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Effects of Supplementary Pollination on Macadamia Nut Set, Retention and Yield in Murang'a County, Kenya

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Abstract

Macadamia is a promising prime dessert nut with the potential of alleviating poverty and enhancing food security in Kenya. Nut set and subsequent development of nuts to maturity is dependent on pollination which is mediated by animals, and honey bees are the dominant macadamia flower visitors. However, macadamia is pollen deficit as not all flowers set develop to mature nuts, thus supplemental pollination results to better nut yields. There is limited information in Kenya among the smallholder macadamia growers on the importance of supplementing pollination to enhance nut yields. This study was conducted at Kandara Macadamia Research Centre and in a smallholder macadamia farm located 15 km from the research centre, which was purposively selected from July 2021 to May 2023. Assessment of the influence of pollinators and supplementing pollination to nut set, retention and final yields was done. Honey bee, (*Apis mellifera* L.) colonies were also introduced at the Macadamia Research Centre to enhance pollination and mitigate deficits. Racemes were bagged to exclude pollinators, others left open to unlimited pollinator access while others received supplemental hand pollination. The results demonstrate that macadamia is pollen limited and pollination is highly reliant on insect pollinators. There were significant differences ($p < 0.001$) among the bagged (pollinator exclusion), open and hand pollinated racemes in both farms. The initial nut set and retention was increased significantly (21.54%) in hand pollinated racemes compared to those that were left to open pollination (unlimited pollinator visits) depicting pollination deficit in farm B. Introduction of supplementary honey bee colonies at the Kandara Macadamia Research Centre, resulted to higher nut set, retention, nut-in-shell and kernels. Macadamia growers are encouraged to introduce honey bee colonies in their farms to improve yields and also address pollination deficits.

Keywords: insect pollinators, honey bee, pollinator exclusion, pollen, pollination deficit

1. Introduction

Pollination is a significant ecosystem service, with insects accounting for 85% of all pollen transfer and is critical for plant reproduction and survival (Kämper et al., 2021; Ricketts, 2008). According to Klein et al. (2007), about 70% of the food crops depend on animal-mediated pollination. Globally, there is a growing number of crops which fully depend on pollinators, making them critical for food production and nutrition (Klatt et al., 2014; Aizen et al. 2008). Fruits, seed set and nutritional value in several crops has been shown to increase as a result of pollination services (Klatt et al., 2014; Bommarco et al., 2012). Flowering plants are mainly dependent on animals for pollination (Ollerton et al., 2011) with majority of the main crops being highly reliant on pollinators for optimal seed or fruit production (Perrot et al., 2019; Ratto et al., 2018; Aizen et al., 2009). The quantity or quality of pollen deposited on flower stigmas has decreased over the years as a result of anthropogenic disturbance, resulting to reduction in yields (Bennett et al., 2020). According to Dainese et al. (2019) there is insufficient insect mediated pollination in about 29 crops. Studies have indicated global declines in various insect pollinator populations thus placing pressure on food production due to pollination deficits (Patel et al., 2021; Klein et al., 2018; Potts et al., 2016; Aizen & Harder, 2009; Gallai et al., 2009). Pollen limitation is common in plants and studies have shown that 63% of species studied are pollen inadequate (Sargent & Ackerly, 2008; Knight et al., 2005). The number of various insect species visits to flowers influences both the quantity and quality of yields in various crops, including macadamia.

