Breeding New Cultivars for the Australian Macadamia Industry

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Abstract. In 2017, five new cultivars specifically selected for Australian conditions were released. These were developed from an improvement program initiated by Commonwealth Scientific and Industrial Research Organisation in the early 1990s. Progeny seeds were produced by crossing industry standard cultivars with other cultivars with elite kernel production per unit projected canopy area. Seedlings were planted at two densities (2 m and 4 m along rows) in field trials at Bundaberg in 1997 and 1998, and Northern New South Wales in late 1997, along with replicated plants of parents grafted onto seedling rootstocks. Trials were assessed for commencement of flowering, growth, yield, kernel recovery, and components of kernel quality over 8 years. Best linear unbiased predictions of clonal values were obtained for each individual progeny using a pedigree-based mixed linear model. A bio-economic model was used to estimate economic weights for a selection index of clonal values to identify elite candidates. Final approval of 20 candidates for second-stage assessment was made by an industry committee using selection index rankings and observations of tree field performance and kernel quality.

Macadamia is a rapidly developing horticultural industry in subtropical regions. The macadamia tree produces a high value kernel that is consumed as a snack, confectionary, ingredient in bakery products or ice cream, or as oil. Macadamia is the only member of the Australian flora that has been developed as an international horticultural food crop. The crop initially was commercialized in Hawaii in the early 20th century, following introduction into the islands in the late 19th century. Australia is major producer of macadamia, following expansion of the industry from the 1970s (Hardner et al., 2009).

Selection of superior germplasm supports sustainable crop production. Genetic variation has been demonstrated for important production and kernel quality traits (Hardner et al., 2001, 2002). Macadamia is commonly propagated by grafting scions onto seedling rootstocks; therefore, total (both additive and nonadditive) genetic variation may be targeted in selection.

Cultivars and selections developed by the University of Hawaii/Hawaiian Agricultural Research Station in Hawaii from the 1930s are a major source of germplasm for world macadamia production (Hardner, 2016; Hardner et al., 2009). Initially, Hawaiian candidate cultivars were selected from early commercial seedling orchards and then clonally propagated for further evaluation. In Australia, the selection of superior germ-

plasm appears to have been started in the 1940s, with a comprehensive orchard survey undertaken in the 1950s to identify potentially superior germplasm (Hardner et al., 2009). A private breeding program was initiated in Australia during the 1970s, using some of the earlier superior Australian germplasm developed by Norm Greber (Bell et al., 1988; Hardner et al., 2009). Regional variety trials have been used from the 1980s to collect more robust quantitative data on the relative performance of elite Hawaiian and Australian material (Hardner et al., 2001, 2002; Stephenson, 1990a).

To date, the Australian macadamia industry has relied predominately on Hawaiian germplasm, which is derived from a narrow genetic base (Steiger et al., 2003) that has been selected under production environments different to those experienced in Australia. The need for an industry-supported breeding program to develop new cultivars adapted specifically to the Australian production environments was identified in the early 1990s (Hardner and McConchie, 1999; Stephenson, 1990b; Winks, 1983). The Australian macadamia breeding program adopted a quantitative genetic-focused approach that employed improved experimental design, structured populations to support analysis with quantitative genetic-based linear mixed models, and selection index to identify candidates with the greatest likelihood of delivering improved

profits to the Australian industry (Hardner and McConchie, 1999; Hardner and Peace, 2010; Mehlenbacher, 2003; Topp et al., 2016). The breeding strategy comprised two phases: 1) evaluation of recombinant seedling progeny to identify candidate cultivars for further testing; and 2) evaluation of candidate cultivars in clonal regional variety trials to identify cultivars for release.

Five cultivars from this program were released to the Australian macadamia industry in 2017. This paper reviews the methods used for the selection of the 20 candidate cultivars that subsequently were established in the second-stage clonal regional variety trials from which these final cultivars were selected.

Materials and Methods

Crossing and production of progeny. Crossings were undertaken in 1994 and 1995 between parents selected based on performance as cultivars in regional variety trials, complementarity (i.e., one parent deficient and one parent elite for particular traits), and industry feedback on commercial performance (Table 1). Five industry standard cultivars (A4, A16, H246, H344, and H660, where the prefix “A” indicates developed by the Hidden valley Plantation program, and “H” indicates selected by the University of Hawaiian program), and seven less-common and newer selections that produced high kernel per unit projected canopy area (Daddow, H781, H614, H816, H842, H849, Own Venture) were used as parents. Selection background of the parents is described in Hardner et al. (2009) and Hardner (2016). Reciprocal crosses were made; however, details are not included here, as this factor was not accounted for in the prediction of clonal effects.

Crosses were made in September of each year using the technique described by Urata (1954). Racemes of male and female parents were isolated with a paper bag several days before anthesis. Pollen was obtained by accessing bags on the selected male parents, following anthesis of more than 20% of the flowers, and rubbing a 20-cm diameter glass over the raceme. Pollination was undertaken by opening bags that had been placed on the selected females and re-rubbing the tube with collected pollen over open maternal flowers. Bags were removed 1 week after pollination.

Mature fruit were collected in April of the following year. Following collection and without storage or any other pretreatment, the fibrous husk was removed and individual nuts (seeds) were sown into 60-cm square forestry tubes for germination. Around the start of the following summer (i.e., December), germinated seedlings were transferred into 5-L plastic pots to promote better root development.

