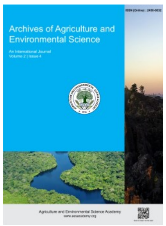
Archives of Agriculture and Environmental Science 8(4): 498-503 (2023)
https://doi.org/10.26832/24566632.2023.080406

e-ISSN: 2456-6632

This content is available online at AESA

Archives of Agriculture and Environmental Science

Journal homepage: journals.aesacademy.org/index.php/aaes



ORIGINAL RESEARCH ARTICLE

Contribution of insect flower visitors on macadamia nut set, retention and yield in central Kenya

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ARTICLE HISTORY

Received: 18 September 2023
Revised received: 02 November 2023
Accepted: 18 November 2023

Keywords

Central Kenya
Insect flower visitors
Macadamia
Nut-in-shell yield

ABSTRACT

The aim of this study was to evaluate the contribution of insects that visit macadamia flowers to nut set, retention, nut-in-shell, and kernel yields. The study was conducted at the Macadamia Research Centre in Kandara, Murang'a County, in three flowering cycles (cropping), from August 2020 to May 2022. Nut set, retention, and yield were assessed by randomly selecting twelve trees that were in full bloom at the study orchard in each of the flowering cycles. On each of the twelve trees, four branches of the same size were selected and tagged for the study. The branches were about 1 to 1.5 metres high from the ground. On each branch, one raceme at the bud stage was randomly selected and one of the four treatments administered. The treatments were (i) bagged during the day with mesh nets, (ii) bagged at night, (iii) bagged throughout the flowering season, excluding all insects, and (iv) racemes were left unbagged, thus having unlimited flower visitation by insects. There were significant differences on nut-in-shell yield (mass) ($P \leq 0.05$) in flowers that were unbagged (68.23 ± 4.03), bagged at night (61.50 ± 3.51), bagged during the day (6.53 ± 1.05) and those that were bagged throughout (4.45 ± 0.95). Racemes that had flower visitors fully excluded resulted in low nut-in-shell production. The initial nut set, retention, and ultimately the nut-in-shell yields were significantly increased in flowers that were left unbagged, thus insects had unlimited access. Macadamia nut set, retention, and ultimate yield (nuts-in-shell and kernel) is largely dependent on the presence of insect flower visitors.

Citation of this article: Njue, N. I., Muthomi, J. W., Chemining'wa, G. N., & Odanga, J. J. (2023). Contribution of insect flower visitors on macadamia nut set, retention and yield in central Kenya. *Archives of Agriculture and Environmental Science, 8*(4), 498-503, https://dx.doi.org/10.26832/24566632.2023.080406

INTRODUCTION

Pollinator-dependent crops account for 75% of all food crops grown worldwide and include some of the most expensive and nutritious commodities (Eilers *et al.*, 2011; Chaplin-Kramer *et al.*, 2014; Garibaldi *et al.*, 2022; Potts *et al.*, 2016). The degree to which crops rely on insect pollinators varies greatly; for example, *Macadamia integrifolia* yields can be increased by up to 185% after insect pollination (Grass *et al.*, 2018). According to Bommarco *et al.* (2012), insects' presence on flowers of oilseed rape increases yields by 18%, while in strawberry, yields can be increased by more than 70% (Hodgkiss *et al.*, 2018). Pollination is a critical ecosystem service for plant reproduction, with insects accounting for 85% of all pollen transport (Gill *et al.*, 2016; Potts *et al.*, 2016; Kamper *et al.*, 2021). Insect pollination contributes the most to total crop output (Klein *et al.*, 2007). Pollination accounts for 87.5% of angiosperm production worldwide (Ollerton *et al.*, 2011).

