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Full Length Research Paper

Benzyladenine delays immature fruit abscission but does not affect final fruit set or kernel size of *Macadamia*

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Macadamia **is a mass-flowering subtropical rainforest tree that is widely cultivated for its edible kernels.** ***Macadamia*** **flowers are borne on pendant racemes of 100 - 300 flowers but typically less than 2% of the flowers produce mature fruits and kernels. This study investigated the use of plant growth regulators to reduce abscission of flowers and immature fruit and to increase final fruit set of** ***Macadamia*****. Pre-anthesis applications of the cytokinin, benzyladenine at 200 mg/L, increased initial fruit sets (2 weeks after anthesis) across four experiments from 8 - 17% (for control racemes) to 27 - 61% (for treated racemes). Post-anthesis applications of benzyladenine increased fruit retention up to 8 weeks after anthesis, but no treatment increased fruit retention beyond the final phase of immature fruit drop at 10 weeks post-anthesis. Benzyladenine delayed abscission of immature** ***Macadamia*** **fruit but it had no effect on final fruit set, nut-in-shell weight or kernel weight.**

Key words: Auxin, benzylaminopurine, cytokinin, fruit drop, gibberellin, nut, paclobutrazol, plant growth regulators, pollen tubes, Proteaceae.

INTRODUCTION

Macadamia cultivars are derived from two freely hybridising species, *Macadamia integrifolia* and *M. tetraphylla*, indigenous to the subtropical rainforests of eastern Australia. Both species and their hybrids are grown commercially in South Africa, Australia, Hawaii and Brazil. *Macadamia* flowers are borne on pendant racemes produced in the leaf axils (Wilkie et al., 2009). Each raceme comprises between 100 and 300 flowers, and fertilisation occurs within 7 days of anthesis (Ito, 1980; Sedgley, 1983). Rapid abscission occurs during the following week, commonly involving more than 80% of the flowers (Sakai and Nagao, 1985; Trueman and Turnbull, 1994a, b). This precedes a period of immature fruit drop up to 8 - 10 weeks after anthesis (Sakai and Nagao, 1985; Trueman and Turnbull, 1994b) during which fertilised fruits abscise (Sedgley, 1981). Fruits reach maturity approximately 24 weeks post-anthesis (Nagao and Sakai, 1988; Trueman et al., 2000) and are later harvested from the ground, dehusked to yield nut-in-shell (NIS), and cracked to provide the kernel (Walton and Wallace, 2008, 2009). Typically, less than 2% of flowers remain after the period of immature fruit drop to produce mature fruits (Trueman and Turnbull, 1994a; Wallace et al., 1996).

Plant growth regulators are used on many tree crops to manipulate immature fruit drop, increase fruit set or fruit size, and loosen or remove fruits (Bangerth, 2000; Bubán, 2000; Wertheim, 2000; Stover and Greene, 2005; Burns et al., 2008). The only growth regulator currently used for *Macadamia* is the ethylene-releasing compound, ethephon, which induces abscission of mature macadamia fruits in preparation for harvest from the orchard floor (Gallagher and Stephenson, 1986; Stephenson and Gallagher, 1987; Nagao and Sakai, 1988; Trueman et al., 2002; Trueman, 2003a, b). An auxin, naphthalene acetic acid (NAA) at 1, 10, or 100 mg L^{-1}, has been tested for reducing immature fruit drop of *Macadamia* but no effects were found on the initial or final numbers of fruit set per raceme (Williams, 1980). There are currently no recommendations for the use of growth regulators to reduce immature fruit drop or increase nut or kernel size of *Macadamia*. With the exception of applications employed to produce late season effects, most growth regulators are applied to tree crops within a four week period after

