The Effect of Supplementary Pollination on Nut Set of *Macadamia* (Proteaceae)

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The effects of supplementary pollination on initial and final nut set and nut weight of the *Macadamia* cultivars, 'Hawaii Agricultural Experiment Station 246' and 'Hidden Valley A4', were assessed over 3 years at an orchard in eastern Australia. The final nut sets of racemes bagged to exclude insect pollinators were low in all 3 years of the study for both cultivars. This demonstrated the importance of exposure to insect visitors to increase nut set of these cultivars. However, the improved initial nut set by supplementary cross pollination of 246 in all 3 years of the study showed that insect pollination is inefficient compared to hand pollination. Furthermore, supplementary cross pollination of 246 increased final nut set by 57–97% in 1989 and increased nut weight by 15·0% and kernel weight by 20·0% in 1991. Cross pollination of A4 did not result in any consistent pattern of initial nut set and did not improve final nut set, but increased nut weight by 11·6% and kernel weight by 18·4%, with a higher percentage kernel recovery in 1991. In addition, supplementary self pollination of A4 increased nut sets in both 1989 and 1990. Yield and quality of both cultivars may benefit from increasing pollen transfer in the orchard.

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INTRODUCTION

Macadamia, a member of the family Proteaceae, is cultivated for its edible nuts. There are at least seven species of *Macadamia* in Australia (Gross and Hyland, 1993), but only two species, *Macadamia integrifolia* Maiden and Betche and *M. tetraphylla* L. A. S. Johnson, and their hybrids, are grown commercially. These species are indigenous to the subtropical rainforests of the east coast of Australia.

Macadamia, like many tropical trees, is mass flowering, and produces many more flowers than fruits. Flowers are borne in pendulous racemes consisting of 100–300 flowers. *Macadamia* flowers are protandrous (Sedgley, Blesing and Vithanage, 1985) and partially self incompatible (Sedgley, 1983), and the initial nut set of many commercial cultivars is reduced when self pollination is compared with cross pollination (Urata, 1954; Ito and Hamilton, 1980; Sedgley *et al.*, 1990). However, more than 90% of the nuts that set at 3 weeks post anthesis (initial nut set) abscise by 8 weeks post anthesis (Sakai and Nagao, 1985). Ovaries that abscise have been found to be fertilized and normal in development (Sedgley, 1981) and it is not clear whether increases due to cross pollination at initial nut set produce increased final nut set. Recently, Trueman and Turnbull (1994*a*) have demonstrated that artificial cross pollination may in some circumstances increase final set, weight and kernel recovery of a commercial *Macadamia* cultivar.

Several studies in Hawaii have claimed that pollination by the honeybee, *Apis mellifera* L., was responsible for increases in yield. Shigeura, Lee and Silva (1970) found an increase in yield when honeybees were placed in an orchard. Shigeura (1967, 1968), Ito, Hunter and Hamilton (1970) and Ito and Hamilton (1980) inferred that transfer of cross pollen by honeybees was responsible for higher yield and better nut quality observed in a mixed block planting compared with a pure block planting. Treatments were confounded in these studies and reported increases in yield may have been due to year or site effects.

In Australia, the major pollinators in commercial *Macadamia* plantations are from two genera of social bees: the introduced honeybee, *Apis mellifera*, and native bees of the genus *Trigona* (Vithanage and Ironside, 1986). The behaviour of these species of bees influences their effectiveness as pollinators. Pollen collectors of both genera make consistent contact with the stigma of *Macadamia* (Heard, 1994) since pollen is presented on the swollen tip of the style adjacent to the stigma. Nectar-collecting honeybees only occasionally make contact with the stigma and nectar-collecting *Trigona* never make contact with the stigma. Since contact with the stigma is necessary for effective pollination, the type of floral resource gathered will be important in determining the effectiveness of pollination.

This study was undertaken to assess the effect of cross and self pollination on initial nut set and final nut set, to compare pollination by bees with artificial pollination and assess the efficiency of insect pollinators, and to examine the relationship between initial nut set and final nut set of *Macadamia*.

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MATERIALS AND METHODS

Study site

All experiments were carried out at Hidden Valley plantations, Beerwah, (26°50′ S 152°56′ E), between Aug. 1989 and May 1992. Trees of two cultivars of *Macadamia* were used: 'Hawaii Agricultural Experiment Station 246' (246), approximately 25 years old, and 'Hidden Valley A4' (A4), approximately 10 years old. Pollen from two other cultivars, 'Hidden Valley A16' (A16) and 'Own Choice', was used to cross pollinate when necessary. Cultivar 246 was in a pure block with a closed canopy between trees, and A4 was in a small block surrounded by other cultivars, with an open canopy.

Experimental design

In 1989 and 1990, eight trees of each cultivar were selected, and on each tree, four branches of similar diameter with approximately 30–40 racemes were selected. Every raceme on a branch was tagged. In order to examine the contribution of early flowering to nut production, two experiments were conducted on 246 in 1989, one during the sparse flowering in late Aug. and the other during the heavy flowering in mid-Sep. Four large branches were treated for the Aug. flowering and four smaller branches, occupying approximately one third of the canopy area of the larger branches, were treated for the September flowering. One tree was excluded from the experiment in September due to asynchrony in flowering. Branches were randomly assigned to one of four treatments with each tree receiving all treatments. All racemes on the branch received the same treatment. In 1991, 125 racemes were selected per tree on each of four trees and 25 racemes per tree were randomly assigned to one of five treatments. The treatments were: (1) bagging of flowers to prevent insect pollination; (2) racemes open to pollinators (control); (3) racemes open to pollinators, with additional hand pollination with pollen from another cultivar (supplementary cross); (4) racemes open to pollinators, with additional hand pollination with pollen from different trees of the same cultivar (supplementary self); (5) racemes bagged to exclude pollinators and hand pollinated with pollen from different trees of the same cultivar (bagged and selfed). Bags were replaced after each pollination. This treatment was performed in 1991 only.