Macadamia is the main lucrative nut crop grown for its edible kernel, which has great nutritional benefits and is native to Australia (Trueman, 2013). The main countries where it is currently grown are Australia, Hawaii, Kenya, and South Africa (Quiroz *et al.*, 2019). Macadamia has pendant racemes that are 10–20 cm long with 100–300 protandrous flowers, which are self-incompatible (Trueman, 2013). Macadamia flowers profusely, but yields are low as only 3% of the initial flowers set mature to form nuts due to, among other physiological factors, pollination deficits (Howlett *et al.*, 2019). Most of the nuts abscise within the first two months after nut set (Lavi *et al.*, 1996; Howlett *et al.*, 2015). Nut yields may be improved by addressing factors that lead to nut dropping, such as pollination (Howlett *et al.*, 2015). Insects are the main agents of pollen transfer in macadamia, and the number of visits by various insect species influences both the quantity and quality of macadamia nut yields (Khalifa *et al.*, 2021). There are diverse invertebrates such as bees, wasps, beetles, and butterflies that forage for nectar or pollen in macadamia flowers (da Silva *et al.*, 2020). However, the honey bee (*Apis mellifera*) is dominant and present in all the main areas where there is cultivation of macadamia (Evans *et al.*, 2021). Although *A. mellifera* is the most abundant macadamia flower visitor, there are other bee species that contribute to macadamia pollination. Pollination by more than one bee species, such as honey bees, carpenter bees, stingless bees, feral bees, and social and solitary bees, results in better pollination (Klein *et al.*, 2003; Khalifa *et al.*, 2021).

Pollination in macadamia is mainly animal-mediated, as the stigma is small in size and has sticky pollen, demonstrating minimal possibility of wind pollination (Heard, 1993). Therefore, macadamia flowers greatly benefit from insect visitation, with bees being the most abundant visitors globally (Howlett *et al.*, 2015; Kamper *et al.*, 2021). According to Delaplane *et al.* (2013), the exclusion of flower visitors has been recognized as a technique for measuring agricultural pollinator dependency. Studies on pollinator dependency in a variety of crops, including macadamia nuts, have been conducted using mesh bags to exclude insects (Grass *et al.*, 2018). Elimination of insect flower visitors results in a reduction of macadamia nut set and yields (Tavares *et al.*, 2015). Low insect visitation on flowers or reduced activity in a macadamia orchard may result in insufficient pollen transfer and hence poor pollination (Anders *et al.*, 2023; Tavares *et al.*, 2015). Flowers left with unlimited insect visitor access have been shown to increase by 304% and 23% in nut set and nut-in-shell yields, respectively (Anders *et al.*, 2023). Abscission of nuts and lack of nut development to maturity after flowering are signs of insufficient ovule fertilization (Trueman *et al.*, 2022). The pollination of macadamia mainly happens during the day, so nocturnal insects such as bats and flying insects have little impact on the pollination of macadamia blossoms (Heard, 1993; Blanche *et al.*, 2006). Wind could be a contributor to pollen transfer in macadamia (Tavares *et al.*, 2015). However, no one has attempted to distinguish the contribution of wind-borne macadamia pollen from pollen transferred by other agents, despite the possibility that wind is a particularly significant agent of pollination on macadamia (Blanche *et al.*, 2006). Although most experiments have not taken wind pollination into account, Urata (1954) argued that the role of windblown pollen in macadamia pollination should not be discounted. Blanche *et al.* (2006) quantified the initial fruit or nut set as a sign of successful pollination. Production of self-pollinated nuts has been shown to decrease due to gametophytic incompatibility that inhibits pollen tube growth (Trueman, 2013). There is no information on how flower visitors' presence or absence influences the nut set, retention, and yields (nut-in-shell and kernel) of macadamia in Kenya.

The lack of knowledge on insect flower visitors and their contribution to macadamia orchards in Kenya presents a huge gap in assessing the impact of pollinator guilds on macadamia production. To improve the nut yield of macadamia, this study highlights the effects of insect flower visitors' presence or exclusion through bagging on nut set, retention, and yield. Specifically, this study assessed (i) the effects of insect flower visitors on macadamia nut set in Murang'a county, (ii) the effects of insect flower visitors on macadamia nut retention in Murang'a county, and (iii) the effects of insect flower visitors on macadamia nut-in-shell and kernel yields in Murang'a county. This knowledge is intended to form the basis for macadamia pollination and can be utilized to improve nut yields in Kenya.

MATERIALS AND METHODS

Study area

Field experiments on the effect of flower visitors on nut set, retention, and yield were conducted for three cropping cycles between August 2020 and May 2022 in a homogenous macadamia orchard at the Kandara Macadamia Research Centre in Murang'a county within central Kenya. The study area was located between 0°59'43.9″S, 37°03'31.0″E, and 1°00'00.7″S, 37°03'39.2″E, in East Africa. Kandara is a sub-county within Murang'a county that has deep and well-drained red or brown nitosol soils (Jaetzold *et al.*, 2006). Total monthly rainfall and mean temperature data for the study area ranged from 1.2 to 254.2 mm and 17.4 to 22 °C, respectively. The study area has four weather seasons, namely: cold season that occurs during the months of June, July, and August; dry season (January, February, and September), short rains (October, November, and December, and long rains (March, April, and May).