anthesis (Bubán, 2000; Wertheim, 2000; Flaishman et al., 2001; Greene, 2001; Stover and Greene, 2005; Watanabe et al., 2008). Sedgley et al. (1990) suggested that *Macadamia* yields could be increased by achieving maximal initial fruit set prior to the subsequent period of immature fruit drop. Trueman and Turnbull (1994a) and Wallace et al. (1996) subsequently showed that supplementary cross-pollination of *Macadamia* increases initial fruit set, and that increased initial set is sometimes translated into higher final set. In the present study, four growth regulators (a cytokinin, benzyladenine (BA); a gibberellin (GA_3); a gibberellin synthesis inhibitor, paclobutrazol (PBZ; that is, 1-(4-chlorophenyl) 4,4-dimethyl-2-(1, 2, 4-triazoll-yl) pentan-3-ol); and an auxin, NAA) were applied to *Macadamia* racemes immediately pre-anthesis to test their ability to affect initial and final fruit sets. Experiments in subsequent years determined the effects of single or repeated cytokinin applications (pre-anthesis and/or 3 weeks post-anthesis) on pollen tube penetration, initial fruit set, final fruit set, and nut-in-shell (NIS) and kernel size.

MATERIALS AND METHODS

Four experiments were conducted at two orchards in eastern Australia, using *Macadamia* cultivars, '246' ('Keauhou'), '660' ('Keaau') and 'A4' ('Hidden Valley A4'). Experiments 1 and 4 were performed at Hidden Valley Plantations, Beerwah, Queensland (26°50'S 152°56'E) and Experiments 2 and 3 were performed at Wollongbar, New South Wales (28°49'S 153°23'E) in an orchard managed by *Macadamia* Plantations of Australia Pty Ltd.

General method

Racemes were selected and tagged approximately 4 day pre-anthesis (Figure 1A), and the number of flowers per raceme was counted (Figure 1B). Growth regulators were applied in ethanol: water (1/1, v/v) solutions by spraying racemes until runoff (approximately 3 mL per raceme), each raceme being partially enclosed in a sheet of aluminium foil during spraying to reduce spray drift. An ethanol: water (1/1, v/v) solution was used as the control in each experiment. Initial fruit set (14 day post-anthesis) (Figure 1C) and final fruit set (between 105 and 135 day post-anthesis) (Figure 1D) were determined for each raceme in all experiments. Fruit sets were also determined on additional days in Experiments 2 - 4 (below). Mature fruits from Experiments 3 and 4 were harvested at 221 day and 199 day post-anthesis respectively. These fruits were dehusked to provide the nut-in-shell (NIS) (Figure 1E) and then cracked to provide the kernel (Figure 1F). NIS and kernel weights were recorded for each fruit.

Two additional racemes per treatment from each tree in Experiments 2 - 4 were collected 7 day post-anthesis for examination of pollen tube growth. The flowers were fixed in glacial acetic acid / ethanol (1/3, v/v), and later rinsed in water for 1 h, autoclaved for 15 min in 10% sodium sulphite, rinsed in water for another hour, and then placed in decolourised aniline blue. Twenty-five flowers per raceme were randomly selected for microscopic examination, and each was dissected longitudinally with a single scalpel cut along the length of the style before being squashed gently in a drop of decolourised aniline blue. Each flower was then examined for pollen tube penetration to the base of the style.

Experiment 1

Twenty-seven racemes were selected and tagged on each of five cv. 246 trees. Eight treatments (BA at 50 or 200 mg L^{-1}, GA_3 at 50 or 200 mg L^{-1}, PBZ at 500 or 2000 mg L^{-1}, and NAA at 10 or 50 mg L^{-1}) and a nil-hormone control were each applied 1 day pre-anthesis to three racemes per tree. All racemes were pollinated using cv. 'H2' ('Hinde') pollen, employing the test-tube pollination method described by Trueman and Turnbull (1994a). Fruit sets were determined 14 days and 110 days later.

Experiment 2

Ninety racemes were selected and tagged on each of five cv. 660 trees. Two treatments (BA at 50 or 200 mg L^{-1}) and a nil-hormone control were each applied 4 days pre-anthesis to 30 racemes per tree. Flowers were not hand-pollinated. Fruit sets were determined 14, 21, 39 and 105 days post-anthesis.

Experiment 3

In the following year, 120 racemes were selected and tagged on each of five cv. 660 trees, and all racemes were sprayed both 3 day pre-anthesis and 21 days post-anthesis. Thirty of the racemes per tree were allocated to each of four treatments: '0/0', '0/200', '200/0' and '200/200', where the first and second figures represent the BA concentration (in mg L^{-1}) of the pre-anthesis and post-anthesis spray, respectively. Flowers were not hand-pollinated. Fruit sets were determined 14, 21, 39, 56, 70 and 135 days post-anthesis, and fruits were harvested 221 day post-anthesis for measurement of their NIS and kernel weights.