Macadamia (*Macadamia integrifolia*, *Macadamia tetraphylla*, and their hybrids) is the main profitable nut crop grown in Kenya for its edible kernel which has great nutritional benefits and is native to Australia (Quiroz et al., 2019; Trueman, 2013). The crop was not agriculturally grown until in the mid-19th century, but nuts were used by the indigenous Australian people due to their high oil content (Nock et al., 2019). The demand for macadamia nut has continued to increase globally due to their treasured culinary resource (Shabalala et al., 2022) and an increase in populations conscious of healthy eating habits (Bandason et al., 2022). Pollination is one of the limiting factors to increased macadamia nut production (Kämper et al., 2021). Macadamia is a mass flowering nut tree which has pendant cylindrical racemes that are 10-20 cm with 100-300 flowers that have female and male parts maturing at different times, thus reducing chances for self-pollination (Howlett et al., 2015; Trueman, 2013). Despite macadamia flowering profusely, yields are low as only 3-4% of the flowers mature to form nuts due to among other factors pollination deficits (Grass et al., 2018). The bloom period of macadamia is short and takes an average of five days and the flower have a high pollen requirement, meaning for successful fertilization, more pollen grains have be deposited on the stigma (Howlett et al., 2015). The transfer of pollen in macadamia is mainly animal mediated as the stigma is small in size and has sticky pollen (Trueman, 2013; Heard, 1993) thus greatly benefit from the insect visitation for pollination. Bees are the most common and abundant macadamia flower visitors globally (Kämper et al., 2021; Howlett et al., 2015). Bees, particularly honey bees, pollinate the majority of crops globally (Rader et al., 2009; Klein et al., 2007). However, diverse invertebrates such as bees, wasps, beetles and butterflies have been shown to forage for nectar or pollen in macadamia flowers. Honey bee (*Apis mellifera*), is the most dominant and is 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 insect species that contribute to macadamia pollination. Pollination by more than one bee species, such as honeybees, carpenter bees, stingless bees, feral bees, social bees, and solitary bees, result in better pollination (Fründ et al., 2013; Klein et al., 2003).

In macadamia, high nutlet abscission and subsequent final nut set per raceme is related to inadequate pollination (Trueman et al., 2021), and pollination supplementation has been shown to increase nut yields with up to 92% (Trueman et al., 2022). The proportion of pollen tube germination in inflorescences with supplemental pollination increases resulting to nut formation within 14 to 21 days after pollen transfer (Wallace et al., 1996). Eusocial bees, such as honey bees, *Apis mellifera* as well as bumble bees such as *Bombus terrestris*, and solitary gregarious species have been domesticated and their nests can be placed in farmlands for crop pollination (Kremen et al., 2004; Delaplane & Mayer 2000). The introduction of colonies or nests of managed bee species helps mitigate pollination deficits in crops (Garibaldi et al., 2017; Geslin et al., 2017). Honey bees and stingless bees are the main managed pollinators that have been introduced to crops, including macadamia orchards (Halcroft et al., 2013). Managed honey bee colonies can be placed in orchards easily during the peak macadamia flowering seasons (Goodwin, 2012), and this increases the pollinator populations (Garratt et al., 2014; Trueman, 2013), which results in increased flower visitation and pollen deposition on the stigma, thus addressing pollen limitation.

Fruit set or seed set comparison between flowers receiving supplementary pollination and flowers receiving natural or open pollination is the recognized method for quantifying pollen limitation (Trueman et al., 2022; Bennett et al., 2020). Fruit set is generally increased in flowers receiving supplemental pollen by an average of 63% (Bennett et al., 2020). Supplementing blooms with pollen in tree crops is not a common practice (Knight et al., 2006). Pollen supplementation is typically done on a small subset of the tree's flowers (Khanduri et al., 2019; Pearse et al., 2015). Macadamia racemes require about 150 honey bee visits, and it is recommended to have about 5-8 colonies (bee hives) per hectare for adequate pollination (Howlett et al., 2015). Pollination management should be viewed as a production factor as it affects crop yield and many of its components, including fruit set and seed set, fruit quality (*e.g.*, size, aspect, sugar content, flavor, and nutritional content), seed quality (*e.g.*, germination rate, oil content), and other characteristics. Supplementing macadamia pollination is not a common practice in Kenya, and the possibility of augmenting the fields with managed honey bees other than in commercial production systems in order to increase macadamia yield has not yet been investigated. It is critical to understand the extent to which macadamia yields can be enhanced through supplemental pollination in Kandara, Murang'a County. This will boost macadamia nut productivity and profitability among smallholder farmers in Kenya. This study was therefore conducted to assess the effect of supplementary pollination (hand pollination and pollination with honeybee colonies) on nut set, retention, and yield in Kandara, Murang'a County, and determine if macadamia has a pollination deficit.

2. Materials and Methods

2.1 Study Area and Weather Seasonality

This study was conducted at the Kandara Macadamia Research Centre and on one smallholder farm, purposively randomly selected that had more than ten trees and was located 15 kilometres from the Macadamia Research Centre. The area is located between 0º59′43.9″S, 37º03′31.0″E and 1º00′00.7″S, 37º03′39.2″E, in East Africa. Kandara is a sub-county within Murang'a county that has deep and well drained red or brown nitosols soils (Jaetzold et al., 2006). Total monthly rainfall and mean temperature data of the study area ranged from 1.2 mm to 254.2 mm and 17.4 ^{o}C to 22 ^{o}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 season (October, November and December, and long rain season (March, April and May).