Racemes were bagged by enclosing in 0·5 mm × 1·0 mm mesh bags or glassine paper bags from the stage of style looping (approx. 2 d pre-anthesis) until all sepals had withered (approx. 10 d post-anthesis). Racemes that received hand pollination were treated after the method of Ito and Hamilton (1969), with a glass test tube 25 mm internal diameter and 300 mm long. Pollen was applied to the inner surface of the test tube by rubbing it against a freshly opened raceme. The racemes to be pollinated were placed in the test tube and the tube was rotated, allowing pollen to make contact with the stigma. Two racemes were treated using this method before the test tube was rinsed in 100 % ethanol. This method has been shown to be effective in primarily altering the type of pollen rather than the number

of pollen grains on the stigma (Trueman and Turnbull, 1994*a*). Hand pollinated racemes were treated as above every 2 d from anthesis until all sepals had fallen. Cultivar 246 was cross pollinated with A4 in the main flowering in all three years, and with Own Choice in the early flowering in Aug. 1989. Cultivar A4 was pollinated with A16 in 1989 and 1990 and, due to asynchrony in flowering, 246 in 1991.

Initial nut set (INS) counts for each raceme were conducted 21 d after the last pollination of the raceme in 1989, and 14 d and 21 d after the last pollination of the raceme in 1990 and 1991 for all racemes except those that were bagged in 1990. Floral abscission and ovary swelling of bagged racemes had not occurred at 14 d in 1990 and counts were conducted at 21 d. Final nut set (FNS) counts were conducted in mid-Jan., approximately 4 months after flowering. Nuts from all treatments were bagged in Mar. 1992, and allowed to develop until maturity. Mature nuts were collected from the bags in June and allowed to dry. Nut in shell (NIS) and kernel were weighed individually and individual kernel recovery, a quality factor used by the industry, was calculated by dividing kernel weight by NIS weight.

Pollinator visits

Insect visits were monitored on A4 and 246 for 10 min each hour between 0600 h and 1700 h for 4 d during the flowering season in 1989 (spaced over 11 d of the flowering season), between 0900 h and 1700 h for 11 d in 1990 (spaced over 44 d) and between 0800 h and 1700 h for 5 d in 1991 (spaced over 18 d). Two study areas were examined each day when flowering was intense, and one was examined between 30 Aug. 1990 and 21 Sep. 1990 when flowering was sparse. Each study area consisted of a section of canopy approx. 1·0 m³ on trees of 246, or A4, or both when flowering of the two cultivars overlapped. Study areas were 0·2–1·5 m above the ground. Each study area contained approx. ten racemes which had reached anthesis. Study areas were selected to ensure that floral stage, abundance and density of flowers were comparable. In each study area, the number of visitors, species of visitor and type of resource gathered were recorded for the 10 min period each hour. Two *Trigona carbonaria* Smith hives were placed in the orchard in 1990 and one in 1991, within 500 m of the study sites. No honeybee hives were placed in the orchard in any year.

Statistical analysis

The appropriate log or square root transformation was performed on the INS data for the control, supplementary self and supplementary cross pollination treatments in order to achieve a normal distribution, and analysed using an analysis of variance procedure of GENSTAT with trees regarded as blocks. The assumptions of analysis of variance were checked by examining plots of residuals against fitted values. Differences between means were assessed using Tukey's HSD test.

Initial nut sets of the bagged racemes and the bagged and selfed racemes, with the exception of A4 data in 1989 and

1991, were not normally distributed and were excluded from the analysis of variance. Data for A4 in 1989 required an unbalanced ANOVA and were analysed using the GLM procedure of SAS and tested against the type-three sum of squares.

All FNS data were analysed as contingency tables tested against the χ^2 statistic since they displayed Poisson distributions. Very low FNSs were observed for the bagged and bagged and selfed racemes and these were excluded from the analysis in all cases except 246 early flowering in 1989 and main flowering in 1990, in which cases the distribution was similar to the other treatments. Differences between means were assessed against the χ^2 statistic, using the Dunn-Sidäks correction. NIS weights, kernel weights and individual kernel recoveries were analysed with an analysis of variance and the differences between means assessed using Tukey's HSD test.

