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

Nicholas I. Njue¹*, James W. Muthomi¹, George N. Chemining’wa¹ and James J. Odanga²

¹Department of Plant Science and Crop Protection, University of Nairobi, P.O. Box 30197 - 00100, Nairobi, KENYA
²Invertebrate Zoology Section, National Museums of Kenya, P.O. Box 40658 - 00100, Nairobi, KENYA
*Corresponding author’s E-mail: nickzireri@gmail.com

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 Kendara 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. Kendara 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...
the study orchard. On each of the twelve trees, four branches
were selected when trees were in full bloom and with inflores-
cences/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 inflores-
cences/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 stand-
ardized 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 visi-
tors 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 flow-
ers. 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 assess-
ment 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 through-
out, 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 immedi-
ately de-husked at the study site and transported to a laborato-
ry 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 improvised 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).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Nut set in 3 seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sept 2020</td>
</tr>
<tr>
<td>Unbagged</td>
<td>14±1.14a</td>
</tr>
<tr>
<td>Bagged at night</td>
<td>12.83±0.55b</td>
</tr>
<tr>
<td>Bagged during the day</td>
<td>3.5±0.51c</td>
</tr>
<tr>
<td>Bagged throughout</td>
<td>1.25±0.3d</td>
</tr>
<tr>
<td>p value</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Nut retention in 3 seasons</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sep-20</td>
</tr>
<tr>
<td>Unbagged</td>
<td>7.33±0.93a</td>
</tr>
<tr>
<td>Bagged at night</td>
<td>6.5±0.72b</td>
</tr>
<tr>
<td>Bagged during the day</td>
<td>0.75±0.18c</td>
</tr>
<tr>
<td>Bagged throughout</td>
<td>0.56±0.15d</td>
</tr>
<tr>
<td>p value</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Means ±SE followed by the different letter(s) within the same column are significantly different at P<0.05.
Herbert et al. (2019) found that the nuts and kernels produced is also affected by pollination. This is because each flower needs adequate pollination to achieve the maximum yield of macadamia nuts and kernels. Khalifa et al. (2020) showed 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. (2022) concluded that managing the orchard environment to ensure optimal conditions for pollination, such as adequate moisture and temperature levels, is important for macadamia growers to ensure that their trees are 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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**REFERENCES**


