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Review

# The reproductive biology of macadamia

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ABSTRACT

Macadamia is a widely-grown tree crop that produces edible kernels with high oil content. The macadamia kernel is the single embryo of the fruit, and so factors that influence fruit set and embryo development are critical regulators of yield and quality. This review summarises over 75 years of research on floral induction, floral structure, pollen transfer, the breeding system and fruit development of macadamia, highlighting features such as insect pollination and partial self-incompatibility that limit orchard productivity and affect kernel quality.



**Contents**



## 1. Introduction

The genus, *Macadamia* (Proteaceae), is comprised of four evergreen tree species endemic to the rainforests and rainforest fringes of subtropical eastern Australia (Mast et al., 2008; Neal et al., 2010; Shapcott and Powell, 2011). The kernels of two species, *M. jansenii* and *M. ternifolia*, are inedible due to the presence of high levels of cyanogenic glycosides, and so macadamia cultivars are derived from two freely-hybridising species, *M. integrifolia* and *M. tetraphylla*, that contain low levels of cyanogenic glycosides in their mature kernels (Storey, 1985; Gross and Weston, 1992; Dahler et al., 1995). Macadamia is grown extensively in commercial plantations in Australia, South Africa, Brazil, Hawaii, Kenya and Costa Rica, and most cultivars have been derived from selection programmes in Hawaii and Australia that identified superior-yielding seedling trees (Nagao and Hirae, 1992; Stephenson and Gallagher, 2000; Peace et al., 2003; Steiger et al., 2003; Hardner et al., 2009). These cultivars are propagated clonally by grafting onto seedling rootstocks, although tissue culture methods have been developed recently for macadamia seedlings (Cha-um et al., 2011). Orchards are typically comprised of two or more cultivars, often with a principal cultivar and the other cultivars planted in 'pollinator' rows. However, macadamia is sometimes planted in partial or complete blocks of a single cultivar (Ito and Hamilton, 1980; Stace, 1986; Trueman et al., 2002). The commercial product of macadamia is the single embryo of the fruit, and so limitations to fruit set and embryo development have important economic consequences for macadamia growers. This review describes the processes of floral initiation, flowering, pollination and fruit development in

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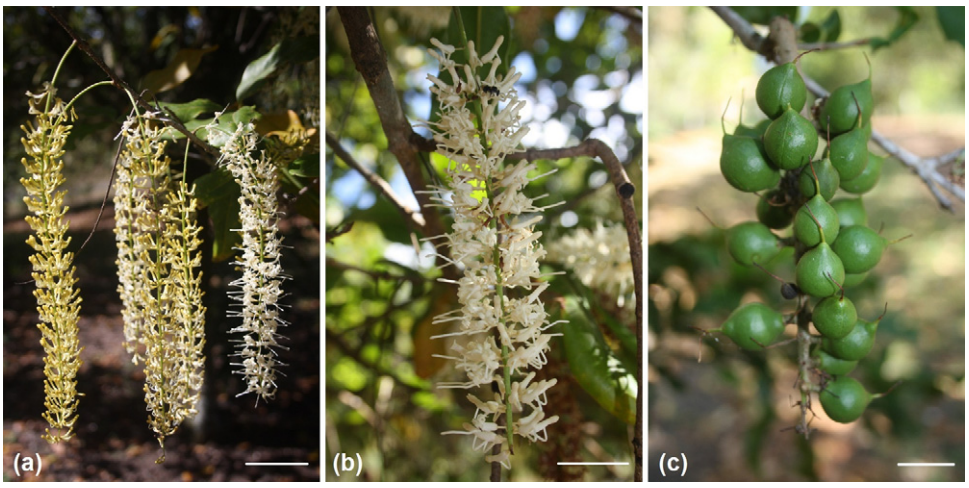


**Fig. 1.** (a) Macadamia racemes progressing from pre-anthesis (left raceme) to anthesis (right raceme). Scale bar = 30 mm; (b) raceme in which most flowers have opened. A small stingless bee (*Tetragonula* sp.) is foraging at flowers near the top of the raceme. Scale bar = 15 mm; (c) A macadamia infructescence at the stage of immature fruit drop. Scale bar = 10 mm.

macadamia, focussing on factors that might limit fruit set, nut yield and kernel quality.