2.2 Study Crop and the Plant Flowering Patterns

The species grown Kandara area is *Macadamia integrifolia*, an evergreen tree that grows to a height of about 12.5 metres to 16.0 metres with a base width of lower branches being between 3.2 metres to 6.6 metres. Macadamia trees bloom throughout the year in central Kenya, with the months of August, September, and October having intense flowering and the months of January, February, March, April, May, June, July, November, and December having sparse blooming. The study was conducted during dense flowering (August) in 2021 and 2022. Dense and sparse floral patterns were classified by percentage blossoming, with flowering less than 50% considered sparse and flowering 50% and higher considered dense.

2.3 Study Design

This study was conducted at two sites (i) KALRO, Macadamia Research Centre, Kandara and marked as farm A and (ii) smallholder farm within Kandara sub-county, (marked as farm B) which was purposively selected, located 15 kilometres from the Macadamia Research Centre and had more than ten mature macadamia trees for two cropping cycles from August 2021 to May 2023. Five honeybee colonies, sourced from the National Beekeeping Institute (Lenana), Ministry of Agriculture, were introduced at the Macadamia Research Centre (farm A) just before the onset of the peak flowering season in July, as described by Howlett et al. (2015) that 1 hectare of macadamia orchard requires 5-8 honey bee colonies while no colonies were introduced the smallholder farm (farm B, control). In the month of August, ten trees were selected and, on each tree, six branches of almost similar size and level from ground with inflorescences at bud stage were randomly selected. In each farm, a total of 60 branches were selected each year (120 branches for the two farms), and 20 branches per farm received similar pollination treatment. A total of 240 branches were selected for this experiment in 2021 and 2022. Each branch was assigned one of the following treatments (i) open pollination (unlimited insects' visitation) (ii) bagged with a mesh cloth to prevent any insect access but allow wind and self-pollination (iii) inflorescences open to pollinators and received supplemental hand pollination with pollen collected from a different tree. Inflorescences were bagged using mesh nets of approximately 0.5 mm to 0.8 mm from the bud stage until the sepals had withered, fourteen days after flowers had opened. Hand pollination was done as per the method described by Wallace et al. (1996), where a glass test tube of 25 mm diameter and 300 mm height was used. Pollen was collected from freshly opened flowers by revolving the flowers inside the surface of the test tube. The test tube with pollen grains was then immediately placed on inflorescences and rotated to allow the stigma of the flowers to be pollinated come into contact with the pollen. After treating two flowers, the test tube was rinsed using 100% alcohol (Wallace et al., 1996). This process was repeated every three days until the sepals on the treated flowers withered or fell. The initial nut set was counted twenty-one days after flowers had withered. The final retention was taken when the nuts were four months old when no more abscission was happening. Nuts from all treatments were thereafter bagged one month to maturity for ease of collection. Nuts were then allowed to develop to maturity, then collected from the bags, dried, and individual nut and kernel weights taken. Weight of the individual dried nuts-in-shell was then measured to the nearest 0.01 g using a digital weighing scale. The weighed macadamia nuts were, thereafter, manually cracked and weights of individual kernels taken using the digital weighing scale at the Entomology Laboratory in the University of Nairobi's Department of Plant Science and Crop Protection. Kernel recovery, a quality factor used by the industry was computed by dividing kernel weight by nut-in-shell weight and expressed as a percentage (Hardner et al., 2001).

2.4 Data Analysis

Pollination treatment effects on nut parameters (nut set, retention, nut-in-shell mass and kernel mass) was assessed using generalized linear mixed-effects models (GLMM), which was fitted using the lme4 (Bates et al., 2015) in R statistical package (R Development Core Team, 2018). Pollination treatments were used as a fixed effect to test for differences in the mean number of nut set, nuts retained, nut-in-shell and kernel yields between open, bagged, and hand pollination. Nut set, retention, nut-in-shell and kernel yields were counts, thus Poisson distribution was used whereas, for kernel recovery and pollination deficit, which were proportions, Pearson was used. Kernel recovery was evaluated as the percentage of the kernel weight compared to nut-in-shell weight. Pollination deficit which is the percentage of the difference between nut set in hand and open pollination treatments, was evaluated to determine whether hand pollinated racemes showed a higher nut set than open-pollinated flowers in the control farm (farm B, without honey bee supplementation). To test if the pollination deficit was reduced in farms supplemented with honey bee colonies, model to test for the interactive effects of pollination treatment (hand versus open pollination) and honey bee supplementation (with or without additional honey bee colonies) was constructed. T-test was used to compare nut set, retention and yield between the two farms (farm A, supplemented with bee colonies and farm B, no colonies introduced). Means were separated using Tukey's test and were regarded as significantly different at $P < 0.05$. Means are reported with standard errors. All data analyses were computed using R statistical software, version 4.2.1 (R Development Core Team, 2018).