Establishment of field trials. Three field trials were established with a subset of the progeny available from the 1994 and 1995 crossings at two sites—Bundaberg (B) and Alstonville (T)—within the two main production regions of macadamia in Australia (Table 2). At the Bundaberg site (B), the B97 trial was planted as a single section in Mar. 1997 at a density of 5 m between planting

rows and 2 m spacing along planting rows (Table 2). A total of 263 own-rooted seedlings from the 1994 crossing program were established as single-tree plots within each of 25 blocks. Seedlings were allocated to blocks on the basis of full-sib family, with one seedling per family per block and some unbalance across blocks. A single replication of the own-rooted cuttings of the cultivar A4 also was planted in each block.

A second trial at Bundaberg (B98) was planted in Aug. 1998 with 688 own-rooted seedlings from the 1995 crossings, and 77 individual plants of scions of 10 of the parents grafted onto the industry standard H2 seedling rootstocks (Table 2). The trial was planted in two sections, with each section blocked by planting row. Planting rows were 5-m apart. Plants were established at two planting densities—2 m and 4 m spacing within alternating planting rows. Seedlings were randomly allocated to each block on the basis of full-sib family with, generally, one family per block. Grafted parents were allocated on the basis of scion genotype and replicated across blocks.

Similar to B98, the Alstonville trial (T98) was planted in two sections, with planting rows separated by 5 m and with blocks of either 2 m or 4 m planting densities along planting rows

(Table 2). However, the dimension of a block within a section was three rows by 10 plants (placed at a given planting density along a row within blocks), in contrast to B98, where blocks were allocated to whole planting rows. A total of 561 seedlings from the 1995 crossing program and 107 individuals of scions of 10 of the parents grafted onto H2 seedling rootstocks were planted in this trial. Seedlings and grafted parents were allocated to blocks similar to that done for the B98 trial.

Trees were trained to a central leader within the first year, and those with a single leader were topped to encourage side shoots. Growth of trees was vigorous, particularly at the Bundaberg location, and canopy management was applied at age 6 years following harvesting. For a given trial (B97), or section within a trial (B98 and T98), a coordinate system was defined by a grid of planting rows by tree positions within rows.

Data collection. Projected canopy diameter perpendicular to planting rows [canopy width (CW)] was assessed 5 years after planting, before any canopy management. Yield per tree of nut-in-shell at 1.5% moisture content (NIS) was assessed in all trials from age 5 years to age 8 years after planting. For all years, fruits that had abscised before the start of March were removed before yield assessment. At ages 5 and 6 years, trees were harvested in a single operation around April by collecting all fruits that had already abscised and stripping the remaining fruits [wet-nut-in-husk (WNIH)] from the tree. At ages 7 and 8 years, harvesting was undertaken by visiting the tree at intervals separated by 6 weeks (mid-April, end-May, mid-July, end-August) to harvest the abscised WNIH from the ground. The WNIH that remained in the tree at the final harvest in August also were collected by stripping the tree. It was assumed that fruit collected directly under a tree were produced by that particular tree. At the T98 trial, a major rain event in 2005 (7 years after planting) washed away nuts on the ground between the end-May and mid-July harvest (third harvest).

Individual tree NIS was estimated by separately dehiscing each harvest-by-tree collection of WNIH, assessing total mass of wet-nut-in-shell, subsampling 50 nuts, drying the sample to 1.5% moisture content (NIS), and then using the unique ratio of NIS to wet-nut-in-shell of the sample to convert the entire collection and to estimate NIS for each harvest-by-tree. At age 7 years, the mass of late dropping nuts (i.e., nuts that were remaining on the tree at the last harvest, LDNM) per tree also was recorded, in addition to the contribution this made to total annual individual tree yield.

Total kernel recovery (TKR) was assessed for each tree from the 2004 (age 7 years at B97 and age 6 years at B98 and T98) annual harvest by subsampling 50 nuts from the total harvest, weighing NIS, cracking these, weighing total kernel mass, and calculating the percentage ratio. In 2003, 50 nuts also were subsampled from the total harvest, cracked to extract kernel, sorted to remove

commercially unacceptable kernel using industry standard guidelines, and then used to assess percentage of whole kernel by mass and mass of individual whole kernels [whole kernels by mass (WKM)]. In 2006, kernel samples were prepared and assessed for shriveled kernel rating (SK) using a four-point scale based on industry standards.

Prediction of genetic values. Clonal values of progeny candidates were predicted on the basis of a genetic model that included additive (described using historical pedigree records) and full-sib family genetic effects. Analyses incorporating simultaneously information across trials and planting densities within trials were performed for the phenotype of a particular trait measured at a given age, according to the following general mixed linear model that modeled genetic effects for each site-by-planting density combination and residual effects at each section-within-trial level (with B97 being represented by only one section):

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_u\mathbf{u} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_f\mathbf{f} + \mathbf{r}$$

where $\mathbf{y}$ was the vector of observations for all trials, $\mathbf{b}$ was a vector of fixed effects, which include the general mean, site, trial-within-site, section-within-trial-within-site, planting density, site $\times$ planting density interaction, propagation group (i.e., own rooted seedlings vs. grafting onto seedling rootstock) and, to account for global environmental trend in each section, linear covariates across the planting rows and columns of the coordinate grid defined for each section within a trial; $\mathbf{X}$ was the design matrix that mapped the observations onto the fixed effects; $\mathbf{u}$ was the vector of random nongenetic effects, which included block within a section and, where adequate, to account for lack-of-fit, row, and column effects for each section within a trial; $\mathbf{Z}_u$ was the matrix that mapped the observations onto the nongenetic random effects; $\mathbf{a}$ was the vector of additive genetic effects for individuals (including ancestors) in each site-by-density; $\mathbf{Z}_a$ was the matrix mapping the observations onto the additive genetic effects; $\mathbf{f}$ was the vector of full-sib family effects (i.e., specific combining ability of the crosses) for each site-by-density; $\mathbf{Z}_f$ was the design matrix for full-sib family effects; and $\mathbf{r}$ was a vector of unknown random residual spatial effects for each observation within each section-within-trial level. Residuals spatial effects were modeled as an anisotropic first-order autoregressive process (Costa e Silva et al., 2001; Dutkowski et al., 2002; Gilmour et al., 1997).