Experiment 4

Forty racemes were selected and tagged on each of five cv. A4 trees. The treatments were the same as Experiment 3, except that the pre-anthesis treatment was applied 1 day pre-anthesis, and there were ten racemes per treatment within each tree. Flowers were not hand-pollinated. Fruit sets were determined 14, 21, 39, 56, 70 and 114 days post-anthesis, and fruits were harvested 199 days post-anthesis for measurement of their NIS and kernel weights.

Statistical analyses

Analyses of variance were performed on the pollen tube penetration, fruit set, NIS weight and kernel weight results, regarding trees as blocks in randomised block designs, and using square or cube root transformations where necessary to achieve normality of the distributions. Post-hoc least significant difference (LSD) tests were performed only when significant differences were detected by analysis of variance. Means are reported with standard errors, and treatment differences were regarded as significant at $P < 0.05$.

RESULTS

Experiment 1

The percentage of cv. 246 flowers that initially set fruits (that is, 14 days post-anthesis) was significantly increased by pre-anthesis BA sprays, but was not significantly affected by GA_3 or PBZ sprays (Figure 2).

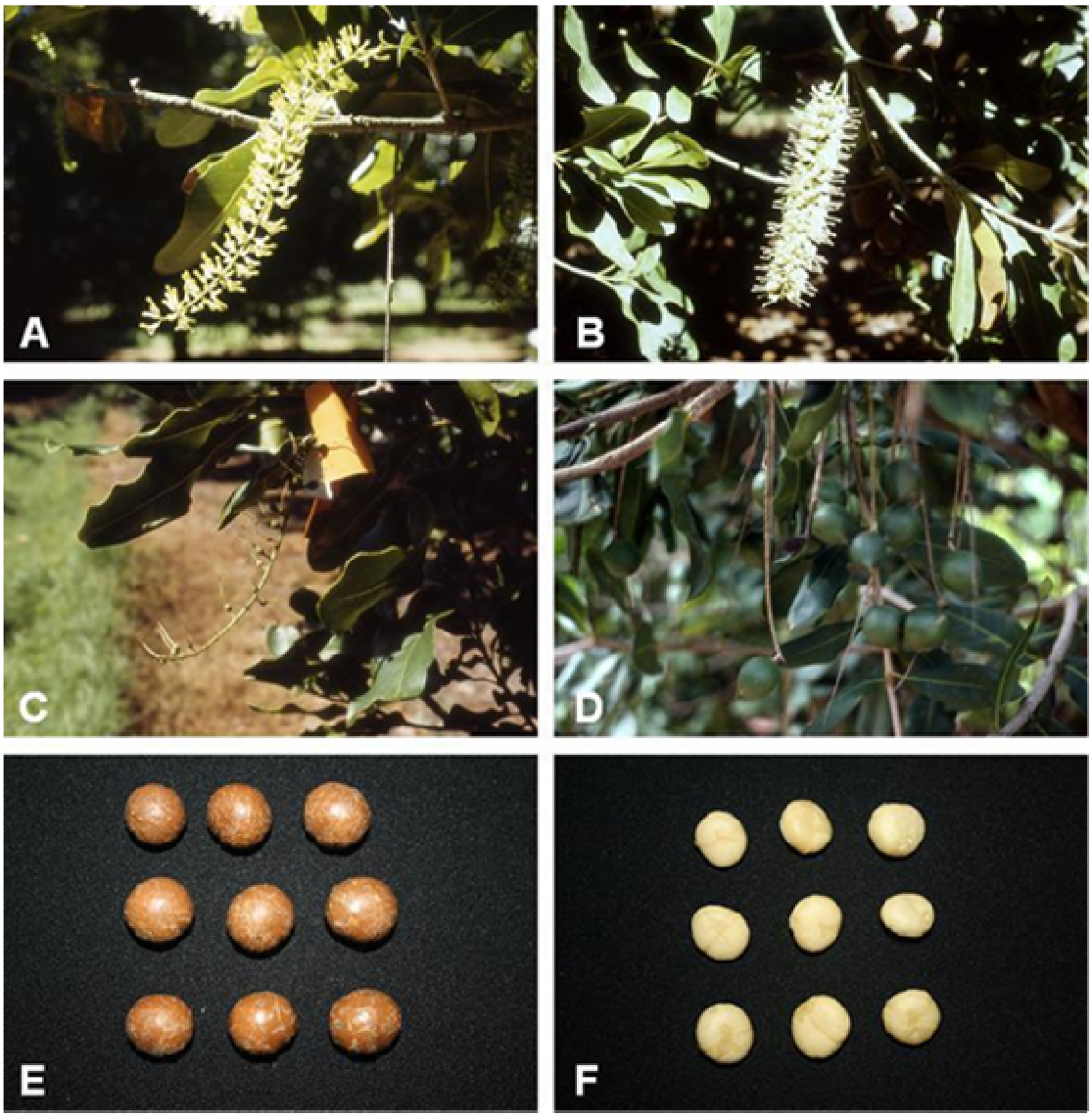