RESULTS

Cultivar 246 initial nut set

There were consistent differences in INS of 246 due to pollination treatment for all three years of the study,
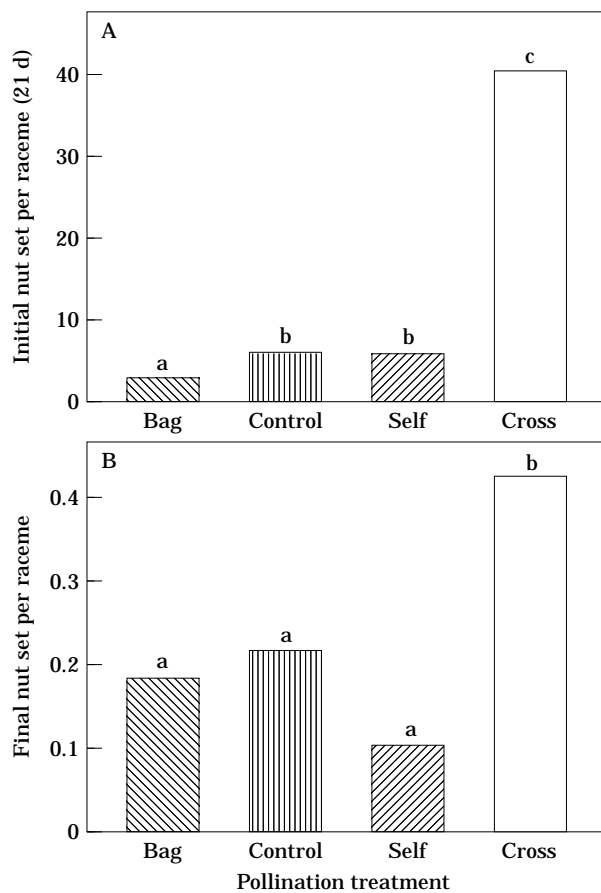

FIG. 1. Initial (A) and final (B) nut sets of treated racemes of 246 opening in August 1989 (prior to main flowering). Number of racemes receiving supplementary cross pollination (cross) = 47, supplementary self pollination (self) = 59, control racemes = 60, bagged (bag) = 37. Treatment means with different letters were significantly different ($P < 0.05$).
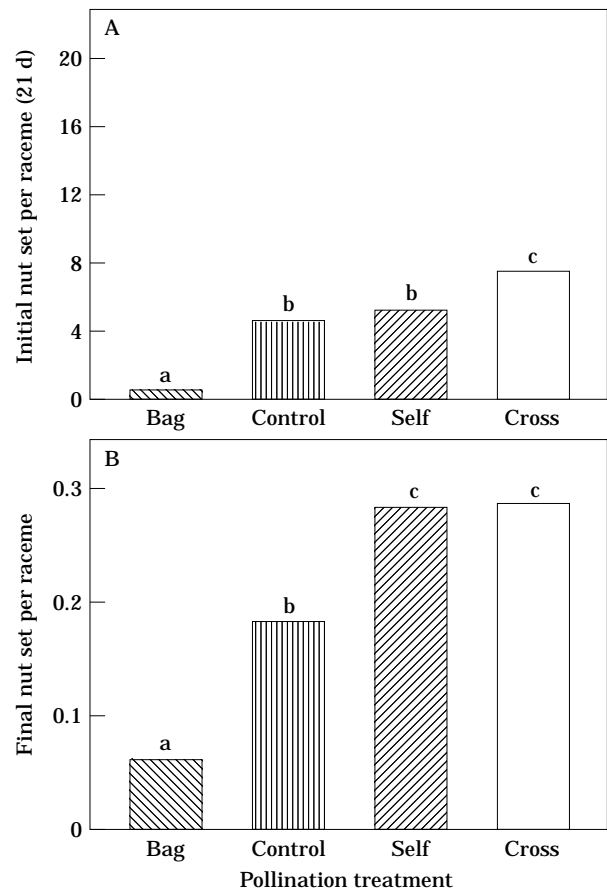

FIG. 2. Initial (A) and final (B) nut sets of treated racemes of 246, 1989. Number of racemes receiving supplementary cross pollination (cross) = 247, supplementary self pollination (self) = 282, control racemes = 282, bagged (bag) = 118. Treatment means with different letters were significantly different ($P < 0.05$).

although these differences varied in magnitude. In all cases observed, racemes that received supplementary cross pollination set significantly more nuts ($P < 0.01$) than those receiving any other treatment (Figs 1A, 2A, 3A, B and 4A, B). Supplementary self pollinated racemes did not set significantly more nuts than racemes that were open pollinated only (control), with the exception of 1990 (Fig. 3B). In all years the bagged racemes set very few nuts, with most racemes having an INS of zero (Figs 1–4). In addition, bagged and selfed racemes set very few nuts, and sets of these treatments were not significantly different in 1991 (Fig. 4A, B).