The variance of $\mathbf{y}$ was defined as

$$\text{var}(\mathbf{y}) = \mathbf{V} = \mathbf{Z}_u\mathbf{G}_u\mathbf{Z}_u^T + \mathbf{Z}_a\mathbf{G}_a\mathbf{Z}_a^T + \mathbf{Z}_f\mathbf{G}_f\mathbf{Z}_f^T + \mathbf{R}$$

where $\mathbf{G}_u$ was the variance-covariance matrix of the random nongenetic effects using a diagonal matrix with independent variances for each factor-by-section, $\mathbf{G}_a$ was the variance-covariance matrix of the random additive genetic effects among site-by-planting densities, $\mathbf{G}_f$ was the variance-covariance matrix of the

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Table 1. Numbers of progeny from crossing among 12 parents over two crossing seasons (1994 and 1995), and established in progeny trials for evaluation and selection of candidate cultivars for phase 2 evaluation. Italicized numbers represent those planted in the 1995 trials.

Female	Crossing season	Male									
		A4	A16	H246	H344	H660	H781	H814	H816	H842	H849
Own Venture	94	23	21	19				17	17		
Daddow	95	28	36	35	33	20	35	15	27	34	32
A4	94		13	16				17	17		
	95		11	14	19	34	27	11	25	17	36
A16	94			17				16	18		
	95			40	20	20	41	32	30	37	21
H246	94							16	18		
	95				12	14	14	17	27	8	22
H344	95					12	12	12	15	22	23
H660	95						19	27	32	26	22
H781	95							17	16	14	20
H814	94								18		
	95								33	14	5
H816	95									25	23
H842	95										15

Table 2. Design of progeny trials planted at two sites (B = Bundaberg, T = Alstonville) detailing trials, distance between planting rows [Row (m)], plant within planting rows [Space (m)], number of blocks (nBlock), number of seedling progeny (nProg), number of plants of propagated parents (nPar), and total number of plants (nPlants). For nPar, the number of unique parent genotypes is given in parentheses.

Site	Trial	Row (m)	Space (m)	Planting date	nBlock	nProg	nPar	nPlants	Notes
B	B97	5	2	Mar. 1997	25	263	25 (1)	288	Irrigated
B	B98	5	2	Aug. 1998	12	480	65 (10)	545	Irrigated
		5	4	Aug. 1998	10	208	12 (8)	220	Irrigated
T	T98	5	2	Nov. 1997	19	343	67 (10)	410	
		5	4	Nov. 1997	10	217	36 (10)	253	
Total						1511	205 (10)	1716	

random full-sib family effects among site-by-planting densities, and $\mathbf{R}$ was the variance–covariance of the residual effects of the observations within each section-within-trial. Under the applied general mixed linear model described previously, connections across trials and planting densities for additive genetic effects occur via the incorporation of the numerator relationship matrix (Henderson, 1977; Henderson and Quaas, 1976). Restricted maximum likelihood estimates of (co)variance parameters were obtained by using the average information restricted maximum likelihood algorithm implemented in the software ASReml (Gilmour et al., 2006).

Initial analyses were undertaken for each trial to review normality of residual distributions and significance of spatial model terms following appropriate transformation of phenotypic observations to achieve normality (Table 3). Significant spatial effects identified by the within-trial analyses were included in the subsequent multitrial analyses. Different structures were used in the multitrial analyses to model the variance–covariance matrices for additive genetic and full-sib family effects, including a single-order factor analytic parameterization (Costa e Silva et al., 2006, 2017; Hardner et al., 2010; Smith et al., 2001) (Table 3).

Total genetic variance for each trait at given site and planting density (vG_{sp}) was estimated as $vA_{sp} + 4 \times vF_{sp}$, where vA_{sp} and vF_{sp} were the estimated additive genetic and full-family variances, respectively, for the each unique combination of the s^{th} site and p^{th} planting density (noting that vA_{sp} and vF_{sp}

were the common additive or family variance estimates across trials within site for a given planting density). This genetic model assumed that epistasis was negligible and additive and dominance effects for a particular trait were equivalent between seedling and grafted plants, after removal of a general average propagation effect. Narrow-sense heritability and individual broad-sense heritability were estimated for each trait at the t^{th} trial by p^{th} density as:

$$h_{tp}^2 = \frac{vA_{sp}}{vA_{sp} + vF_{sp} + vR_t}$$

$$H_{tp}^2 = \frac{vG_{sp}}{vA_{sp} + vF_{sp} + vR_t}$$

where vG_{sp} , vA_{sp} , and vF_{sp} were defined as previously, and vR_t was the pooled residual variance for the corresponding t^{th} trial, estimated as the average of the respective residual variance estimates obtained for the sections within the t^{th} trial. For a given trait, total genetic correlations between sites and planting densities were estimated as:

$$rG_{sp,s'p'} = \frac{\text{cov}G_{sp,s'p'}}{\sqrt{vG_{sp}vG_{s'p'}}}$$

where $\text{cov}G_{sp,s'p'}$ was the total genetic covariance between the p^{th} planting density at the s^{th} site and the p'^{th} planting density at the s'^{th} site, and vG_{sp} and $vG_{s'p'}$ were defined as previously.

