



Pollen-parent affects fruit, nut and kernel development of *Macadamia*

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ABSTRACT

The genotype of the pollen that fertilizes the ovule is known to affect the characteristics of fruits and nuts for many species, a phenomenon known as the xenia effect. Cross-pollination increases fruit set, nut mass, kernel mass and kernel recovery of macadamia nuts at maturity when compared with self-pollination. However there is limited information on the xenic effects of different macadamia cultivars used as cross pollen-parents on the fruit components and fruit development. The aim of this study was to clarify in what nut components and at what developmental stages xenic effects occurred. Two large-seeded macadamia cultivars, 'HAES 246' and 'HV A16', were used as maternal trees and pollen-parents were 'HAES 246', 'HV A16' and 'HAES 814', a small-seeded cultivar. Pollen-parents affected the mass of both the syngamous tissue of the kernel (embryo) and the tissues of maternal origin; i.e. the husk (pericarp) and shell (testa). Xenic effects were detected in the endosperm 6 weeks after pollination and in fruit, nut and kernel size and mass from 10 weeks after pollination until maturity. Nut mass, kernel mass and kernel recovery of macadamia were increased significantly by a different pollen-parent. The HV A16 pollen on HAES 246 flowers produced an increase of 11% nut mass compared with HV 814 pollen on HAES 246 flowers. This would increase the gross margin of a farm producing 4.5 t/ha of nuts by \$2574/ha at typical 2018 prices. Macadamia growers and the macadamia industry would benefit from identification and use of the most beneficial cross-pollen sources available.

1. Introduction

Cross-pollination is vital for producing sufficient food for the global human population since more than three quarters of the world's major food crops depend on cross-pollination for optimal production (Klein et al., 2007; Klatt et al., 2014). Cross-pollination of crops is also important for human health and reducing the levels of cross-pollination has the potential to seriously impact human nutrition (Chaplin-Kramer et al., 2014; Ellis et al., 2015; Smith et al., 2015; Brittain et al., 2014). The type of pollen-parent has many effects on crop yield and characteristics. Cross-pollination increases yield over self-pollination for many crops including olive, grape, mango and apple (Shemer et al., 2014; Sabir, 2015; Perez et al., 2016; Sapir et al., 2017). Different pollen-parents affect many characteristics of fruit and seeds including size, shape, colour and other properties such as sugar and oil composition, a phenomenon termed xenia (Denney, 1992; Wallace and Lee, 1999; Pahlavani and Abolhasani, 2006; Liu, 2008; Kodad et al., 2009; Seal et al., 2013; Piotto et al., 2013).

Xenic effects on fruit are sometimes attributed to an increased number of developing seeds from more successful pollination by better pollen-parents (George and Nissen, 1986; Kahn et al., 1994; Keulemans

et al., 1996; Taber and Olmstead, 2016). Different pollen-parents increase fruit size, sugar content, fruit set and seed number for many-seeded fruits mandarin (Wallace and Lee, 1999; Wallace et al., 2002) and blueberry (Gupton and Spiers, 1994; Taber and Olmstead, 2016). However, xenic effects also occur in single-seeded fruits; e.g., 'Teague', 'Topa-Topa' and 'Ettinger' cross-pollens increase fruit and seed mass compared with self-pollen on pollinated 'Fuerte' avocados (Degani et al., 1990). 'Kalibar8' and 'Kalibar11' pollen-parents increase nut and kernel mass compared with self-pollen on 'Fertile de Coutard' and 'Negret' hazelnuts (Fattahi et al., 2014). Most research into the effect of pollen-parents has compared cross-pollen with self-pollen and there is little information comparing different cross-pollen sources.

There are at least seven species of *Macadamia* (Proteaceae) in Australia (Gross and Hyland, 1993) but only two species *M. integrifolia* (Maiden and Betche) and *M. tetraphylla* (L.A.S. Johnson) and their hybrids are grown commercially (Trueman, 2013). Macadamia is a single-seeded nut crop indigenous to the sub-tropical rainforests of eastern Australia (Hardner et al., 2009, 2012). Macadamia is cultivated in Australia, South Africa, Hawaii, Brazil, China and other countries (Trueman, 2013; Howlett et al., 2015). *M. integrifolia* and *M. tetraphylla* readily hybridize (Peace, 1997). Commercial macadamia cultivars are

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clonal, propagated mainly by grafting and to a limited extent by cuttings. The fruit of the edible macadamia consists of a fibrous pericarp ('husk') covering the seed ('nut') (Stroschen, 1986). The edible embryo ('kernel') is encased in the hard integument ('shell') of the seed (Stroschen, 1986; Trueman, 2013).

Macadamia flowers are pollinated by insects (Heard, 1994; Wallace et al., 1996; Trueman, 2013). Macadamia flowers are known to be self-incompatible, with pollen from the same cultivar (i.e. the same genotype) resulting in poor fruit set (Sedgley et al., 1990). Cross-pollen, i.e. pollen from a different cultivar increases fruit set, nut mass, kernel mass and kernel recovery of macadamia compared with self-pollen (Ito and Hamilton, 1980; Sedgley et al., 1990; Wallace et al., 1996; Meyers, 1997; Vithanage et al., 2002). Supplementary cross-pollination of macadamia increases final fruit set and nut mass compared with open-pollination (Trueman and Turnbull, 1994; Wallace et al., 1996). There is only limited research into the effect of different cross-pollen cultivars as pollen-parents (Meyers, 1997). Details of when and where xenia manifests during the development of macadamia fruit and fruit components have not been studied.