Figure 1. *Macadamia* flowers prior to anthesis (A) and at anthesis (B); *Macadamia* fruits at 14 d post-anthesis (C) and at final fruit set (D); and *Macadamia* nut-in-shell (E) and kernels (F).

Initial fruit sets of 28.7 ± 3.4% and 61.1 ± 3.8% were attained on racemes treated with BA at 50 mgL^{-1}and 200 mg L^{-1}, respectively, compared with 17.3 ± 2.0% for control racemes. Treatment with NAA at 10 mg L^{-1} caused a significant reduction in initial fruit set, with a mean of 5.9 ± 1.2%. Final fruit sets did not differ significantly among treatments.

Experiment 2

Initial fruit sets of cv. 660 racemes were significantly increased by a pre-anthesis spray of BA at 200 mg L^{-1}, but not by BA at 50 mg L^{-1} (26.9 ± 0.9% and 10.9 ± 0.4%, respectively, compared with 10.6 ± 0.7% on control racemes) (Figure 3). Fruit sets on racemes treated with BA at 200 mg L^{-1} remained significantly greater than the controls at 21 days post-anthesis but not at 39 days post-anthesis or final set. Final fruit sets were 0.61 ± 0.07%, 0.54 ± 0.06% and 0.64 ± 0.06% for the 0 mg L^{-1}, 50 mg L^{-1} and 200 mg L^{-1} BA treatments, respectively.

Experiment 3

A single pre-anthesis spray of BA at 200 mg L^{-1} (200/0 treatment) significantly increased fruit sets of cv. 660 racemes at 14, 21 and 39 days post-anthesis but the effect was not maintained to 56 or 70 days post-anthesis or to final set (Figure 4). The initial fruit set on BA-treated