Clonal values for a trait were predicted for each individual for each site and planting density as:

$$g_{sp} = a_{sp} + f_{sp} + dwf_{sp}$$

where a_{sp} was the predicted additive genetic effect, f_{sp} was the predicted effect for the corresponding full-sib family of the individual, and dwf_{sp} was the predicted within-family dominance effect for the p^{th} density at the s^{th} site. This model assumed that the estimated parameters were similar to the true underlying genetic parameters. To predict dwf_{sp} for each site and planting density, dwf_{sp} was initially only obtained for those individuals with observations as:

$$dwf_{sp*} = \frac{3 \times vF_{sp}}{vR_{tq}} r_{tq}$$

where r_{tq} was the residual of the observation record for the individual in the q^{th} section of t^{th} trial, vR_{tq} was the residual variance estimated for the same q^{th} section of the s^{th} trial, and vF_{sp} was the estimated full-sib family variance for the p^{th} density and s^{th} site corresponding to the observation of the individual. The prediction of dwf_{sp} for an individual in other site-by-densities was obtained as:

$$dwf_{sp} = \frac{d f w_{sp*}}{\sqrt{vF_{sp*}}} rF_{sp*,sp} \sqrt{vF_{sp*}}$$

where, $rF_{sp*,sp}$ was the correlation among family effects between the site and planting density for which the residual was derived (sp^*) and a different site-by-planting density (sp).

Selection methods. A linear objective function was used to obtain a combined selection index (Hazel, 1943; Smith, 1936) for ranking of selection candidates. The

Table 3. Transformations used to obtain normal distribution of residuals, and genetic and residual variance–covariance models used to predict additive genetic and full-sib family effects for canopy width (CW), age of first crop (AFC), total mass of nut-in-shell yield per tree (NIS), mass of late dropping nuts (LDNM), total kernel recovery (TKR), proportion of whole kernels by mass (PWKM), mass of individual whole kernels (WKM), and shriveled kernel rating (SK).

Trait	Age (yr)	Units	Transformations			Models		
			B97	B98	T98 ²	Additive	Family	Residual
CW	5	m	ID	ID	ID	fa(SP)	fa(SP)	at[TQ]:spatial
AFC	8	years	ID	ID	ID	fa(SP)	diag(S)	at[TQ]:spatial
NIS	5	kg	ln(y + 0.02)	ln(y + 0.02)	na	at[S, 'B']:us(P)	at[S, 'B']:v	at[TQ]:spatial
NIS	6	kg	ln(y + 0.01)	ln(y + 0.01)	ln(y + 0.01)	fa(SP)	at[S, 'B']:us(P)	at[TQ]:spatial
NIS	7	kg	ln(y + 3)	ln(y + 3)	ln(y + 1.5)	fa(SP)	fa(SP)	at[TQ]:spatial
NIS	8	kg	ln(y + 0.02)	ln(y + 5)	ln(y + 5)	fa(SP)	fa(SP)	at[TQ]:spatial
LDNM	7	kg	(y + 0.01) ^{-0.415}	(y + 0.01) ^{-0.415}	(y + 0.01) ^{-0.415}	fa(SP)	us(S)	at[TQ]:spatial
TKR	6&7	g/100 g	ID	ID	ID	v	na	at[TQ]:spatial
PWKM	5&6	g/100 g	ID	ID	ID	us(S)	us(S)	at[TQ]:spatial
WKM	5&6	g	ID	ID	ID	us(S)	v	at[TQ]:spatial
SK	8&9	rating (0, 1, 2, 3)	ID	ID	ID	v	v	vR

²Note: NIS for age 7 years at T98 was missing, due to a rain event that precluded the third harvest.

ID = identity transformation; fa = factor analytic parameterization of a variance-covariance matrix; S = site; P = planting density; SP = site by planting density; TQ = section within a trial; at[TQ] = conditional on a section within a trial; spatial = variance-covariance matrix for modeling random residual effects, modeled as spatially correlated (assumed to follow a first-order separable autoregressive process) residuals; diag = diagonal variance-covariance matrix (i.e., considering heterogeneous variances across trials, and assuming trial correlations to be all equal to zero); na = not included in model; at[S, 'B'] = factors conditional to Bundaberg level of site (S); us = unstructured covariance matrix; v = single variance component (i.e., homogeneous variance across site-by-density levels, and assuming correlations among dimensions equal to one); vR = common variance of spatially independent residuals assumed across trials.

selection index value for each candidate was estimated as the sum of the candidate's economic value for each objective trait, estimated as the product of the predicted clonal values by the respective estimated economic weight.

Traits included in the selection objective were CW (m) at age 5 years, age of first crop (AFC, years), cumulative NIS yield to age 8 years (CNIS8, kg), late dropping nut mass at age 7 years (LDNM, kg), TKR (g/100 g), proportion of whole kernels by mass (PWKM, g/100 g), average whole kernel size (WKS, mm), and SK (0–3), planted at a density of 4-m spacing along rows at Bundaberg. Clonal values for CNIS8 were predicted by summing clonal values of individual age NIS. Clonal values for WKS were predicted as follows:

$$g_{WKS} = \frac{g_{WKM}}{\sqrt{vG_{WKM}}} r_{G_{WKS}, WKM} \sqrt{vG_{WKS}}$$

where vG_{WKS} was the total genetic variance for WKS (estimated as 0.270), $r_{G_{WKS}, WKM}$ was the estimated total genetic correlation between whole kernel mass and WKS (estimated as 0.96), vG_{WKM} was the total genetic variance for whole kernel mass (estimated in this study), and g_{WKM} was the predicted clonal value of the individual for whole kernel mass.