Study crop

Macadamia integrifolia is the main species grown in the orchard, which is an evergreen tree that grows to a height ranging between 12.5 and 16.0 metres and with the base width of lower branches ranging between 3.2 and 6.6 metres. In central Kenya, the macadamia trees bloom throughout the year, with the months of August, September, and October having dense flowering, whereas January, February, March, April, May, June, July, November, and December have sparse blooming. The dense and sparse flowering patterns were described by percentage blossoming, where flowering less than 50% was regarded as sparse and flowering 50% and above was termed dense during the survey.

Assessment of nut set and retention

To assess the effect of insect flower visitors on macadamia nut set and nut retention, twelve trees were randomly selected at

Figure 1a, b. *Fully bloomed macadamia tree (a) and bagged inflorescence (b) in Kandara, Murang'a County in August 2020.*

Figure 2a, b. *Mature macadamia nuts (a) and bagged mature nuts before harvest (b) in Kandara, Murang'a County in March, 2021.*

the study orchard. On each of the twelve trees, four branches were selected when trees were in full bloom and with inflorescences/racemes located on the outer side of the canopy. The selected four branches were of almost same size in diameter and located at about 1 to 1.5 metres from the ground. One inflorescences/raceme at the bud stage was selected per branch and tagged for study. All the selected inflorescences, at the bud stage, were then bagged with fine mesh nets until the flowers matured. The mature inflorescences were then bagged with a fine mesh net measuring 30 centimeters by 15 centimeters (Figures 1a, b) that was then strengthened with a wire frame to avoid bruising the florets and secured with a wire tie. This standardized procedure was repeated on each of the twelve trees for four experimental treatments, namely: (i) bagged during the day from seven a.m. to six p.m. in order to exclude insect flower visitors during the day; (ii) bagged at night from six p.m. to seven a.m. in order to exclude insect flower visitors at night; (iii) bagged throughout the flowering period to exclude all insect flower visitors from accessing the macadamia flowers; and (iv) not bagged throughout the flowering stages in order to provide unlimited insect flower visitors access to the macadamia flowers. The nut set was recorded after fertilization, twenty-one days after flower abscission, and this experiment was conducted three times, of September 2020, February 2021 and Oct 2021. Nut retention on all treatments was observed four months after nut set (February 2021, July 2021 and March 2022) after the nut set experiment when nuts were no longer abscising.

Assessment of nut-in-shell yield

One month before harvesting (eighth month after nut set), specifically in March 2021, November 2021 and May 2022, mature nuts (Figure 2a) were bagged with a recyclable bag. This was to allow fully matured nuts to drop into the bag for assessment of nut yield. This experiment was repeated for each of the four treatments described in the nut set experiment. In the experiment, each of the four treatments was assigned a bag with a different colour namely: (i) blue for bagged during the day, (ii) white for bagged at night, (iii) green for bagged throughout, and (iv) red for the unbagged flowers. Yield was assessed by recording the weights of individual nuts-in-shell that were collected at the end of the successful protocol for each of the four treatments on nut set and nut retention (Figure 2b). The macadamia nuts harvested from each treatment were immediately de-husked at the study site and transported to a laboratory at the department of Plant Science and Crop Protection at the University of Nairobi, where they were dried at 38°C for seven days in an oven. The weight of the individual dried nuts-in-shell was then measured to the nearest 0.01g using a digital scale, while length and width were measured using a vernier calipers.

Assessment of kernel yield

The nuts were thereafter cracked manually using an improved nut cracker, and the weights of individual kernels were taken using a digital scale to the nearest 0.01 g, and length and width were measured using a vernier calipers.

Data analysis

To compare the effects of bagging, unbagging, bagging throughout, and bagging flowers at night on the mean nut set, retention, nut-in-shell, and kernel weight, pollination treatment was used as a fixed effect. Means of nut set, retention, nut-in-shell weight, kernel weight, and nut-in-shell length, width, and kernel length and width were subjected to analysis of variance (ANOVA). To test for significant differences, the means were separated using Tukey's test. The data analyses were computed using R statistical software (R Development Core Team, 2018).