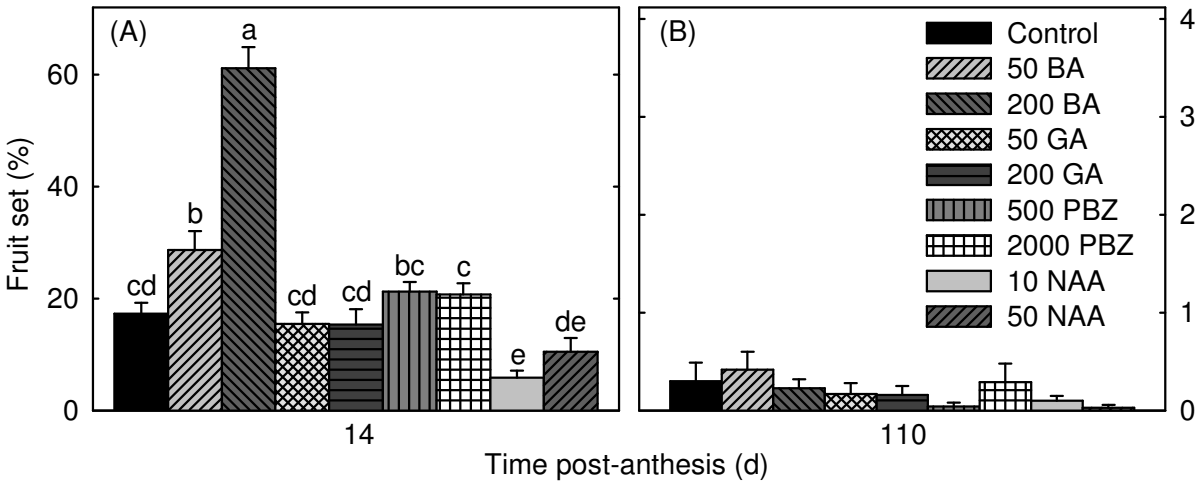

Figure 2. Effect of pre-anthesis applications of benzyladenine (BA) at 50 or 200 mg L^{-1}, gibberellic acid (GA) at 50 or 200 mg L^{-1}, paclobutrazol (PBZ) at 500 or 2000 mg L^{-1}, or naphthalene acetic acid (NAA) at 10 or 50 mg L^{-1} on the percentage of *Macadamia* cv. 246 flowers in Experiment 1 retained as fruit at (A) 14 d post-anthesis and (B) 110 d post-anthesis. Means (+ SE) with different letters are significantly different (ANOVA and LSD test, $P < 0.05$, n = 15).

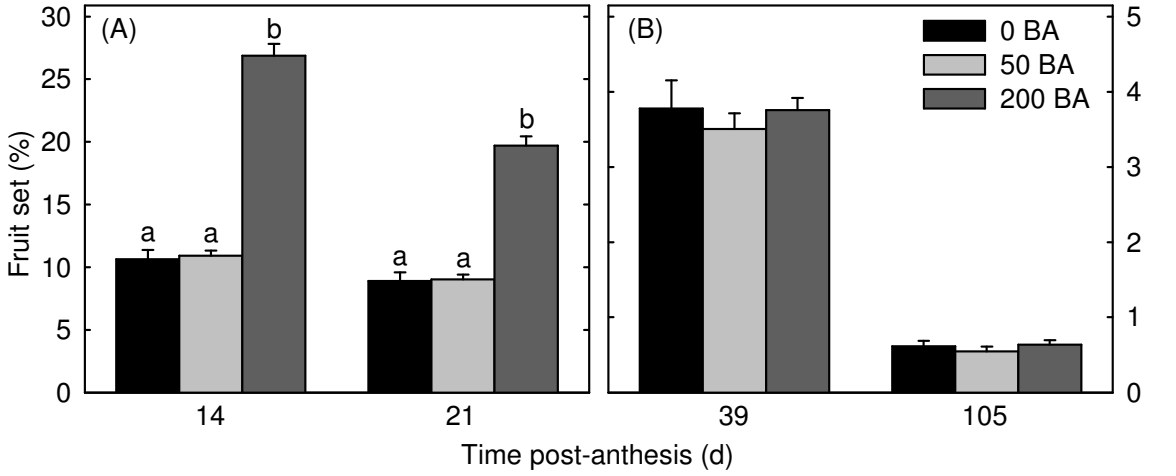

Figure 3. Effect of pre-anthesis benzyladenine applications (at 0, 50 or 200 mg BA L^{-1}) on the percentage of *Macadamia* cv. 660 flowers in Experiment 2 retained as fruit at (A) 14 d and 21 d post-anthesis and (B) 39 d and 105 d post-anthesis. Means (+ SE) with different letters are significantly different (ANOVA and LSD test, $P < 0.05$, n = 150).

racemes was 50.0 ± 1.0%, compared with 13.7 ± 0.6% on control racemes. A single BA spray 21 days post-anthesis (0/200) significantly increased fruit sets at 39 and 56 days post-anthesis but the effect was not maintained to 70 days post-anthesis or final set. The same was the case for the double BA treatment (pre-anthesis plus 21 days post-anthesis sprays) (200/200) even though fruit sets at 39 d post-anthesis were significantly greater for this treatment than for either of the two single-spray treatments. Final fruit sets for the 0/0, 0/200, 200/0 and 200/200 mg L^{-1} BA treatments were 0.53 ± 0.05%, 0.54 ± 0.05%, 0.42 ± 0.05% and 0.43 ± 0.05%, respectively.