A bio-economic model that included costs and returns of production and processing for a 100-ha orchard from establishment to 20 years after planting similar to that described in Hardner et al. (2006) was used to estimate the economic weights of the selection traits. The economic weight of LDNM at age 7 years was estimated by assuming that the ratio of LDNM to total harvest at this age would be maintained at all ages. Economic weights were expressed as the change in the profitability index (ratio of discounted profit to discounted costs) from a unit increase in the objective trait. The estimated economic weights used in this study were $w_{CW} = -0.143$, $w_{AFC} = 0.065$, $w_{CNIS8} = 0.031$,

$w_{LDNM} = -0.104$, $w_{TKR} = 0.11$, $w_{PWKM} = 0.001$, $w_{WKS} = 0.006$, and $w_{SK} = -0.255$. To evaluate the contribution of each trait to the selection index value, correlations between the predicted clonal value of an individual for each objective trait and the selection index were calculated.

The final step in selection of the 20 candidate cultivars to progress to the regional variety trial was a review by a selection committee of macadamia growers and processors from the Australian industry of the selection index–derived rankings against observations of tree field vigor and structure, and presence of stick-tights (dead fruit that have failed to drop, Akinsanmi et al., 2012) made during a field walk, and quality traits (i.e., extent of shriveledness, color, glossiness, size, kernel discoloration, insect damage) of a sample of raw kernel. This assumed that broad-sense heritability of these traits was relatively high with little environmental effect, so that the raw observation reflected the true underlying clonal value of the individual. Candidates were considered from the highest ranked to identify those for which there was a strong reason to not progress based on field observation or raw kernel appearance.

Results

There was substantial cross-over interaction between site and planting density for NIS yield per tree at 6 years, TKR, percentage of whole kernel by mass, and average whole kernel mass (Fig. 1, Table 4). On average, canopies were wider at age 5 years, and AFC and mass of late dropping nuts were lower at the Bundaberg site compared with Alstonville. Differences between trials were greater than differences between planting densities for CW, age to first yield, mass of late dropping nuts, and NIS yield at ages 5, 6, and 8 years. When converted, yield per hectare was greater for the 2-m planting spacing, except for T98 at age 8 years.

Estimates of phenotypic variance of almost all traits (except NIS yield at age 8 years) were consistently greater for the 4-m planting density at the Alstonville trial (T98) compared with the other trials (Table 5). The estimate of the common phenotypic variance of SK across trials was 0.05.

Estimates of narrow-sense heritability of CW were greater at the trial at the Alstonville site (average 0.36) compared with those for trials at Bundaberg (average 0.15); however, individual broad-sense heritability was similar across all trials (average 0.58) (Table 5), indicating that dominance was relatively larger for this trait at Bundaberg. Estimates of heritabilities of CW were similar among the two planting densities examined here.

Estimates of narrow-sense heritability of AFC ranged from 0.02 to 0.32 (average 0.16) and tended to be lower at Bundaberg compared with Alstonville, and at the 2-m planting density compared with 4 m (Table 5). Nonadditive genetic effects also were stronger at Bundaberg than Alstonville for this trait, with estimates of individual broad-sense heritability being greater at Bundaberg, but there was no large difference in individual broad-sense heritability between planting densities.

Estimates of narrow-sense heritability of total mass of nut-in-shell yield per tree ranged from 0.05 to 0.59 and from 0.21 to 1.09 for individual broad-sense heritability (Table 5). At the Bundaberg site, narrow-sense heritability and individual broad-sense heritability estimates were lowest at age 6 years, with the strength of dominance effects varying among ages and tending to be greater in the 4-m planting density compared with that for 2 m, at least at ages 6, 7, and 8 years. Narrow and broad-sense heritability estimates for total mass of NIS tended to be lower in the 2-m planting densities. Estimates of narrow-sense heritability and individual broad-sense heritability for mass of late dropping nuts at age 7 years at Bundaberg

were slightly greater for the 4-m planting density (Table 5). Interpretation of genetic parameters for the total mass of nut-in-shell yield at Alstonville was complicated by the missing third harvest at age 7 years.

The average across sites and planting densities of narrow- and broad-sense heritability estimates for TKR were 0.21 and 0.24, respectively (Table 5). Also for this trait, the ratio of the additive genetic variance to the total genetic variance ranged between 0.81 and 1.00. The narrow-sense heritability and individual broad-sense heritability estimates tended to be greater at the Bundaberg site compared with Alstonville, and for the 2-m planting density compared with 4 m.

Estimates of narrow- and broad-sense heritability of proportion of whole kernel by mass (averages of 0.05 and 0.09) were lower than for TKR (Table 5). The magnitude of estimates of narrow-sense heritability for mass of individual whole kernels were similar to those for TKR, whereas estimates of individual broad-sense heritability were somewhat greater.

For CW, AFC, NIS at age 7 years (including yield for the missing third harvest at the Alstonville trial), and average whole kernel mass, the estimated total genetic correlations between the 4-m planting density at Bundaberg and the corresponding trait performances at the same site for the 2-m

planting density and at Alstonville for both planting densities were relatively high (above 0.7) (Table 6). However, for NIS at age 5 years, the total genetic correlation between the 4-m and the 2-m planting densities at Bundaberg was lower (0.62), as were all the correlation estimates for NIS at age 6 years. For NIS at age 8 years, the genetic correlation estimate between the 4-m planting density at Bundaberg and the 2-m planting density at the same site was high (0.89), but lower (0.60, 0.76) correlation estimates were obtained with both planting densities at Alstonville. Clonal values for TKR at the 4-m planting density for Bundaberg were highly correlated (0.92, 1.00) with those at the 2-m planting density for both sites, but less strongly correlated with the 4-m planting density at Alstonville. For the proportion of whole kernels by mass, the total genetic correlations between the 4-m planting density at Bundaberg and either planting density at the Alstonville site were very low (0.09).