3. Results

3.1 Nut Set

There were significant differences in nut set among the racemes that received hand, open and bagged pollination treatments in farm A. Number of nuts set were significantly higher in hand and open pollination treatments than in bagged treatments in farm B. However, in both farms, hand pollinated racemes set significantly more nuts ($p < 0.001$) than the other two treatments (Figure 1). The intercept estimate was 1.5875 with a standard error of 0.1441. The z-value was 11.02, indicating a significant effect of the pollination treatment ($p < 0.001$). The hand pollination treatment estimate was 2.1743 with a standard error of 0.1507. The z-value is 14.43, indicating a significant effect ($p < 0.001$). The open pollination treatment estimate was 2.0820 with a standard error of 0.1515. The z-value was 13.74, indicating a significant effect ($p < 0.001$) (Figure 1).

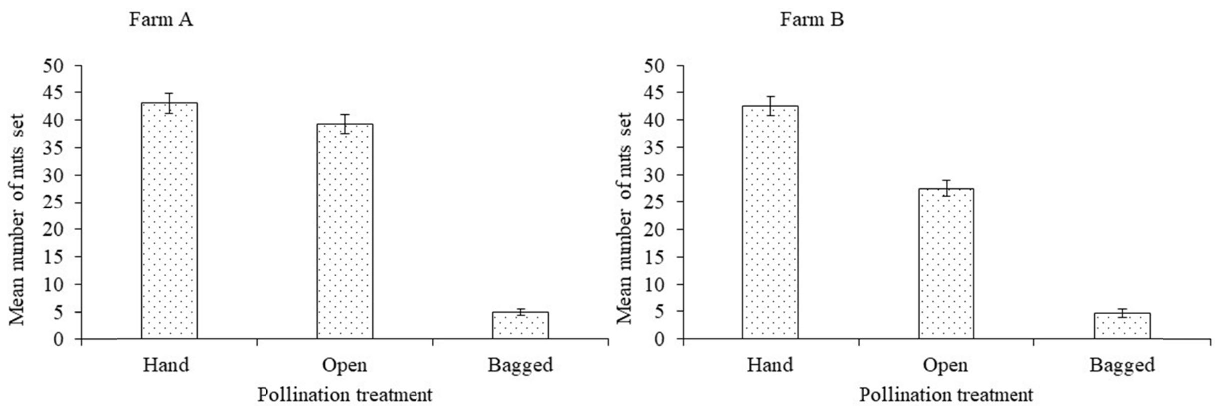

Figure 1. Mean±SE number of nuts set after flowering at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022. Error bars in the graph represent ±standard error of mean

Nut set was significantly higher in open pollinated racemes (39.3±1.71) in farm A that had honey bee colonies supplementation compared to farm B (27.5±1.53) that did not have colonies (t-test = 4.715; $p < 0.001$) (Figure 2).

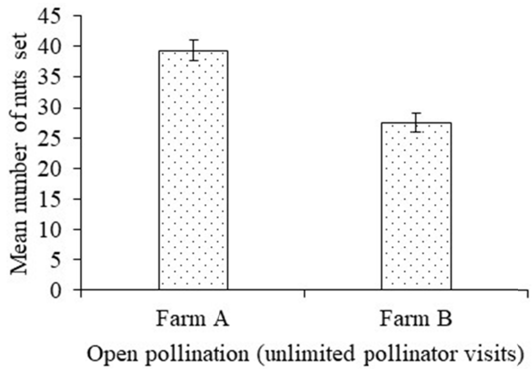

Figure 2. Mean± SE number of nuts set on open pollinated racemes at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022. Error bars in the graph represent ±standard error of mean

3.2 Nut retention

The racemes that received open pollination and hand pollination had significantly higher nut ($p < 0.001$) retention than those that were bagged. The intercept estimate was 0.9147, with a standard error of 0.2008. The z-value was 4.554, indicating a significant effect ($p < 0.001$). The hand pollination estimate was 2.4266, with a standard error of 0.2086. The z-value was 11.631, indicating a significant effect ($p < 0.001$). The open pollination estimate was 2.3105 with a standard error of 0.2097. The z-value was 11.020, indicating a significant effect ($p < 0.001$) (Figure 3).