## 2. Floral induction

Macadamia has three buds in every leaf axil that can potentially develop into shoots or inflorescences (Storey, 1985; Wilkie et al., 2009a). Usually only one of the buds develops in each leaf axil and, since there are three leaves per node in *M. integrifolia* and four leaves per node in *M. tetraphylla*, three or four inflorescences develop per node in these species and their hybrids (Storey, 1985). The inflorescence is a pendant raceme (Fig. 1a) bearing between 100 and 300 flowers, with whorls of six pairs of flowers at each node of the rachis (Storey, 1985; Joubert, 1986; Trueman and Turnbull, 1994a). Floral initiation in the orchards of eastern Australia occurs during late autumn or winter when minimum temperatures are between 11 °C and 15 °C (Moncur et al., 1985; Olesen, 2005; Wilkie et al., 2010). Macadamia buds undergo little growth for 50–96 d after initiation (Moncur et al., 1985) possibly because of unfavourable environmental conditions such as cool temperature and low solar irradiance (Moncur et al., 1983). Raceme elongation commences in mid-late winter (Moncur et al., 1985) and peak anthesis usually occurs in late winter or early spring (Heard, 1993; Nagao et al., 1994; Trueman and Turnbull, 1994a,b; Wallace et al., 1996; Wilkie et al., 2009a).

The effects of photoperiod on floral initiation in macadamia are not known, although macadamia may be day-neutral as *M. integrifolia* produces flowers all the way from the Equator to 40°S. Floral initiation of potted trees at a controlled day temperature of 25 °C occurs at a wide range of night temperatures (5 °C, 10 °C, 15 °C and 20 °C) although raceme production during a return to low ambient temperatures (mean 10.5 °C at night) is much greater in trees that have been exposed to the warmest (20 °C) nights (Stephenson and Gallagher, 1986). However, in trees that have already initiated floral buds, further raceme production occurs at night temperatures of 12 °C, 15 °C and 18 °C but it is almost completely inhibited at 21 °C (Nakata, 1976). Removal of an entire season's racemes can invoke an earlier and more intense flowering in the following season (Stephenson et al., 1989), trunk girdling before floral buds become visible can almost double the number of racemes produced in that season (Nagao and Sakai, 1990), and application of the growth retardant, uniconazole, greatly increases flowering of young trees (Nagao et al., 1999). These results suggest that carbohydrate availability may also affect floral initiation.

Mature macadamia trees can produce up to 2500 racemes in a flowering season (Moncur et al., 1985; Moncur, 1988; McFadyen et al., 2011; Olesen et al., 2011). In many cultivars, some racemes are produced on stems less than 1 year old, but most are produced on wood at least 2 years old in areas of the canopy that are heavily shaded (Nagao et al., 1994; Wilkie et al., 2009a; Olesen et al., 2011). However, some cultivars such as A4 produce many racemes on young stems at the outer edge of the canopy (Wilkie et al., 2009a). Racemes tend to be produced on less-vigorous and shorter stems; e.g. <30-cm length in cultivar 660, <60-cm length in cultivars A38 and 695, and <80-cm length in cv. A4 (Wilkie et al., 2009a).

Canopy pruning is required to allow machinery access and improve spray penetration in macadamia orchards (McFadyen et al., 2004, 2005). Yield can be strongly affected by the timing of canopy pruning because pruning disturbs the cycle of recurrent vegetative flushes, subjecting the new flush to different conditions of temperature and irradiance and altering carbohydrate availability (Olesen et al., 2006; Wilkie et al., 2009b, 2010). This, in turn, affects stem elongation, raceme production and abscission of the young fruit (Olesen, 2005; Wilkie et al., 2009b, 2010; Olesen et al., 2011; McFadyen et al., 2011, 2012a,b). Pruning times, such as early autumn, that provide an immature vegetative flush in late autumn and early winter can inhibit raceme production and reduce yield (Wilkie et al., 2010). Other pruning times, such as early to mid-spring, that provide an immature vegetative flush during early fruit development can increase abscission of young fruit and also reduce yield (McFadyen et al., 2011, 2012a).

## 3. Floral structure

Macadamia flowers at anthesis are typically about 15 mm long including a 3-mm pedicel, with one anther attached by a short filament to each of four petal-like perianth segments (Scholefield, 1982; Storey, 1985; Joubert, 1986). The pistil consists of a unicarpellate, superior, pubescent ovary and a slender style with a club-shaped tip, on which rests the small stigmatic area (Urata, 1954; Storey, 1985; Wallace et al., 1992). The ovary contains two orthotropous ovules (Sedgley, 1981; Strohschen, 1986). Macadamia styles begin to elongate and bend about 6–7 d before anthesis, and the mid-portion of the style protrudes through the abaxial suture between two perianth segments 2–5 d before anthesis (Urata, 1954; Sedgley et al., 1985). Anther dehiscence occurs 1–2 d before anthesis (Urata, 1954; Sedgley et al., 1985) and the triaperturate pollen is deposited in clumps on the stigma and upper