There were 118 progeny (7.8%) with a selection index value greater than the average of the 10 cultivars (Own Venture, Daddow, A4, A16, H246, H781, H814, H816, H842, H849) also evaluated in the progeny trials (Fig. 2). Twenty nine progeny ranked above the best cultivar (H816). The correlation between predicted clonal values for cumulative NIS yield to 8 years and the selection index value was 0.84. The next most impor-

tant traits were mass of late dropping nuts ($r = 0.28$), age to first crop (-0.15), SK (-0.14), and proportion of whole kernels by mass (-0.12). Predicted clonal values for TKR were virtually uncorrelated with selection index value (-0.07). The average of the predicted profitability index of the top 20 ranked progeny was 42% greater than the average for the tested cultivars, and the average of predicted profitability index for the top 5 ranked progeny was 68% greater. Five of the top 25 progeny ranked by selection index were rejected by the industry selection review panel (Table 7).

Discussion

This study is the first to employ quantitative genetic approaches to develop improved germplasm in macadamia. Previous approaches generally have used phenotypic observations of single plants to select candidates for further clonal testing. However, phenotypic observations confound genetic and environmental effects, and accuracy of phenotypic selection is low if elite individuals are selected from unreplicated candidates, particularly for low heritability traits (i.e., traits for which the phenotype is more influenced by environmental effects).

In retrospect, the incorporation of different planting densities in the design of the field trials undertaken in this study may not be the most efficient approach for identifying elite candidates for selection. Progeny trials in tree crops are expensive partly because the field experiments are large and also because plants must be assessed for several years, as early productivity is not well correlated with yield potential in the long term (Hardner et al., 2002). The first trial in this study (i.e., B97) was established at 2-m planting density in an attempt to reduce costs per hectare. However, it was subsequently realized that the genetic correlation between trees planted at 2-m spacing and those at a wider spacing within a planting row (which is more conventional for production orchards) was not known. In addition, at later ages, it was difficult to be absolutely certain that fruits from neighboring trees were not included in the harvest of individual trees planted at a density of 2 m within a row, highlighted by the generally lower phenotypic variance and narrow- and broad-sense heritability estimates for NIS at later ages in the 2-m planting densities. Hence, later trials were established with a

Fig. 1. Back-transformed (for details of transformation for analysis, see Table 3) estimated mean yield at four ages (5, 6, 7, and 8 years), two sites (B = Bundaberg, T = Alstonville) planted at two densities (2 m and 4 m along a planting row). Note that yield at age 7 years at Alstonville was missing the third harvest.

Table 4. Estimated back-transformed averages for canopy width (CW), age of first crop (AFC), mass of late dropping nuts (LDNM), total kernel recovery (TKR), proportion of whole kernels by mass (PWKM), mass of individual whole kernels (WKM), and shriveled kernel rating (SK) by planting density (2/4) by site (B.T) (e.g., B.2 = 2-m planting density at Bundaberg site).

Trait	Age (yr)	Units	B.2	B.4	T.2	T.4
CW	5	m	4.83	4.79	3.85	3.92
AFC	8	year	5.07	5.17	5.92	5.86
LDNM	7	kg	0.01529	0.03138	0.00251	0.00774
TKR	6&7	g/100 g	37.11	38.08	37.08	36.04
PWKM	6&7	g/100 g	42.35	44.83	52.47	50.93
WKM	6&7	g	2.76	2.85	2.97	2.81
SK	6&7	0–3	1.45	1.45	1.65	1.65

Table 5. Estimated phenotypic variance (vP), narrow-sense heritability (h^2), and individual broad-sense heritability (H^2) for transformed (see Table 3 for details) canopy width (CW, m), age of first crop (AFC, years), total mass of nut-in-shell yield per tree (NIS, kg), mass of late dropping nuts per tree (LDNM, kg), total kernel recovery (TKR, g/100 g), proportion of whole kernel by mass (PWKM, g/100 g), and mass of individual whole kernels (WKM). Results are given by trial (B97, B98, and T98) and (.) planting density (2/4) (e.g., B97.2 = Bundaberg B97, planting density 2 m).

Trait	Age (yr)	vP					h^2					H^2				
		B97.2	B98.2	B98.4	T98.2	T98.4	B97.2	B98.2	B98.4	T98.2	T98.4	B97.2	B98.2	B98.4	T98.2	T98.4
CW	5	0.55	0.58	0.62	0.52	0.94	0.13	0.12	0.19	0.40	0.32	0.67	0.64	0.62	0.51	0.53
AFC	8	0.16	0.40	0.32	0.49	1.37	0.05	0.02	0.32	0.25	0.16	0.29	0.11	0.44	0.25	0.16
NIS	5	1.95	3.50	4.25			0.34	0.19	0.37			0.72	0.40	0.37		
NIS	6	1.79	2.54	3.14	3.19	7.44	0.07	0.05	0.18	0.21	0.33	0.45	0.32	0.60	0.21	0.33
NIS	7	0.07	0.11	0.20	0.21	0.63	0.41	0.27	0.50	0.21	0.48	0.67	0.43	1.04	0.58	0.69
NIS	8	0.05	0.07	0.13	0.04	0.08	0.56	0.39	0.59	0.22	0.11	0.81	0.57	1.09	0.24	0.50
LDNM	7	4.48	4.04	4.29	1.89	5.26	0.27	0.30	0.34	0.13	0.38	0.34	0.38	0.42	0.22	0.42
TKR	(2004)	11.80	15.41	15.25	17.88	32.40	0.30	0.23	0.23	0.20	0.11	0.35	0.27	0.23	0.20	0.13
PWKM	(2003)	289.92	368.02	368.02	580.39	1100.63	0.04	0.03	0.03	0.10	0.05	0.12	0.10	0.10	0.10	0.05
WKM	(2003)	0.28	0.35	0.35	0.49	0.86	0.30	0.24	0.24	0.22	0.12	0.49	0.40	0.40	0.33	0.19