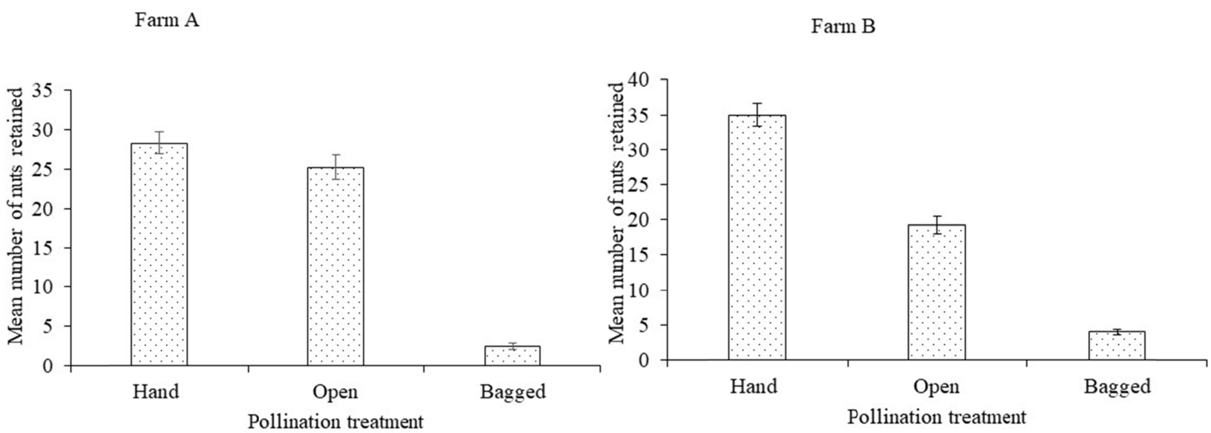

Figure 3. Mean±SE number of nuts retained to maturity at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022. Error bars in the graph represent ±standard error of mean

Racemes that received open pollination and honey bee colonies supplementation (farm A) had significantly higher nuts retained (25.2±1.53) compared to those that received open pollination but no honey bee colonies supplementation (19.3±1.27) in farm B (t-test = 4.413; $p = 0.0016$) (Figure 4).

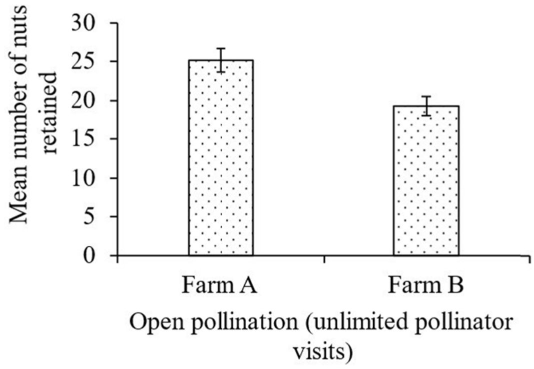

Figure 4. Mean±SE number of nuts retained to maturity on open pollinated racemes at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022. Error bars in the graph represent ±standard error of mean

3.3 Nut-in-Shell and Kernel Yield

The inflorescences that received open pollination and hand pollination had significantly higher nut-in-shell ($p < 0.001$) than those were bagged. Nut in shell yields differed significantly between the two farms for all treatments. The were significant kernel weight differences among the pollination treatments (Hand, Open and bagged) ($F_{2, 27} = 78.67$, $p < 0.001$) (Table 1). The treatment groups exhibited varied mean yields, with the hand pollination showing the highest mean yield, followed by the open pollination, whereas the bagged racemes had the lowest mean yield. Bagged racemes had significantly lower nut-in-shell and kernel yields than those that received any other treatment in both farms. Supplemented inflorescences produced more nuts than those that were bagged and open pollinated ones (Table 1).

Table 1. Mean±SE nut-in-shell and kernel weights on bagged, open and hand pollinated racemes at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022.