Experiment 4

A single pre-anthesis spray of BA at 200 mg L^{-1} (200/0) to cv. A4 racemes significantly increased fruit sets at 14 and 21 d post-anthesis but not at 39, 56 or 70 days post-anthesis or at final set (Figure 5). The initial fruit set on the BA-treated racemes was 47.9 ± 2.0%, compared with 7.7 ± 0.9% on the control (0/0) racemes. A single BA spray 21 days post-anthesis (0/200) had no significant effect on fruit sets at 39, 56 or 70 days post-anthesis or at final set. The double BA treatment (pre-anthesis plus 21 days post-anthesis sprays) (200/200) significantly increased fruit sets at 39 and 56 days post-anthesis but

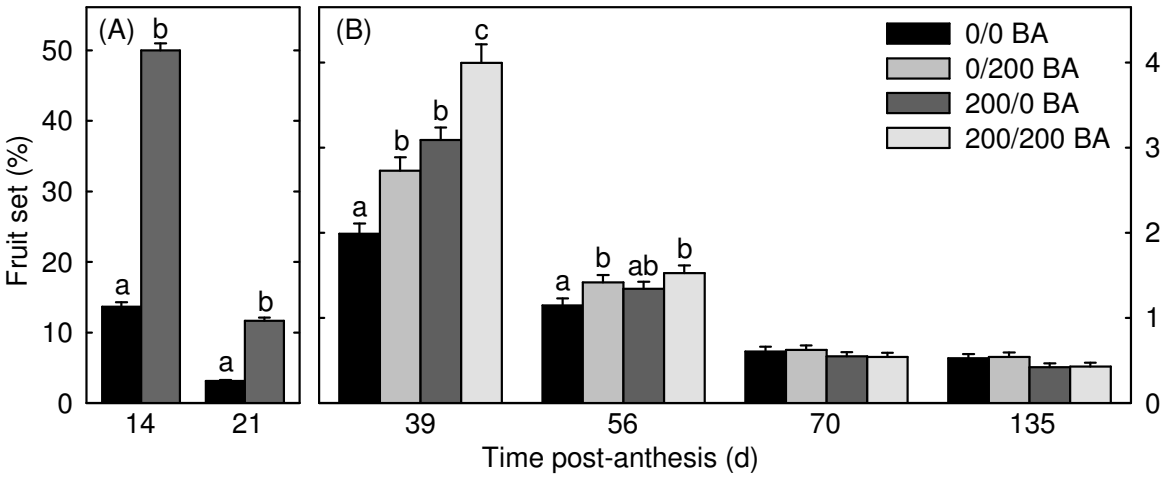

Figure 4. Effect of single or repeat benzyladenine applications on the percentage of *Macadamia* cv. 660 flowers in Experiment 3 retained as fruit at (A) 14 d and 21 d post-anthesis and (B) 39 d, 56 d, 70 d and 135 d post-anthesis. The first and second numbers (e.g. 0/200) refer to the 3-d pre-anthesis and 21-d post-anthesis treatment concentrations (mg BA L^{-1}), respectively. Means (+ SE) with different letters are significantly different (ANOVA and LSD test, $P < 0.05$, n = 150).