RESULTS AND DISCUSSION

Nut set

Flower visitors had an effect on macadamia nut set in all three seasons (Table 1). Unbagged flowers had the highest mean ± SE number of nuts set (13.67±1.13) whereas those that were bagged throughout had the least (1.31±0.21). There was a significant difference among the four treatments (unbagged, bagged at night, bagged during the day, and bagged throughout) (Table 1) in the mean ± SE number of nuts set per flower (F=50.14, p value <0.0001). Flowers that were bagged throughout had a significantly lower nut set compared to other pollination treatments (Table 1). Macadamia pollination is mediated by insect flower visitors and their presence significantly affected the nut set. Insect flower visitors are essential for successful production of macadamia nuts. Nut set happens after the pollen is transferred from the anthers by insect flower visitors that forage macadamia flowers to a receptive stigma which leads to fertilization and development of the nuts. In this study, exclusion of flower visitors through bagging of macadamia racemes resulted in reduced nut set which supports the findings that insect visitors contribute to nut set (Anders *et al.*, 2023; Evans *et al.*, 2021). Flowers that were bagged during the day and the ones bagged throughout, excluding the flower visitors had few nuts setting per raceme. This indicated that pollen transfer happens during the day and is majorly mediated by insect flower visitors. Racemes that were left open with visitors having unlimited access and the ones bagged only at night had higher nut set indicating that flower visitors that foraged during the day contributed largely to nut set, and there were minimal nocturnal pollen transfer activities. Exclusion of flower visitors from macadamia flowers has been demonstrated to result in decreased nut set and yields (Anders *et al.*, 2023; Tavares *et al.*, 2015). Initial nut set is an indicator of possible expected yields if other agronomic aspects as nutrients, weather and pests are well addressed. The findings concur with Olesen *et al.* (2011) and Trueman (2013) who showed that macadamia pollination is animal mediated and insect pollinators significantly influence nut set

Nut retention

Flower visitors had an effect on macadamia nut retention, with flowers that had unlimited visitation (unbagged throughout) having significantly higher nut retention than those that were bagged at night, bagged during the day and those that were bagged throughout. There was statistical difference among the four groups in mean number of nut retention (F=50.14, p value <0.0001) (Table 2). After nut set, to realize yields, the nuts must be retained on the trees and develop into mature nuts. Successful pollination results in more nuts being retained up to maturity as the ones that are not adequately pollinated drop off (Wallace *et al.*, 1996). Flowers that had unlimited insects access (unbagged) and those that were bagged at night had more nuts being retained to maturity. This indicates that they were sufficiently pollinated therefore minimal abscission after nut set (Tavares *et al.*, 2015), as insufficient pollen transfer causes poor nut retention. The racemes bagged throughout and those that were bagged during the day, denying insects access resulted to very low nuts being retained to maturity.

Table 1. Mean macadamia nut set 21 days after anthesis in Kandara, Murang'a County in three seasons (August 2020-May 2022).

Treatment	Nut set in 3 seasons		
	Sept 2020	Feb 2021	Oct 2021
Unbagged	14±1.14a	18.08±1.04a	20.25±1.45a
Bagged at night	12.83±0.55b	17.25±1.25b	19.67±1.26b
Bagged during the day	3.5±0.51c	2.42±0.53c	3.17±0.42c
Bagged throughout	1.25±0.3d	2.08±0.24d	2.17±0.43d
p value	<0.0001	<0.0001	<0.0001

Means ±SE followed by the different letter(s) within the same column are significantly different at P≤0.05.

Table 2. Mean macadamia nut retention before harvest in Kandara, Murang'a County in three seasons (August 2020-May 2022).

Treatment	Nut retention in 3 seasons		
	Sep-20	Feb-21	Oct-21
Unbagged	7.33±0.93a	6.75±0.66a	7.33±0.54a
Bagged at night	6.5±0.72b	6.33±0.57b	6.83±0.71b
Bagged during the day	0.75±0.18c	0.91±0.29c	0.67±0.18c
Bagged throughout	0.58±0.15d	0.5±0.19d	0.33±0.14d
p value	<0.0001	<0.0001	<0.0001

Means ±SE followed by the different letter(s) within the same column are significantly different at P≤0.05.