	Farm A		Farm B	
	Nut-in-shell weight (g)	Kernel weight (g)	Nut-in-shell weight (g)	Kernel weight (g)
Hand pollination	264.01±17.64a	94.99±11.68a	241.17±13.35a	82.90±4.85a
Open pollination	240.80±15.20b	79.94±14.29a	186.81±11.60b	59.67±4.85b
Bagged to exclude insects	21.71±3.61c	7.08±2.18b	20.72±2.88c	6.28±0.99c
p value	<0.001	<0.001	<0.001	<0.001

Note. Means±SE followed by the different letter(s) within the same column are significantly different at $P \leq 0.05$ (Student's T-test).

Racemes in farm A that received supplementary honey bee pollination had significantly higher nut-in-shell weight (240.80±15.20) and kernel weight (79.94±14.29) than those in farm B (nuts-in-shell 186.81±11.60 and kernel weight 59.67±4.85b) (nut-in-shell weight, t-test = 3.95; $p = 0.03$, kernel weight, $t = 4.762$; $p = 0.001$) (Figure 5).

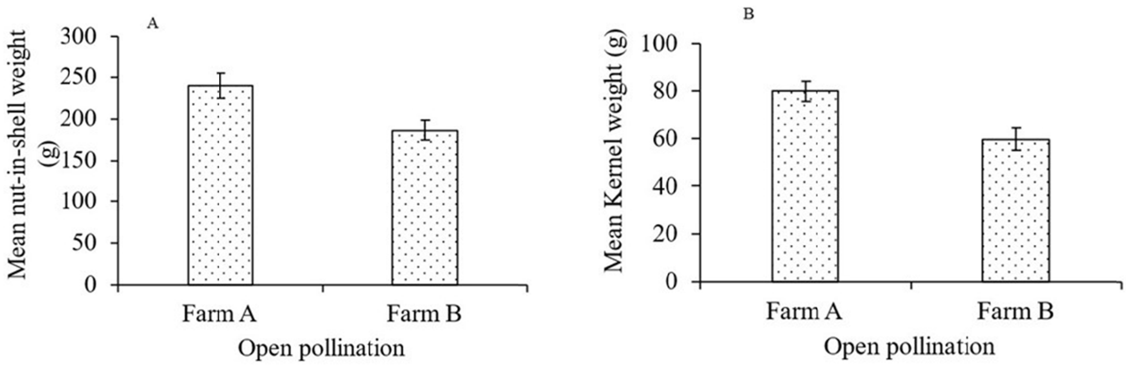

Figure 5. Mean±SE weight of nut-in-shell and kernel on open pollinated racemes at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022. Error bars in the graph represent ±standard error of mean

3.4 Kernel Recovery

Kernel recovery was significantly better (35.14% and 31.71%) in racemes that received open pollination compared to bagged racemes in both farm A and B respectively. Farm A that had honey bee supplementation had significantly better kernel recovery compared to the farm B that was not supplemented (Table 2). Bagged racemes had the lowest kernel recovery.

Table 2. Mean±SE kernel recovery (%) in racemes that were bagged, open and hand pollination at KALRO, Macadamia Research Centre in Kandara, Murang'a county (farm A) and smallholder macadamia farm (farm B) in 2021 and 2022.

	FARM A	FARM B
	Kernel recovery (%)	Kernel recovery (%)
Hand pollination	36.4±1.23a	34.66±1.39a
Open pollination	35.14±1.48b	31.71±0.75b
Bagged to exclude insects	30.0±3.61c	30.0±0.68c
p value	<0.001	<0.001

Note. Means±SE followed by the different letter(s) within the same column are significantly different at P ≤ 0.05 (Student's T-test).

3.5 Pollination Deficit

There was a reduction in nut set between open pollination and supplemental hand pollination treatment up to 21.54% indicating pollination deficit. However, the deficit varied among the blocks that received hand and open pollination treatments (Table 3).

Table 3. Macadamia pollination deficit (%) in a smallholder macadamia (farm B) at Kandara, Murang'a county in 2021 and 2022.