Table 6. Total genetic correlation estimates between the 4-m planting density at Bundaberg and the corresponding trait performances at the same site for the 2-m planting density (B.2), and the Alstonville site for the 2-m (T.2) and 4-m (T.4) planting densities, for canopy width (CW), age of first crop (AFC), total mass of nut-in-shell yield per tree (NIS) from age 5 to 8 years, mass of late dropping nuts per tree (LDNM), total kernel recovery (TKR), proportion of whole kernel by mass (PWKM), and mass of individual whole kernels (WKM).

Trait	Age (yr)	B.2	T.2	T.4
CW	5	0.72	0.84	0.90
AFC	8	0.83	0.83	0.86
NIS	5	0.62		
NIS	6	0.39	0.51	0.54
NIS	7	0.88	0.88	0.80
NIS	8	0.89	0.60	0.76
LDNM	7	0.95	0.91	0.89
TKR	(2004)	0.92	1.00	0.56
PWKM	(2003)	1.00	0.09	0.09
WKM	(2003)	1.00	0.99	0.99

mix of planting densities, although this complicated the analysis. In addition, because macadamia trees are vigorous, the 5-m spacing between planting rows quickly filled in and required hedging at age 6 years from planting at Bundaberg and 8 years at Alstonville. The genetic correlation between performance following hedging of plants established at high density and production in less-dense conventional production orchards is also unknown. Heavy pruning at the Alstonville site may explain the apparent greater yield per hectare at the greater density at year 8 observed in this study.

Estimates of individual broad-sense heritability for total mass of nut-in-shell yield per tree (NIS) between ages 5 and 8 years reported here are generally greater than in Hardner et al. (2002), who reported estimates below 0.22. This may be because the present study was undertaken with unselected progeny, as genetic variation is expected to be lower in selected populations (Bulmer, 1971), such as the regional variety trials reported in Hardner et al. (2002). However, estimates of dominance genetic variance from seedling populations are also generally less accurate than estimates for additive genetic variance (Hardner, 2017). Estimates of total genetic correlation in annual NIS

between trial sites reported here are greater than previously reported (Hardner et al., 2002). In contrast, estimates of individual broad-sense heritability for TKR, proportion of whole kernels by mass, and mass of individual whole kernels are lower in this study compared with Hardner et al. (2001), implying that the accuracy of prediction of kernel recovery assessment was lower in the current study, possibly due to the use of unreplicated seedling progeny, or unknown sources contributing to variation in kernel recovery that obscure the genetic effect (Hardner et al., 2001).

This study is the first to report genetic parameters for AFC, mass of late dropping nuts per tree, and SK in macadamia. Our low estimate of individual broad-sense heritability for AFC suggests that this trait is not under strong genetic control and, hence, it may be difficult to make progress in this trait from incremental breeding approaches. Individual broad-sense heritability of mass of late dropping nuts per tree is comparable with that of NIS over the harvest. In this study, we employed the Australian macadamia industry's kernel quality rating system that is used to assess extent of shriveled kernel for commercial payment. However, our assessment method considered SK independent of other kernel defect traits, whereas the industry method involves initially sorting kernels into premium-, commercial-, and reject-quality grades and then classifying each lower quality kernel into a particular class of defect, which does not allow each cause of each kernel quality defect to be assessed separately.

Mixed linear model methodology simultaneously incorporating information across trials and planting densities within trials enabled the prediction of the clonal value of individuals for a 4-m planting density scenario at Bundaberg (i.e., B97), by using data from progeny that were only observed in other trials and planting densities. This was possible through the modeling of correlated genetic effects (Falconer, 1952; Henderson, 1977) via the numerator relationship matrix for additive genetic effects and replication of full-sib families across trials and planting densities. However, prediction of genetic values using this framework requires the

knowledge of the true values for genetic variances in each environment and genetic covariances among environments, which in this study were not known and required estimation using the available data (as is the case for most studies in tree crops), introducing further uncertainty of predicted genetic effects (Kackar and Harville, 1981). Here, only between 271 and 480 progeny were evaluated for a particular site and planting density, suggesting that the accuracy of the estimated (co)variance parameters may be low. Generally, the accuracy of estimation of additive genetic parameters (variance and among trial-by-density correlations) and prediction of additive genetic effects will be greater than for family effects. Observations from full- and half-sib seedling progeny and clonally replicated parents contribute to the estimation of additive genetic parameters and prediction of additive genetic effects, whereas estimation of family parameters and prediction of family effects only use observations on individuals from the same family. Therefore, the clonal replication of parents in this study is expected to contribute to improved accuracy of additive genetic effects, but it is likely to have little influence on the prediction accuracy of family effects. Further improvement in the accuracy of genetic parameters would require a larger number of parents and/or progeny, and/or clonal replication of progeny. In addition, it may be more appropriate to directly model (nonadditive) dominance effects using the dominance relationship matrix (Hardner, 2017; Henderson, 1985). An extension to the methods employed here would be to combine all traits into a single analysis, so that the accuracy of prediction for the total genetic worth of individual progeny could be improved through multitrait genetic correlations (Hardner et al., 2016; Henderson and Quaas, 1976; Thompson and Meyer, 1986).

