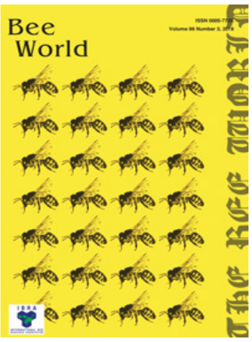

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Introduction

The diet of honey bees consists of protein-rich pollen and sugar-rich nectar collected separately or synchronously from flowers by foraging worker bees (Kajobe, 2006, 2007). These resources are collected in quantities that exceed colony demands and are stored for dearth periods. The nectar is converted into honey and pollen stored as bee bread (Anderson et al., 2014; Nicolson, 2011). While collecting nectar and pollen, bees deposit pollen from anthers to the stigma resulting in pollination and increased fruit set (Vidal, Jong, Wien, & Morse, 2010). In the USA, Morse and Calderone (2000) estimated the value of crop production achieved through pollination by honey bees alone at $14.6 billion. The value of honey production by bees in Africa is 169,306 tons (faostat.org 2013). Some plants have been observed to be heavily visited by the honey bees while others are less frequently visited (Bendifallah, Louadi, & Doumandji, 2013; Couvillon et al., 2015). Nectar and pollen resource depletion induced by prolonged wet seasons or overheating in the dry seasons is known to cause migration or absconding in African honey bees (Hepburn, 2006; Winston, Otis, & Taylor, 1978).

According to Larinde, Adedeji, and Ogbuehi (2014a), the production of honey is dependent on the quality and quantity of floral sources. Studies by Beyene, Abi, Chalchissa, and Tsadik (2016) in Ethiopia also showed that location and hive type interaction has significant effect on honey production per hive. Studies by Abdullahi, Sule, and Chimoya (2011) in Nigeria indicated that bee forage plants are not evenly distributed in the entire surveyed locations.

Uganda has a high potential for honey production not yet exploited. Weeds, pastures, and exotic trees are also used as bee forage in farming areas. Bee forage plants in Uganda have been studied previously (Kajobe, 2006; Kajobe et al., 2009; Kangave, 2015; Katende, Birnie, & Tengnas, 1995). Kajobe (2006) lists heavily visited bee forage of *Apis mellifera* and stingless bees in Bwindi Impenetrable National Park in south western Uganda (*Bidens pilosa, Carapa grandifolia, Croton macrostychus, Entandrophragma excelsum, Markhamia lutea, Prunus africana, Syzigium guinense, Vernonia sp)*. Kangave (2015) lists 46 bee forage plants in selected agro-ecological zones of Uganda. Kajobe et al. (2009) listed plants used by the bees in western highlands and Eastern agro ecological zones. These authors do not relate the dominant bee forage in the studied zones with honey production.

The current production of honey in Uganda is estimated at only 8000–9000 tons (MAAIF/UBOS, 2010; Uepb, 2005). Honey production in Uganda varies from one agro ecological zone to another and within a zone. Northern Uganda records 640 tons of honey annually while central region has the least, 85 tons (Kilimo Trust, 2012; MAAIF/UBOS, 2010). Identifying honey bee floral sources specific to a region is essential in honey production and selection of suitable apiary sites (Abou-Shaara, 2015) as beekeepers can use this information to selectively grow plants that are important to the bees (Kajobe, 2006). A study was done with the aim of identifying bee forages used in honey production by honey bees, *Apis mellifera* in 4 of 10 agro ecological zones (AEZ). Three variables were evaluated for their influence on honey production; (1) preferred pollen and nectar sources and their diversity, (2) compared honey production per hive with AEZ, site and interaction between site and AEZ, and (3) compared bee forage species dominance cover with AEZ, site and interaction between site and AEZ.

Methods

Study sites

The study sites were located in four agro ecological zones of Uganda: The Mid-North Savannah Grassland agro ecological zone (MN), the Lake Victoria Crescent (LVC) agro ecological zone, the Western highlands (WH) agro ecological zone and Kyoga plains (KP) agro ecological zone (Figure 1). The four AEZs were selected based on the differences in vegetation cover, honey production quantities and number of beekeepers (MAAIF/UBOS, 2010).

The four study sites/apiaries in each AEZ were located in one district selected with the help of the respective beekeeping extension workers making a total of 16 apiary sites. In each zone, at least one apiary was located in natural vegetation while others were in farming areas. The sites were decided upon after the apiary owners had demonstrated willingness to participate in the study.

Research design

Both quantitative and qualitative data were collected. Quantitative data included a list of bee plant species and their abundance. Qualitative data was based on observation rewards to pollinators: Nectar (N), Pollen (P), Pollen and Nectar (P + N), and classification of plants in relation to foraging intensity.