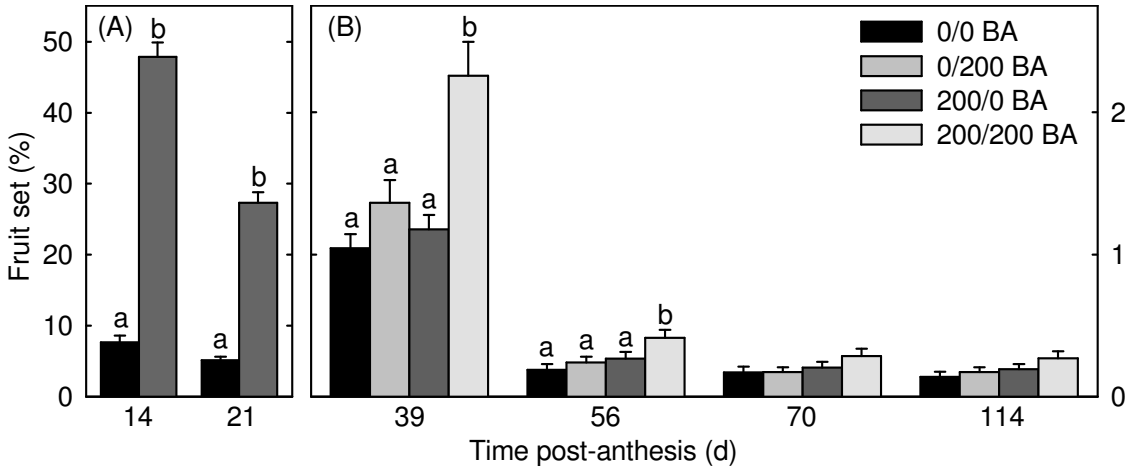

Figure 5. Effect of single or repeat benzyladenine applications on the percentage of *Macadamia* cv. A4 flowers in Experiment 4 retained as fruit at (A) 14 d and 21 d post-anthesis and (B) 39 d, 56 d, 70 d and 114 d post-anthesis. The first and second numbers (e.g. 0/200) refer to the 1-d pre-anthesis and 21-d post-anthesis treatment concentrations (mg BA L^{-1}), respectively. Means (+ SE) with different letters are significantly different (ANOVA and LSD test, $P < 0.05$, n = 50).

the effect was not maintained to 70 d post-anthesis or to final set. Final fruit sets were low for all the treatments: 0.14 ± 0.04%, 0.17 ± 0.03%, 0.19 ± 0.04% and 0.27 ± 0.05% for the 0/0, 0/200, 200/0 and 200/200 mg L^{-1} BA treatments, respectively.

Pollen tubes

Pre-anthesis sprays of BA at 50 or 200 mg L^{-1} did not affect the percentage of flowers bearing a pollen tube at the base of the style (Table 1).

NIS and kernel weights

Sprays of BA at 200 mg L^{-1}, pre-anthesis and/or 21 days post-anthesis, did not affect NIS or kernel weights (Table 2).

DISCUSSION

Initial screening of four different types of growth regulators applied as pre-anthesis sprays showed that only BA (at 50 or 200 mg L^{-1}) increased initial fruit set of

Table 1. Effect of pre-anthesis BA sprays on the percentage of *Macadamia* flowers with a pollen tube at the base of the style 7 d post-anthesis.

	BA concentration (mg L^{-1})		
	0	**50**	**200**
Experiment 2, cv. 660	40.0 ± 4.8	35.2 ± 5.1	33.6 ± 3.1
Experiment 3, cv. 660	23.6 ± 2.2	-	26.8 ± 2.6
Experiment 4, cv. A4	21.2 ± 2.2	-	24.0 ± 1.7

Means (± SE) do not differ significantly in any experiment (ANOVA, $P > 0.05$, $n = 10$ racemes).

Table 2. Effect of pre- and post-anthesis BA sprays on nut-in-shell and kernel weights of *Macadamia*.

	BA concentration (mg L^{-1})			
Pre-anthesis:	0	0	200	200
21-day post-anthesis:	0	200	0	200
Experiment 3, cv. 660				
Nut-in-shell (g)	6.29 ± 0.13	5.95 ± 0.11	6.34 ± 0.15	6.16 ± 0.17
Kernel (g)	2.46 ± 0.06	2.34 ± 0.06	2.40 ± 0.07	2.27 ± 0.09
Experiment 4, cv. A4				
Nut-in-shell (g)	8.00 ± 0.27	8.44 ± 0.36	8.75 ± 0.29	8.26 ± 0.29
Kernel (g)	3.35 ± 0.19	3.59 ± 0.16	3.62 ± 0.17	3.44 ± 0.15

Means (± SE) do not differ significantly in any experiment (ANOVA, $P > 0.05$, n = 56 - 109 fruits [cv. 660] or 9 - 22 fruits [cv. A4]).