The selection index approach used in this study aimed to identify candidates that were predicted to be the most profitable when the worth of a candidate is determined by multiple traits, as there may be different trait combinations with the same overall worth. Selection index contrasts to the concept of an

ideotype, which defines a single selection target of trait combinations. Selection index is also a repeatable and objective method that formalizes the priority of the different objective traits. The economic weights in this study were developed from a detailed bio-economic model of macadamia production and processing (Hardner et al., 2006). However, the assumptions used in this model may be different than those of other enterprises. Further analyses would be useful to understand the sensitivity of predictions to changes in model assump-

tions and uncertainty of genetic parameter estimates for a complex linear model. While the selection index used in this study includes traits associated with raw kernel appearance, no traits are included that are associated with differences in consumer preference for taste, texture, or appearance following roasting. Nevertheless, these traits are difficult and expensive to assess, and a previous study (O'Riordan et al., 2005) found that roasting treatment, rather than genetics or orchard source, had the greatest effect on consumer preference for

these traits. The use of phenotypic observations by the review committee to make decisions to not accept candidates that were ranked highly by the selection index is in contrast to the more formal quantitative genetic approach used to rank selection candidates. Nevertheless, many of the characteristics used to reject candidates were traits that had not been assessed, and this method provided a process for including these traits into the selection decision.

The present study provides learning that can be applied to improve the efficiency of future genetic improvement programs of the crop. First, breeding values predicted using the quantitative genetic methods applied here can be used to more accurately identify parents that are expected to produce progeny with high overall merit. Through this population-improvement approach, the mean of future generations of the breeding program will be greater than the mean of early generations, contributing to ongoing genetic improvement as demonstrated in many other organisms. Second, there may be opportunities to reduce the cost of evaluation through the use of the data generated here to develop alternative methods of assessment and selection. These may include truncation selection of individual with early low yield. This study did not examine genetic correlations among ages within a trait, or between traits, that could be used to evaluate opportunities for earlier age selection. Nevertheless, the assessment strategy adopted in this study was based on genetic parameters for yield and kernel traits estimated in Hardner et al. (2001) and Hardner et al. (2002).

Fig. 2. Frequency distribution of selection index values (H) of progeny in comparison with the mean of the cultivars evaluated in the trials, and the threshold index value for the top 40, 20, and 5 progeny individuals.

Table 7. Predicted clonal values for eight objective traits (AFC = age of first crop, CNIS8 = cumulative NIS to 8 years of age, LDNM = mass of late dropping nuts per tree, CW = canopy width, TKR = total kernel recovery, PWKM = proportion of whole kernel by mass, WKM = mass of individual whole kernels, SK = shriveled kernel rating) of the top 20 candidate cultivars selected for second stage testing. Also shown is the mean of the 10 commercial cultivars also tested in the trials. Strike-through indicates a candidate rejected by the industry selection review committee.

Rank	CW5 m	AFC yr	CNIS8 kg	LDNM7 kg	TKR g/100 g	PWKM g/100 g	WKM mm	SK 0-3
Mean CV	3.6	5.56	12.8	0.030	38.2	49.2	18.4	1.50
1	3.8	5.39	25.0	0.039	36.5	36.8	19.1	1.52
2	3.1	4.99	19.7	0.025	39.9	40.7	18.4	1.37
3	4.0	5.31	23.4	0.018	36.1	34.3	18.1	1.37
4	4.2	5.32	23.8	0.052	36.3	40.6	18.0	1.37
5	3.9	5.35	23.4	0.050	35.9	40.5	17.4	1.49
6	4.6	5.30	24.7	0.067	37.8	32.5	19.4	1.39
7	3.7	5.74	18.6	0.014	35.9	37.2	17.8	1.30
8	3.7	5.46	19.8	0.043	35.5	37.8	17.7	1.35
9	4.1	5.53	21.4	0.067	35.8	40.8	18.6	1.44
10	4.3	5.49	20.8	0.021	37.7	38.7	18.4	1.36
11	4.4	5.03	23.1	0.034	37.7	40.6	18.1	1.49
12	3.5	5.43	17.4	0.069	35.7	40.5	18.2	1.37
13	4.1	5.54	21.0	0.051	35.8	41.2	18.2	1.53
14	4.1	5.45	20.2	0.017	36.4	39.8	17.5	1.40
15	4.1	5.36	18.0	0.034	37.2	39.9	18.8	1.28
16	4.0	5.42	18.8	0.021	36.5	38.7	18.1	1.37
17	4.0	5.42	19.7	0.048	36.3	40.5	17.6	1.49
18	4.4	5.34	21.4	0.049	36.1	39.6	18.0	1.49
19	4.3	5.22	21.2	0.025	36.3	36.6	18.9	1.52
20	4.1	5.46	18.4	0.048	36.0	39.7	17.9	1.36
21	3.5	5.46	16.2	0.059	35.8	38.6	18.8	1.49
22	3.8	5.47	16.8	0.023	38.1	38.2	18.1	1.44
23	4.1	5.45	16.8	0.023	38.5	39.4	18.5	1.35
24	3.9	5.45	17.0	0.028	36.7	39.9	18.2	1.41
25	4.2	5.44	18.8	0.006	34.7	39.6	18.1	1.37

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