Cultivar 246 final nut set

In 1989 FNS was affected significantly by pollination treatment ($P < 0.01$) in the August flowering (Fig. 1B). Supplementary cross pollination of racemes increased final nut set by 97 % in the early flowering season compared to controls, with no significant differences between controls and other treatments (Fig. 1B). The August flowering produced few nuts, contributing only 17·9 % of the racemes and 17·9 % of the final nuts for 246 in 1989, even though
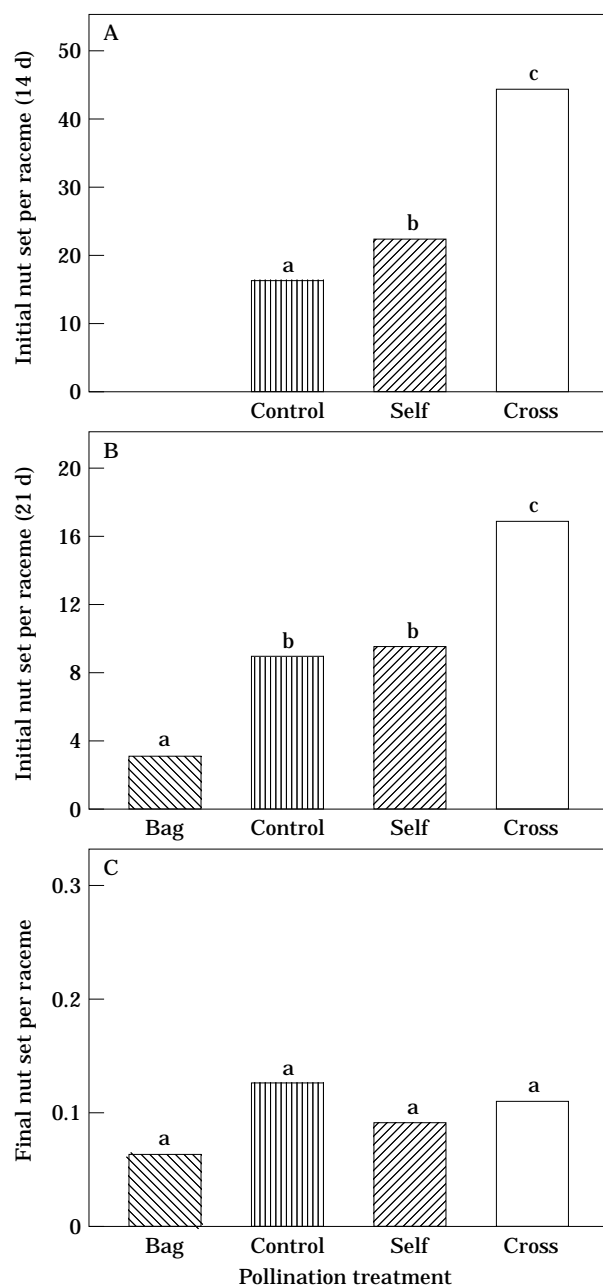
FIG. 3. Initial (A, B) and final (C) nut sets of treated racemes of 246, 1990. Treatments as in Fig. 1. Number of racemes receiving supplementary cross pollination (cross) = 276, supplementary self pollination (self) = 276, control racemes = 273, bagged (bag) = 251. Treatment means with different letters were significantly different ($P < 0.05$).
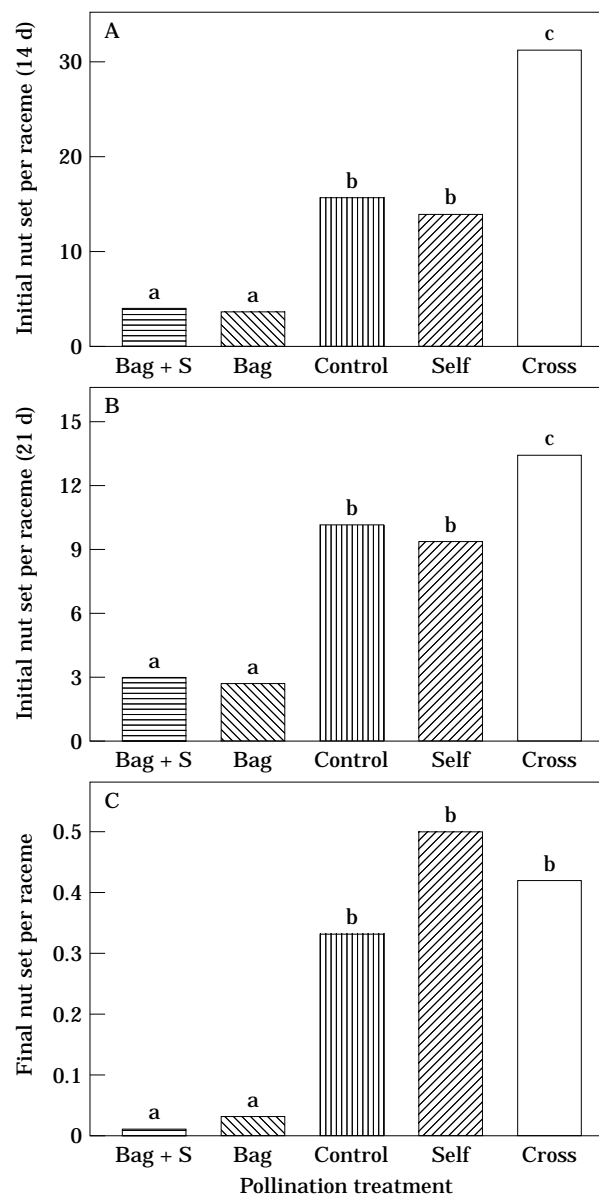

FIG. 4. Initial (A, B) and final (C) nut sets of the pollination treatments for 246, 1991. Treatments as in Fig. 1; bag + s, racemes bagged and selfed. Number of racemes receiving each treatment = 100. Treatment means with different letters were significantly different ($P < 0.05$).

branches occupied approximately three times as much area of canopy as those used in the September flowering.

In the September flowering, racemes that received supplementary cross pollination set 57 % more nuts than the control (significant at $P < 0.05$). Racemes that received supplementary self pollination also set more nuts than the control ($P < 0.05$), and there was no significant difference in nut set between supplementary cross and supplementary self treatments. Bagged racemes set fewer nuts than those of any other treatment with fewer than 0·1 nuts per raceme (Fig.