Data collection (observation of bees foraging at flowers)

Experimental plots measuring 1000 × 1000 m were set up around each study apiary. On each study visit, each experimental plot was divided into nine blocks measuring 333 × 333 m and observations made

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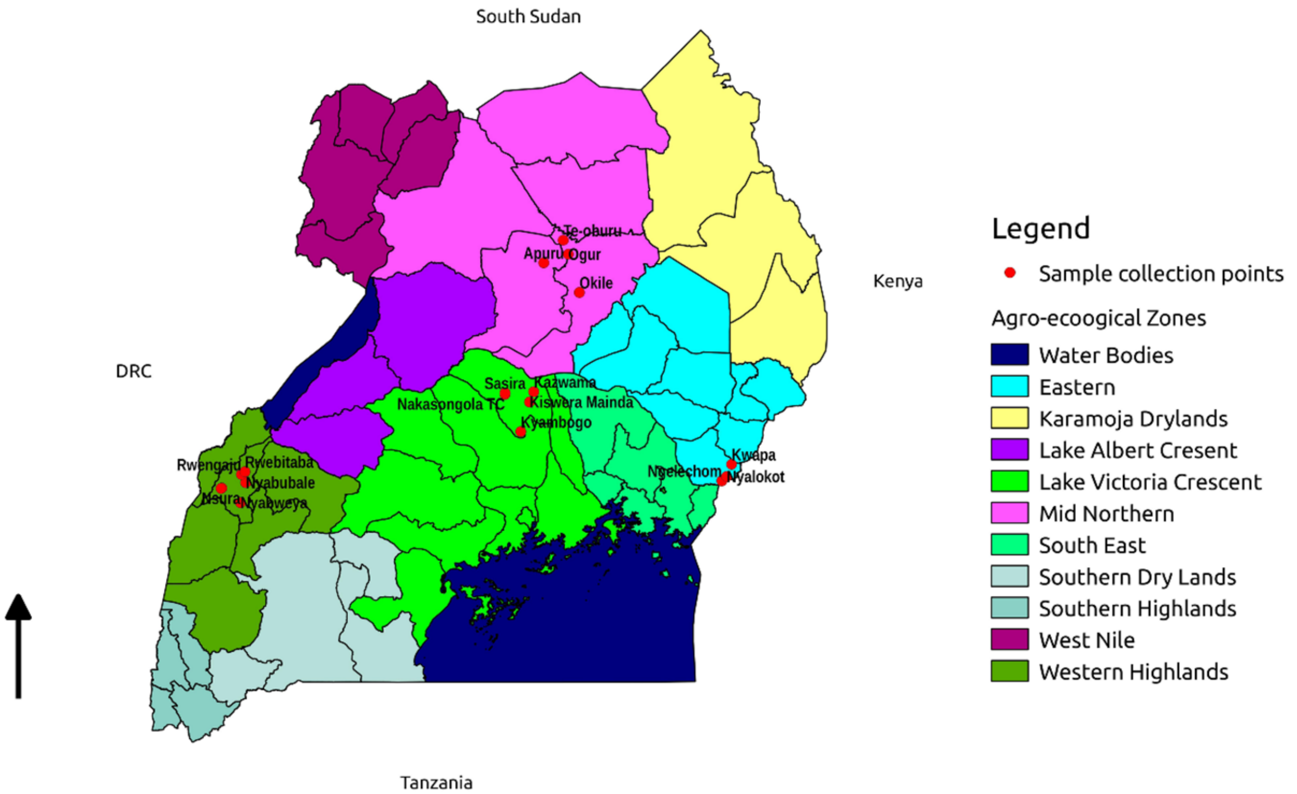

Figure 1. Map of Uganda showing the study sites and different agro ecological zones.

on four blocks selected randomly. Plants seen with flowers within the experimental plots were observed for the presence of foraging honey bees. The target plants were shrubs, trees, agricultural crops, weeds, and pastures. The intensity of the bees visiting flowers of each species at a glance was noted. A plant species was scored as bee forage when at least three bees were seen collecting either pollen or nectar within 10 min. A plant recorded as bee forage at one block when encountered in subsequent blocks was recorded for presence and dominance cover. The observations in each site were repeated monthly from April 2015 to April 2016 to ensure that all the bee forage plants were captured. Observations were done during time of peak foraging activity between 9:00 and 12:00 h. The foraging behavior of bees at flowers was observed to ascertain that the bees were collecting either nectar or pollen; pollen foraging was defined as bees seen running fast over anthers, removing pollen from their hairy bodies and placing it in their pollen baskets, whereas nectar collection was recorded when the bees delved down deep into flowers, or when seen sucking nectar from the outside through corolla tube of tiny flowers with long corollas. Bees foraging on tall trees were observed using a pair of field glasses. The flowering period of each bee forage species was determined through continuous monitoring and recording of flowering patterns including commencement and end of flowering period. Species with multiple flowering seasons were also recorded. This was adapted from methods used by Abdullahi et al. (2011) and Adgaba et al. (2017).

