | 16        | 19           | 30           | 2.62           | 0.9           | 24           | 64           | 4.4         |
| Renown   | 242              | 23           | 2138  | 34  | 3.6 | 187       | 19        | 5           | 40              | 8              | 54        | 31           | 46           | 2.48           | 1.0           | 29           | 252          | 9.0         |

*Average data.

2017 data only.

Cumulative data.
### Supplemental Table 2. Path analysis of relative trait associations with canopy volume. Bold traits indicate direct associations (underlined) with the complex trait as standardized partial regression coefficients. Other traits are associated indirectly and derived from \( r \times \beta \).

| Canopy volume | TCA     | BCA     | BU length | Lateral branching |
|---------------|---------|---------|-----------|-------------------|
| TCA           | 0.72*** | –0.20***| 0.13***   | 0.11***           |
| BCA           | 0.43*** | –0.33*  | 0.17***   | 0.15**            |
| BU length     | 0.40*** | –0.23***| 0.24*     | 0.09**            |
| Lateral branch| 0.35*** | –0.21***| 0.09**    | 0.24*             |
| GU length     | 0.18**  | –0.06NS | 0.11**    | –0.05NS           |
| Nodes         | 0.04NS  | –0.05NS | 0.06NS    | 0.06NS            |
| Internode length | 0.32*** | –0.08NS | 0.06NS    | 0.06NS            |
| BU angle      | 0.10NS  | 0.09NS  | –0.11***  | 0.04NS            |

### Supplemental Table 3. Path analysis of relative trait associations with yield. Bold traits indicate direct associations (underlined) with the complex trait as standardized partial regression coefficients. Other traits are associated indirectly and derived from \( r \times \beta \).

| Yield            | Nuts per tree | Nuts per BU | Raceme length | Canopy volume |
|------------------|---------------|-------------|---------------|---------------|
| Nuts per tree    | 0.97***       | –0.09***    | 0.06***       | 0.05**        |
| Nuts per BU      | 0.69***       | –0.13*      | 0.07***       | 0.02NS        |
| Raceme length    | 0.50***       | –0.08***    | 0.12*         | 0.04*         |
| Canopy volume    | 0.37**        | –0.02**     | 0.04*         | 0.12*         |
| TCA              | 0.41***       | –0.03**     | 0.03**        | 0.10***       |
| BCA              | 0.11NS        | –0.03NS     | 0.02NS        | 0.05***       |
| BU length        | 0.01NS        | 0.01NS      | 0.01NS        | 0.06***       |
| GU length        | –0.17 NS      | 0.04NS      | –0.04*        | 0.03NS        |
| Nodes per GU     | –0.26NS       | 0.03NS      | –0.04**       | 0.01NS        |
| Internode length | 0.19NS        | 0.00NS      | 0.01NS        | 0.06***       |
| Lateral branch   | 0.08NS        | –0.02NS     | 0.04*         | 0.06***       |
| BU angle         | 0.35**        | –0.03**     | 0.05**        | 0.03NS        |
| Racemes per BU   | 0.47***       | –0.08***    | 0.06***       | 0.04*         |
| Raceme diameter  | 0.42***       | –0.08***    | 0.06***       | 0.03NS        |
| Nuts per raceme  | 0.33*         | –0.05***    | 0.03*         | 0.03NS        |
| Avg. nut weight  | 0.41***       | –0.06***    | 0.08***       | 0.06***       |

Multiple regressions for canopy volume \( R^2 = 0.74 \) and \( P < 0.001 \) and for yield \( R^2 = 0.97 \) and \( P < 0.001 \).

*NS, *, **, *** Nonsignificant or significant at \( P \leq 0.05, 0.01, \) or 0.001, respectively.