The aim of this study was to identify what macadamia tissues are affected by different cross-pollens from clonal cultivars and when these effects occur during fruit development. We examined: 1) differences in fruit size and 2) differences in fruit components during fruit development. We expected to see differences not only in the syngamous tissue of the embryo (kernel) and tissues of combined maternal and paternal origin, but also limited effects on purely maternal tissues such as the pericarp (husk) and testa (shell). This study will provide a clearer understanding of the importance of xenia in macadamia, particularly how different pollen-parents affect the economic parameters kernel size, kernel mass and kernel recovery.

2. Materials and methods

2.1. Plant materials

Three commercial macadamia cultivars were used in this study, HAES 246 ('246'), HV A16 ('A16') and HAES 814 ('814'). '246' is a long-established, widely-planted cultivar that was developed in Hawaii, as was '814', which is a less-planted open-pollinated selection of unknown lineage (Hardner et al., 2009). 'A16' is another widely-planted cultivar of unknown lineage that has been developed in Australia. '246' and 'A16' were used as maternal trees. '246', 'A16' and '814' were used as pollen-parents. The cultivars in the current experiments were identified previously as having large differences in nut and kernel size (Meyers, 1997). Cultivars '246' and 'A16' have large nuts whereas '814' has small nuts.

2.2. Experimental design

There were three maternal trees from each of '246' and 'A16'. There were two pollination treatments on each tree. '246' maternal trees were pollinated with 'A16' and '814' pollen and 'A16' trees were pollinated with '246' and '814' pollen, giving three replicates for each pollination treatment for each maternal cultivar.

2.3. Cross-pollen effects on fruit size

Inflorescences on three trees of '246' were cross-pollinated with pollen from 'A16' and pollen from '814'. Three trees of 'A16' were pollinated with pollen from '246' and '814'. Forty racemes on each tree were enclosed in paper bags before anthesis. Twenty racemes on each tree were cross-pollinated with each pollen. Each raceme has 200 to 300 flowers (Wallace et al., 1996). Pollen was collected at anthesis using 30-cm diameter glass test tubes (Trueman and Turnbull, 1994) and transferred to the bagged racemes. Two fruits on three racemes per pollen-parent cross per tree were removed from the tree every 2 weeks

from 2 to 18 weeks after pollination and their diameter was measured.

2.4. Cross-pollen effects on development of fruit components

Twenty racemes on each of three '246' maternal trees were pollinated using 'A16' pollen and an additional 20 racemes were pollinated with '814' pollen as described above. In addition, 20 racemes on each of three 'A16' maternal trees were pollinated with pollen of '246' and '814' as described above. Two fruit were sampled from each of three racemes for each pollen-parent cross on each of the three trees as for 2.3. until week 22, except at week 20 when no fruit were sampled. Fruit diameter was measured then each fruit was dissected. Husk, shell, kernel and endosperm dry mass and nut, kernel and endosperm diameters were measured. Shell hardness at each sampling time was assessed by cutting with a sharp knife. Shells were considered as hardened when they could no longer be cut through with a sharp knife. Racemes were then enclosed in mesh bags to retain mature fruit as they abscised from the tree.

Fruit were dehusked to release the nuts, and nuts were then dried at 45°C for 6 d (Trueman et al., 2000, 2002; Trueman, 2003a,b) in a fan-forced laboratory oven (Memmert GmbH & Co. KG, Schwabach, Germany). Nut diameters were measured, then nuts were cracked manually using a TJs™ nutcracker, and nut mass, shell mass, kernel mass, kernel diameter and kernel recovery were determined. Kernel recovery was calculated by expressing the mass of sound kernel as a percentage of the mass of whole nuts in a sample. Kernels were considered sound if they were free from discolouration, immaturity, insect damage or mould (Walton and Wallace, 2008, 2009, 2010).

2.5. Statistical analysis

Means between different pollen-parent treatments on each maternal cultivar were compared using Student's *t*-tests applied at each sampling time (SPSS version 10.05). Means were considered significantly different at $P < 0.05$.

3. Results

3.1. Cross-pollen effects on fruit size

Fruit resulting from 'A16' pollen on '246' flowers were larger than fruit resulting from '814' pollen from week 14 onwards (Fig. 1a).

Fruit resulting from '246' pollen on 'A16' flowers (A16 × 246) were larger than fruit resulting from '814' pollen (A16 × 814) from week 6 onward, with the exception of at 14 weeks (Fig. 1b).

3.2. Cross-pollen effects on development of fruit components

The diameters of the fruit, nuts and kernels were all greater for the fruit resulting from 'A16' pollen on '246' flowers compared with '814' pollen on '246' flowers from week 10 to week 22, except for week 12 (Fig. 2a–c). Kernel, husk and shell dry mass were all larger for the fruit resulting from 'A16' pollen on '246' flowers compared with '814' pollen on '246' flowers at week 18 and week 22 (Fig. 2d,e,f). Most of the dry matter in the kernels was accumulated after they had expanded to full diameter in week 14 (Fig. 2c and f). The timing of shell hardening was markedly different between the cross-pollens, as 27% of shells resulting from 'A16' pollen on '246' flowers had hardened at week 14 whereas 95% of shells resulting from '814' pollen on '246' flowers had hardened at week 14. All shells had hardened by week 16.

The endosperm dry mass of the fruit resulting from 'A16' pollen on '246' flowers was greater than for '814' pollen on '246' flowers at 6 weeks and at 10 weeks (Table 1). By 10 weeks the embryo diameter was also greater for the fruit resulting from 'A16' pollen on '246' flowers than for '814' pollen on '246' flowers (Table 1). The embryo of the fruit resulting from 'A16' pollen on '246' flowers had expanded by week 10

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