2B). However in 1990 there was no significant difference due to any treatment, and all racemes, including the bagged, set very few nuts (Fig. 3C). In 1991 no significant differences were observed between the control, supplementary self or supplementary cross pollinated racemes but these set many more nuts than those that were bagged or bagged and selfed (Fig. 4C). Pollination treatment affected NIS weight ($P < 0.001$), kernel weight ($P < 0.001$) and individual kernel recovery ($P < 0.05$). Supplementary cross pollination increased NIS weight and kernel weight compared with supplementary self pollination and open pollination alone (control), which were not significantly different (Table 1). In addition, supplementary cross pollination increased individual kernel recovery in comparison to supplementary

TABLE 1. *Mean nut in shell weight, kernel weight and kernel recovery of 246, 1991. Treatment means with different superscript letters (in the same row) were significantly different at* P < 0·05
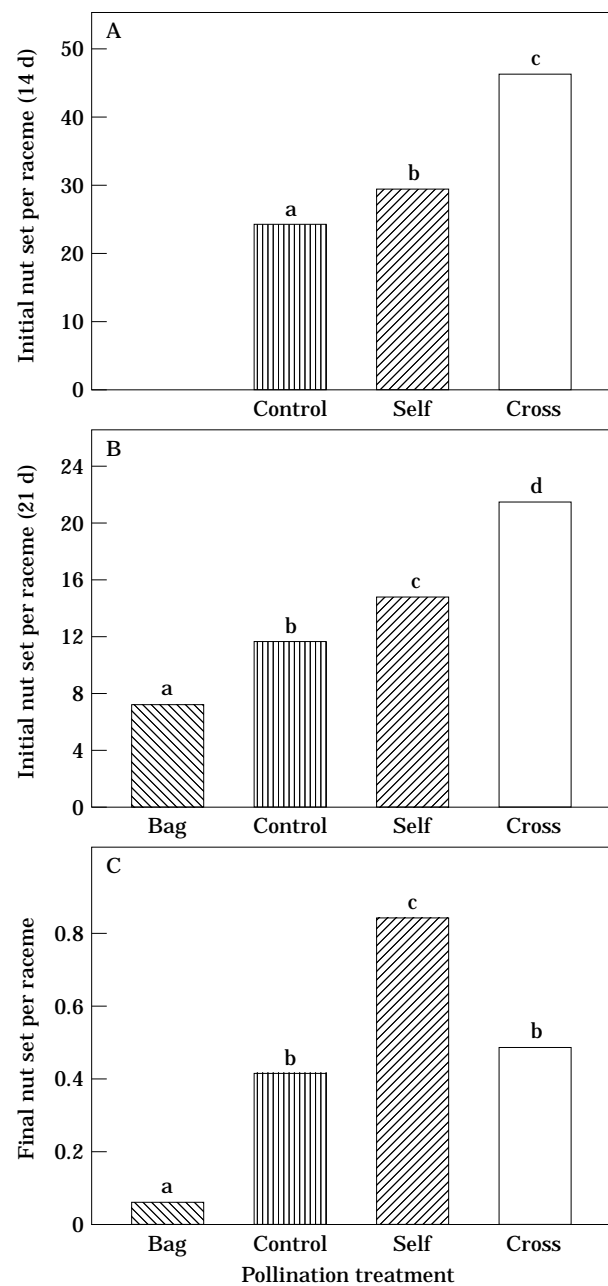
	Treatment		
	Control	Supplementary self	Supplementary cross
Mean nut in shell weight (g)	8·41[a]	8·37[a]	9·67[b]
Mean kernel weight (g)	2·79[a]	2·75[a]	3·35[b]
Mean kernel recovery (%)	33·10[ab]	32·50[a]	34·59[b]
No. nuts harvested	22	45	33
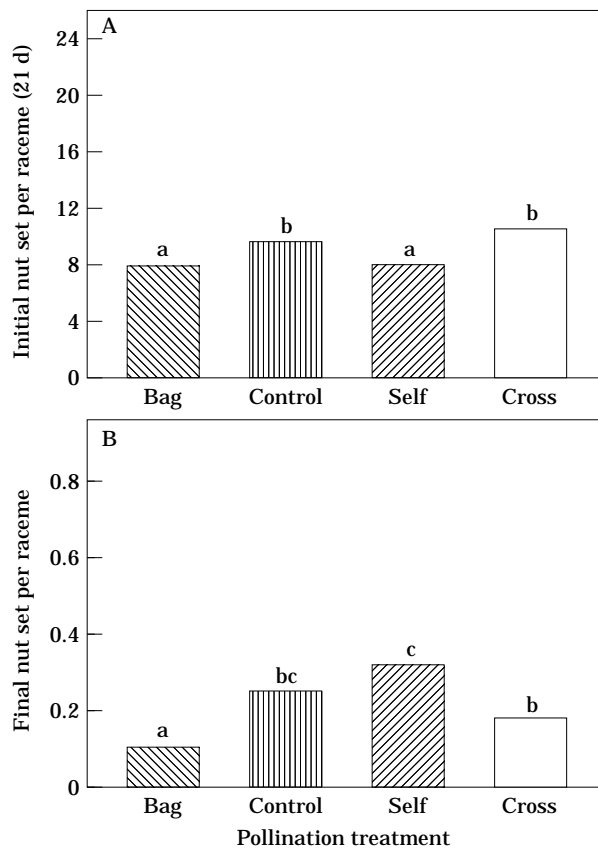
FIG. 5. Initial (A) and final (B) nut sets of treated racemes of A4, 1989. Number of racemes receiving supplementary cross pollination (cross) = 172, supplementary self pollination (self) = 156, control racemes = 154, bagged (bag) = 122. Treatment means with different letters were significantly different ($P < 0·05$).

self pollination (Table 1). Racemes of 246 that were cross pollinated produced nuts that weighed on average 15·0 % more, with 20·0 % more kernel, than those resulting from open pollination.