Table 3. Mean macadamia nut-in-shell and kernel weight (g) in Kandara, Murang'a County in three seasons (August 2020-May 2022).

Treatment	Nut yield (3 seasons)	
	Nut in shell weight (g)	Kernel weight (g)
Unbagged	68.23 ± 4.03a	21.25 ± 1.24a
Bagged at night	61.50 ± 3.51b	19.52 ± 1.07b
Bagged during the day	6.53 ± 1.05c	2.03 ± 0.34c
Bagged throughout	4.45 ± 0.95d	1.47 ± 0.31d
p value	p<0.0001	p<0.0001

Means ±SE followed by the different letter(s) within the same column are significantly different at P≤0.05.

Table 4. Mean length (mm) and width (mm) of nuts-in-shell and kernels in unbagged, bagged at night, bagged at day and bagged throughout inflorescences in Kandara, Murang'a County in three seasons (August 2020-May 2022).

Treatment	Nut-in-shell length	Nut-in-shell width	Kernel length	Kernel width
Unbagged	23.31a	22.06a	16.32a	12.7a
Bagged at night	23.76a	22.21a	16.25a	13.06a
Bagged during the day	22.75a	21.41a	15.63a	13.84a
Bagged throughout	23.14a	21.21a	15a	12.14a

Means ±SE followed by the different letter(s) within the same column are significantly different at P≤0.05.

Previous studies have shown that inadequate pollination can lead to low nut retention in macadamia trees (Penter, 2007, Holwett *et al*., 2015; Holwett *et al*., 2019). On the other hand, when there is adequate pollination, macadamia nut retention is usually high. This is because the fertilized flowers develop into healthy nuts that are able to remain on the tree until they reach maturity (Huett, 2004; Tavares *et al*., 2015). Therefore, it is important for macadamia growers to ensure that their trees are well-pollinated in order to maximize nut retention. This can be achieved by providing suitable habitats for pollinators and by managing the orchard environment to ensure optimal conditions for pollination, such as adequate moisture and temperature levels.

Nut-in-shell and kernel yields

Mean nut-in-shell weights differed significantly among the four treatments (unbagged, bagged at night, bagged during the day and bagged throughout) (F=71.89, p<0.0001). There was statistical difference in mean kernel weights among the four treatments (unbagged, bagged at night, bagged during the day and bagged throughout) (F=74.39, p<0.0001) (Table 3). Macadamia flower visitors contributed to increased yield of nuts-in-shell and kernels. Racemes that were unbagged or bagged at night, thus had unlimited access by diverse flower visitors produced more nuts-in-shell and kernels than those that were either bagged during the day or those that were bagged throughout the flowering period. Studies have shown that the yield of macadamia nuts and kernels is positively correlated with the flower visitor species present in the orchard (da Silva Santos *et al*., 2020; Trueman *et al*., 2022). When there are more species visiting the flowers, more pollen is transferred, leading to larger and heavier nuts and kernels (Khalifa *et al*., 2021; Reddy *et al*., 2022). Adequate pollination is necessary for the maximum yield of macadamia nuts and kernels. This is because each flower needs to be pollinated in order to develop into a nut, and the more nuts that are produced, the greater the potential yield. The quality of the nuts and kernels produced is also affected by pollination (Herbert *et al*., 2019). When the flowers are adequately pollinated, the nuts develop evenly, and the kernels are well-filled, leading to better yields (Howlett *et al*., 2015). Inadequate pollination, on the other hand, can result in poor-quality nuts that are small or malformed, or that have low kernel-to-nut ratios.

Nut-in-shell, kernel length and width

There were no statistical differences (P≤0.05) among the four treatments (unbagged, bagged at night, bagged during the day and bagged throughout) in nut-in-shell length and width as well as kernel length and width of the nuts (Table 4). However, earlier studies have shown that when macadamia flowers are adequately pollinated, the resulting nuts tend to be larger and more uniform in size (Evans *et al*., 2021; Grass *et al*., 2018). This is because adequate pollination leads to the fertilization of more ovules within the nut, which can result in the development of larger and more fully-formed kernels.

Conclusion

The presence of insects that visit flowers of macadamia benefits the crop by increasing nut set, retention, nut-in-shell, and kernel yields. Unlimited insect access to macadamia flowers resulted to better nut yields. Therefore, the findings highlight the significance of flower-visiting insects' in macadamia productivity and profitability in Kenya.

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