Macadamia racemes. Applications of GA_3 and PBZ were ineffective, and 10 mg NAA L^{-1} significantly decreased initial fruit set. Investigations in subsequent years on different cultivars demonstrated the consistency of response to the 200 mg L^{-1} pre-anthesis BA spray, but showed that the 50 mg L^{-1} dose did not consistently affect initial fruit set of cv. 660 racemes. The 200 mg L^{-1} pre-anthesis spray also increased fruit sets at 21 d post-anthesis (and at 39 days post-anthesis on cv. 660 racemes in Experiment 3). Application of BA at a later stage (200 mg L^{-1} at 21 days post-anthesis) increased fruit sets at 39 days and 56 days post-anthesis on cv. 660 racemes, although it was ineffective on cv. A4 racemes. Fruit sets of both cultivars were increased at 39 days and at 56 days post-anthesis by the double (pre-anthesis plus 21 d post-anthesis) 200 mg L^{-1} BA sprays, when compared with control sprays. Indeed, with the exception of the 56 days post-anthesis fruit set on cv. 660 racemes, fruit sets at 39 and 56 days post-anthesis were increased by the double BA spray, when compared with all other treatments.

No treatment increased fruit sets at 70 days post-anthesis or at final fruit set. Abscission of immature *Macadamia* fruit occurs in three distinct phases, with maxima at 2, 6 - 7, and 10 weeks post-anthesis (Trueman and Turnbull, 1994b). Little further abscission occurs until fruits mature approximately 24 weeks post-anthesis (Trueman et al., 2000, 2002). The first phase of immature fruit abscission is strongly related to cross-pollination and fertilisation failure (Trueman and Turnbull, 1994a; Wallace et al., 1996). Severity of the second and third phases is dependent on the level of available carbohydrates, with these phases possibly representing a maternal adjustment of crop load prior to the major period of fruit biomass accumulation (Trueman and Turnbull, 1994b). Therefore, although 200 mg L^{-1} BA pre-anthesis treatments increased fruit sets after the first phase (by 2.5 – 6.2 times) and, in the case of double sprays, after the second phase (by 1.3 – 2.2 times), they did not affect retention of fruits beyond the final phase of immature fruit drop that occurs in the tenth week post-anthesis. Increased fruit retention after the first two phases of immature fruit drop was not the result of increases in the percentage of flowers with pollen tubes in the base of the style, as pollen tube penetration was not affected by BA treatments. In addition, BA sprays at 21 days post-anthesis were highly effective, more than 14 days after fertilization would have been completed (Ito, 1980; Sedgley, 1983; Trueman and Turnbull, 1994a). BA may have affected the sink strength of individual fruits or racemes, directly by increasing sink activity or indirectly by stimulating fruit growth and increasing sink size (Wismer et al., 1995; Bubán, 2000; Yuan and Greene, 2000; Stern et al., 2003). Final NIS and kernel fresh weights were not affected by BA treatments, suggesting that BA had no more than a temporary effect on sink strength.

The most likely effect of BA was to delay abscission of

fruits that were destined to abscise (Peterson et al., 1990; Kuang et al., 1991; Atkins and Pigeaire, 1993). Initial fruit sets following the pre-anthesis BA spray in Experiments 3 and 4 were higher than the percentages of flowers exhibiting pollen tube penetration to the base of the style. Therefore, some unfertilized flowers were retained at 14 d post-anthesis, and would presumably abscise after initial fruit set was recorded. The 21-days post-anthesis BA sprays were generally also effective at delaying fruit drop but the effects were not maintained past the tenth week post-anthesis, as the extra fruits retained at 56 d post-anthesis abscised during the final phase of immature fruit drop.

The possibility of re-applying BA around 56 d post-anthesis, or adding other growth regulators that may affect fruit retention at this critical stage, is worthy of further investigation. BA increases pod set or seed yield in legume crops (Atkins and Pigeaire, 1993; Barclay and McDavid, 1998; Nonokawa et al., 2007), which have racemose inflorescences and high rates of flower and immature fruit abscission that are similar to *Macadamia*. Commercial formulations that combine BA and GA_{4+7} are used widely to increase fruit size and quality of tree crops, particularly apple (Bubán, 2000; Wertheim, 2000; Bound, 2006). This study, however, provides no recommendations for the use of growth regulators as yield manipulators in *Macadamia*, as no treatment affected the final number of fruits, NIS weights or kernel weights.

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