Cultivar A4 initial nut set

In contrast to 246, the patterns of initial nut sets in A4 varied from year to year. In 1989 the number of nuts set at 21 d by the control racemes was not significantly different from supplementary cross pollinated racemes while racemes of these two treatments set significantly ($P < 0·05$) more nuts than supplementary self pollinated and bagged racemes, which were not significantly different (Fig. 5A). However,

FIG. 6. Initial (A,B) and final (C) nut sets of treated racemes of A4, 1990. Number of racemes receiving supplementary cross pollination (cross) = 258, supplementary self pollination (self) = 251, control racemes = 261, bagged (bag) = 237. Treatment means with different letters were significantly different ($P < 0·05$).
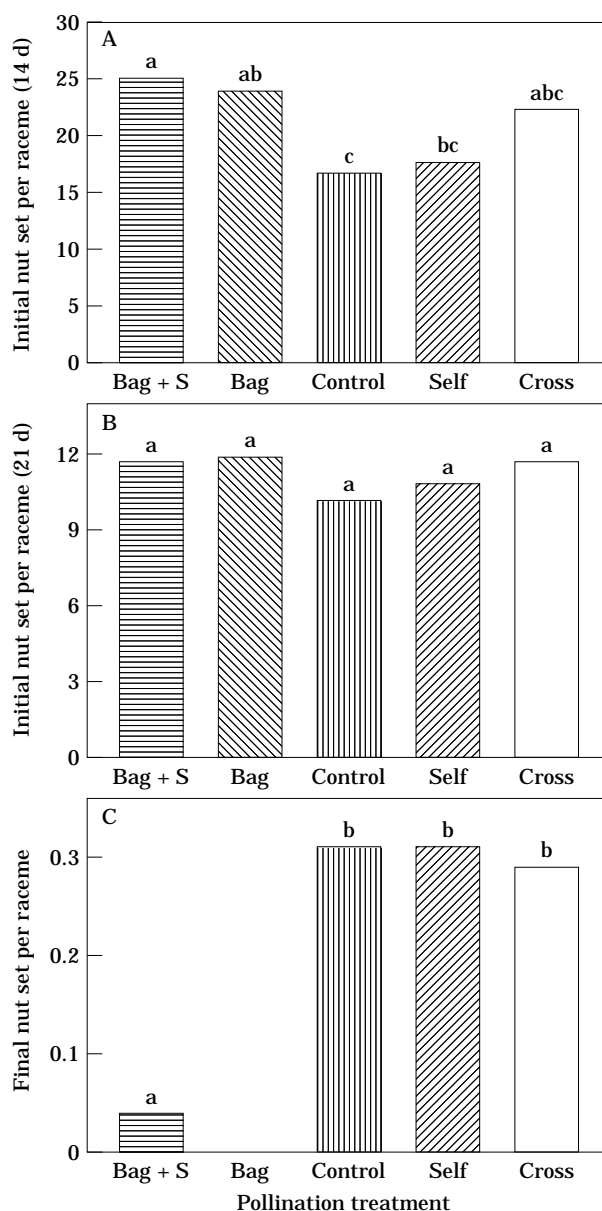
FIG. 7. Initial (A, B) and final (C) nut sets of the pollination treatments for A4, 1991. Treatments as in Fig. 1; bag + s, racemes bagged and selfed. Number of racemes receiving each treatment = 100. Treatment means with different letters were significantly different ($P < 0.05$).

racemes that received supplementary cross and self pollination in 1990 set significantly more nuts than the control racemes, with cross pollinated racemes setting significantly more than self pollinated racemes (Fig. 6 A, B). The bagged racemes in both years set fewer nuts than racemes of all other treatments. The pattern was different again in 1991 at 14 d, with the highest sets in the bagged, and bagged and selfed racemes, and the lowest in the control racemes (Fig. 7 A). However, at 21 d there was no significant difference between any treatments (Fig. 7 B).

Cultivar A4 final nut set

In 1989 and 1990, in contrast to 246, supplementary cross pollinated racemes did not set significantly more nuts than the control. However, racemes that received supplementary self pollination set significantly more nuts than the cross pollinated racemes ($P < 0.05$ in 1989, $P < 0.01$ in 1990) and the control in 1990 ($P < 0.001$) (Figs 5 B and 6 C). In 1991, there was no significant difference between the control, supplementary cross pollinated and supplementary self pollinated racemes (Fig. 7 C). However, there was a significant difference in NIS weight ($P < 0.05$), kernel weight ($P < 0.01$) and individual kernel recovery ($P < 0.01$). Supplementary cross pollination of A4 racemes produced nuts that weighed 11·6 % more than racemes that were open pollinated only, with 18·4 % heavier kernels, and a higher individual kernel recovery ($P < 0.05$, Table 2). There was no significant difference between supplementary cross and self pollination (Table 2), or between supplementary self pollination and controls.

Pollinator visits

Honeybees and *Trigona* sp. were frequent visitors to *Macadamia* racemes at this site (Table 3). Pollen collecting, especially by *Trigona* sp., was often observed. Pollen was a scarce resource after 1000 h and *Trigona* sp. were frequently observed robbing pollen, i.e. removing pollen from unopened or partially opened flowers by chewing through the tip of the perianth tube (see also Heard, 1994).