Farm B			
Block	Hand pollination (nut set)	Open pollination (nut set)	Pollination deficit (%)
1	38	31	10.14
2	49	26	30.67
3	45	18	42.86
4	36	29	10.77
5	39	30	13.04
6	38	27	16.92
7	48	28	26.32
8	52	31	25.30
9	42	34	10.53
10	38	21	28.81

4. Discussion

Pollination by insects led to an increase in nut set compared to the racemes from which insects were excluded. There was a higher nut set in farm A that had supplementary honey bee colonies than in farm B. These results indicate the importance of insect pollinators to the macadamia nut set, which subsequently affects yields. Howlett et al. (2015) established that macadamia pollination is animal mediated. Results from exclusion trials indicate that insect activity on macadamia blooms is necessary for pollination and subsequent nut set (Heard, 1993). Even in orchards where bee populations are exceptionally high, supplemental hand pollination can boost the number of nuts set and the size of the nuts (Howlett et al., 2015; Wallace et al., 1996). Racemes that were bagged and wind pollination allowed resulted in fewer nut sets. Wind has been shown to be an ineffective pollen transfer agent in macadamia as the flower has characteristics of insect pollination such as, a small stigma that is hidden by self-pollen clumps, produces nectar and has sticky pollen (Trueman, 2013; Olesen et al., 2011).

Pollination enhances retention after nut set, as macadamia racemes that were treated with open and supplemental pollination retained nuts significantly higher than those that had insects excluded. This depicts how effective pollination influences macadamia nuts to be retained until they attain maturity. Supplementary honey bees led to increased nut retention, which indicates they are the most important insect pollinators of macadamia in central Kenya. According to Tavares et al. (2015), honey bees accounted for 63% of the insects that foraged macadamia flowers in Hawaii. Successful pollination is a major contributor to the ultimate number of nuts retained, however, nut retention to maturity also depends on available carbohydrates and other agronomic aspects (Wallace et al., 1996; Trueman & Turnbull, 1994). The other agronomic aspects, such as variety, spacing, weather, pruning, irrigation, fertilizer and pesticide applications, play a significant role in macadamia nut yield (Huett, 2004). Moreover, the impact of insect pollination may combine with agronomic parameters, resulting in positive-synergistic correlations (Tamburini et al., 2019; Lundin et al., 2013).

The nut-in-shell and kernel yields increased in racemes with open and supplemented pollination treatments. Hand pollination was comparable to open pollination. Some trees that received hand pollination had higher nut yields than open-pollinated ones, and this could be due to more pollen being carried by hand compared to what was carried by insects (Tavares et al., 2015). This study demonstrates that supplemental pollination increases the initial nut set, retention, and the final nuts harvested under normal orchard management conditions. Overall, the findings indicate that increasing natural pollination levels can boost macadamia yields. Many methods could be used to increase pollination as by establishing hives of *Apis mellifera* in the orchards (Evans et al., 2021; Delaplane et al., 2013). Second, better cultivar interplanting could increase the availability of cross pollen (Kämper et al., 2021; Trueman, 2013; Wallace et al., 1996).

Macadamia trees in farm B expressed a pollination deficit as the racemes that received supplemental hand pollination had better nut sets compared to those that were open pollinated. Hand-pollinated trees, therefore, had better nut retention and ultimately higher nut-in-shell yields, and this could have been due to better placement of pollen grains on the receptive stigmas (Tavares et al., 2015). The study supported earlier findings that macadamia crops are mostly pollen limited and that supplemental pollination is the most efficient way to promote yields (Anders et al., 2023; Trueman et al., 2022; Grass et al., 2018). In macadamia, pollinator dependency and pollination deficits are well recognized, and numerous studies have been carried out to investigate the effects of pollination services on crop yields (Kämper et al., 2021; Grass et al., 2018). Mass-flowering crops such as macadamia are likely to exhibit particularly severe pollination constraints, resulting in poor nut yields due to constrained pollination services (Grass et al., 2018).

5. Conclusion

The results demonstrate that supplemental pollination through introduction of honey bee colonies (hives) and hand pollination in macadamia orchards can increase yields. Addressing pollination deficits through supplemental pollination would therefore result in better nut yields and increased income to smallholder macadamia farmers in Kenya, and consequently improving their livelihood. However, deployment of hand pollination is not practical in a commercial setting, and smallholder farmers should therefore introduce honey bee colonies during peak flowering seasons to ensure successful pollination thus enhancing macadamia nut productivity and profitability.

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Nicholas I. Njue: Proposal development, conceptualization, methodology, data collection, data analysis, data visualization, writing: original draft, and validation. James W. Muthomi; George N. Chemining'wa; John H. Nderitu: Conceptualization, methodology, writing: original draft, and validation. James J. Odanga: Conceptualization, methodology, data visualization and validation.

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