Other insect visitors included *Metriorrhyncus rhipidius* Macleay (Coleoptera; Lycidae), *Monolepta australis* Jacoby (Coleoptera; Chrysomelidae), flies of the family Syrphidae and ants. These visitors were observed infrequently (Table

TABLE 2. *Mean nut in shell weight, kernel weight and kernel recovery of A4, 1991. Treatment means with different superscript letters (in the same row) were significantly different at* P < 0.05

	Treatment		
	Control	Supplementary self	Supplementary cross
Mean nut in shell weight (g)	7·83[a]	8·52[ab]	8·74[b]
Mean kernel weight (g)	3·37[a]	3·77[ab]	3·99[b]
Mean kernel recovery (%)	42·80[a]	44·55[ab]	45·74[b]
No. nuts harvested	23	22	25

TABLE 3. *Numbers of visitors per 10 min per m² of* Macadamia *racemes for each year of study* (n = *total number of 10 min observation periods in each year*). *Mean and standard error provided*

Type of visitor	Year of study		
	1989 (*n* = 88)	1990 (*n* = 136)	1991 (*n* = 45)
Honeybees			
nectar	3·61 ± 0·37	2·40 ± 0·19	5·27 ± 0·63
pollen	0·08 ± 0·03	0·09 ± 0·03	0·29 ± 0·12
both	0·05 ± 0·02	0·09 ± 0·04	0·24 ± 0·46
total	3·74 ± 0·38	2·58 ± 0·19	5·80 ± 0·46
Trigona sp.			
nectar	0·48 ± 0·12	1·71 ± 0·25	2·64 ± 0·58
pollen	0·28 ± 0·09	2·93 ± 0·32	2·73 ± 0·66
both	0·00	0·11 ± 0·04	0·24 ± 0·08
total	0·76 ± 0·16	4·75 ± 0·46	5·61 ± 0·87
Other	0·06 ± 0·03	0·35 ± 0·08	0·16 ± 0·08
Total	4·56 ± 0·46	7·68 ± 0·59	11·57 ± 1·48

3) and will not be discussed further. In 1989 the most numerous visitors were honeybees, with *Trigona* sp. observed infrequently (Table 3). In 1990 *Trigona* sp. was the dominant species, and similar numbers of both species were observed in 1991 (Table 3).

DISCUSSION

The effect of supplementary pollination on nut set and quality

Increases in INS due to cross pollination have been reported for many cultivars of *Macadamia* (Urata, 1954; Ito and Hamilton, 1969; Ito *et al.*, 1970; Ito, Eyre and Cabral, 1983; Sedgley *et al.*, 1990). However, none of these studies examined whether cross pollination increased nut retention at the later stages of development. In all 3 years of our study, supplementary cross pollination increased INS of 246 and, in one of 3 years, of A4. Furthermore, supplementary cross pollination increased FNS in two cases out of four for 246 (Figs 1B and 2B). Cross pollination substantially increased nut weight and kernel weight of both cultivars, and individual kernel recovery of A4. This demonstrates that cross pollination may cause more nuts of *Macadamia* to be retained until maturity and increase other quality factors such as nut size. Similar increases in nut set and weight have been reported by Trueman and Turnbull (1994*a*) for 660 when pollinated with 246 or 333 pollen. These results confirm that differences in nut set and nut quality (i.e. kernel characteristics) observed between pure and mixed blocks (Ito *et al.*, 1970; Ito and Hamilton, 1980) may be due to higher levels of cross pollination in mixed blocks. In many other horticultural crops, including pecan [*Carya illinoensis* (Wangenh.) C. Koch], avocado (*Persea americana* Mill.), chestnut (*Castanea sativa* Mill.), pistachio (*Pistacia vera* L.), date (*Phoenix dactylifera* L.), and lychee (*Litchi chinensis* Sonn.), seeds and mature fruits produced by cross pollination are heavier than those produced by self pollination (Marquard, 1988; Sedgley and Griffin, 1989; Degani *et al.*, 1990; Denney, 1992; Stern *et al.*, 1993).

Supplementary self pollination utilized the same pollination technique as cross pollination, the only difference being the type of pollen used. However, supplementary self pollination of racemes had no effect on INS compared to the control racemes in five out of six cases of 246 (Figs 1A, 2A, 3B and 4A, B), and for A4 in 1991. This confirms that, in these cases, any increases in INS observed in the cross pollinated racemes can be attributed to pollen source (self or cross) rather than pollination technique or number of pollen grains on the stigma.

A surprising result of this study is that supplementary self pollination can increase FNS. Supplementary self pollination increased FNS compared to controls in one of three cases for A4, and equalled the increase due to cross pollination in one of four cases for 246. For A4, when nuts were harvested in 1991, NIS weights, kernel weights, and kernel recoveries were similar to nuts produced by cross pollination.

Some nuts were produced by bagged racemes of both cultivars each year, although both INS and FNS was low. More nuts may be produced by such racemes when there is less competition for resources from cross pollinated nuts; for example, isolated trees and pure blocks sometimes produce a high nut set.

The pollination efficiency of flower visitors

Exposure to flower visitors was important for adequate nut sets of both *Macadamia* cultivars examined in this study. Exclusion of flower visitors (bagged treatment) resulted in the lowest INS in all cases, except A4 in 1991, and lower FNS than any other treatment in five cases out of seven (Figs 2B, 4C, 5B, 6C and 7C). This supports the claim of Shigeura *et al.* (1970) that placing of bees in an orchard may increase yield. However, supplementary pollination increased INS and sometimes increased FNS, NIS weight, kernel weight and kernel recovery in both cultivars examined in this study. The results suggest that natural levels of pollination, due to the activities of flower visitors, were suboptimal. If whole trees respond to pollination in the same way as racemes then improved pollination may increase commercial yields of *Macadamia*.

Several factors may cause inadequate natural pollination, including: (1) low pollinator populations and/or pollinator activity in the orchard, resulting in insufficient visits by pollinators to racemes; (2) insufficient supply of cross pollen in the orchard; (3) bee behaviour resulting in transfer of self pollen but not cross pollen.

High numbers of flower visitors were observed for all years in comparison to other studies (Vithanage and Ironside, 1986; Heard, 1993; Heard and Exley, 1994), except *Trigona* sp. in 1989 (Table 3). Vithanage and Ironside (1986) examined bee visitation rates in three orchards in the area (26° S) and Heard and Exley (1994) examined bee visitation rate in this orchard and many other orchards in the area. Almost all visits observed in the current study were by either honeybees or *Trigona* sp., which are the major pollinators of *Macadamia* (Vithanage and Ironside, 1986). *Trigona* sp. and, less frequently, honeybees were observed in the current study collecting pollen, indicating that bee

behaviour allowed stigma contact and therefore pollination (Heard, 1994). In fact, pollinator activity was so intense that pollen was scarce after 1000 h and many *Trigona* engaged in robbing behaviour. It is surprising that supplementary pollination improved yield in an orchard with such intense pollinator activity. Either *Macadamia* requires more pollinators than observed here for efficient pollination or some other factor limits pollination in this orchard. Many other orchards have lower pollinator populations (Heard and Exley, 1994) and in these orchards increasing pollinator populations may improve yield.

Insufficient supply of cross pollen could account for the inadequacy of natural pollination. Cultivar 246 was planted in pure blocks, and experimental trees were 50–100 m from the nearest cross pollen source. Trees of A4 were up to 50 m from the nearest cross pollen source, although some trees were next to trees of other cultivars. These trees may have received more cross pollen than 246, and consequently final nut sets of A4 were not increased by supplementary cross pollination. Availability of compatible pollen could be increased by improved interplanting of cultivars, rather than planting pure blocks of a single cultivar, and planting cultivars with synchronous flowering.

Bee behaviour may also limit the transfer of cross pollen. In apple (*Malus domestica* Borkh.) orchards, honeybees tended to remain constant to flowers of one cultivar for as long as it was attractive, and established a small foraging range (Free, 1966). In addition, in orchards of dwarf apples, honeybees usually ranged over only about 3 m of one row in one foraging trip where rows made a continuous hedge (Free and Spencer-Booth, 1964). Jackson and Clarke (1991) found that gene flow in almond [*Prunus dulcis* (Mill) D. A. Webb] was restricted to neighbouring halves of cross-compatible trees and suggested that honeybees visited only one cultivar and flew along rows. Most of the cultivated *Macadamia* genotypes can now be identified using isozyme systems (Vithanage and Winks, 1992). This may be a useful tool to determine if seeds result from cross or self pollination, and to examine the pattern of gene flow in the orchard.

The relationship between initial and final nut set

Initial nut set has been used previously as an indicator of cross compatibility and as a predictor of yield (Sedgley *et al.*, 1990). However, current results show it to be unreliable for either of these purposes. Results will depend on when nut counts are taken. Other authors have used 7–10 d (Ito and Hamilton, 1969), 10 d after the last pollination (Ito *et al.*, 1970, 1983), 15–20 d post-anthesis (Urata, 1954) or 21 d post-pollination (Sedgley *et al.*, 1990; Heard, 1993). In this experiment, in some cases differences between treatments were detected at 14 d but no differences were detected at 21 d. In some cases INS may be affected by seasonal influences. In 1989 and 1990 the same pollen source and experimental design produced very different initial nut sets for A4.

Increases in INS due to pollination did not always result in increases in FNS. After INS, the nut retention on a given branch may depend on the available carbohydrate, and may represent a maternal adjustment of crop load, serving to minimize the amount of resources lost by abscission (Trueman and Turnbull, 1994*b*). The current study demonstrates increases in FNS due to pollination under normal orchard conditions where resources are limiting. Increasing resource availability to racemes, for example, by girdling, removing competing flowers or applying fertilizer may result in larger and more consistent increases in FNS due to pollination.

This study, and that of Trueman and Turnbull (1994*a*), collectively report pollination effects on FNS on four cultivars. Many other cultivars are used commercially and different cultivars may have different combining abilities, and this will affect FNS. The combining ability of some cultivars has been examined using INS (Sedgley *et al.*, 1990), but there is a need to investigate combining ability using FNS and nut quality.

Overall, these results demonstrate that improving the natural levels of pollination can increase yields of *Macadamia*. This has implications for orchard design and management. Pollination could be improved in several ways. Firstly, pollinator populations could be increased by placing hives of both *Apis mellifera* and *Trigona carbonaria* in the orchard, and also by careful planning of insecticide spraying regimes to avoid times of peak pollinator activity (Vithanage and Ironside, 1986; Vithanage and Douglas, 1987). Secondly, the availability of cross pollen could be increased by improved interplanting of cultivars (Sedgley *et al.*, 1990). Thirdly, cross pollen transfer in the orchard could be improved by manipulating the behaviour of insects, for example by increasing the number of honeybees collecting pollen or using dispensers to apply pollen to bees leaving a hive (Jay, 1986). In this study, supplementary pollination resulted in yield increases in a *Macadamia* orchard that experienced high bee visitation rates. Many orchards experience very low visitation rates (Heard and Exley, 1994). Such orchards may benefit dramatically from improved orchard design and the introduction of bees.

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