Collection and preparation of specimens for identification

A branch of 12–14 inches length and not more than 10 inches width was collected from shrubs/trees. For herbaceous plants the whole plant including flowers/fruit/pods was sampled. The collected specimens were pressed and dried as described by Lacey, Short, and Mosley (2001). The plant specimens were identified at the Makerere University herbarium.

Honey production at each study apiary was estimated by the amount of honey harvested per hive in kilograms (kg) by the apiary owner from 5 marked honey bee colonies recorded for three harvesting seasons in duration of 2 years. This honey measurement method has been used as a proxy for measuring foraging activity, such that if a sufficient honey yield is collected per period then one knows that the colony foraging behavior is proceeding normally (EFSA, 2016).

Data analysis

All the data was analysed in R (R Core Team, 2014), pie charts of dominant plant species by family were generated from the data on bee forages. The data of land cover by bee forage plants was subjected to a two-way ANOVA, having detected a large variation in plant species dominance cover contributed by AEZ, the validity of the ANOVA analysis was assessed graphically using residuals against fitted values and standardized residuals against theoretical quantiles and found to be within the acceptable model variation. The ANOVA results were then subjected to Tukey HSD multiple range test to identify which AEZs were actually different from each other (Benjamini & Braun, 2002). The honey production data was also subjected to a two-way ANOVA, when the site (apiary) location, but not the AEZ contributed to the observed variation in average honey harvested. The validity of the ANOVA analysis on honey production was assessed graphically using residuals as described above. Pair wise comparisons of average honey production per hive between different sites were done using Tukey HSD multiple range test.

Results

Bee forage species identified

A total of 75 plant species belonging to 31 plant families comprising of shrubs, trees, weeds, and grasses were foraged upon by honey bees during the wet and dry seasons in the study sites. The Fabaceae contributed 21% of the foraged plant species, followed by the family Asteraceae with 12% and Lamiaceae with 7% (Figure 2). The bees collected either

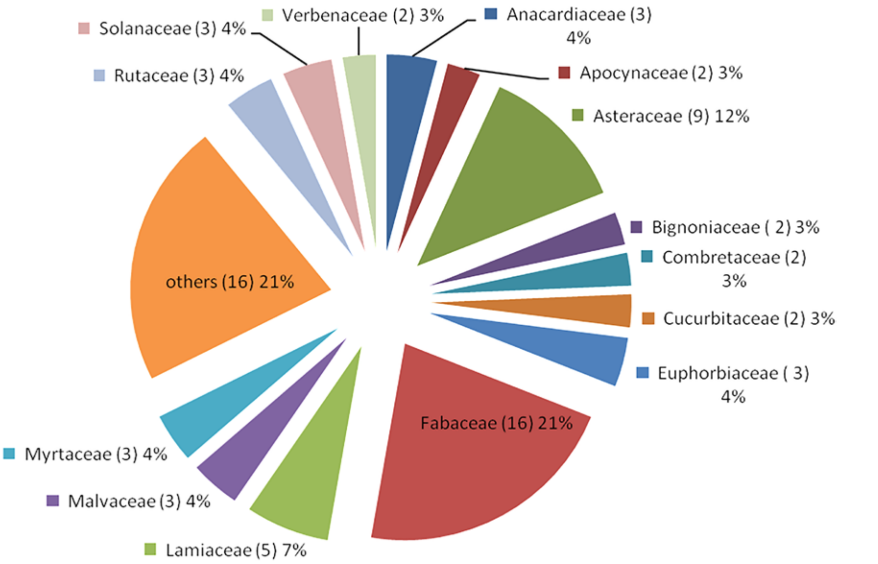

Figure 2. A summary of plant species per family recorded in four agro ecological zones in Uganda between April 2015 and April 2016. The group "others" represents 16 plant families, each family is represented by one plant species.

nectar or pollen or both pollen and nectar from the flowers (Table 1).

The highest number of bee forage species ($n = 62$) occurred at two sites in Nakasongola district (Kazwama and Nakasongola Apiculture Centre) while the lowest number of species ($n = 20$) was found in the Kabarole district (Nsura 2). This shows that all the study sites had a considerable number of bee forage floral species.

The results of top 10 dominant species foraged on by the honey bees in the different AEZs (Supplementary Figure 1) revealed that in Lake Victoria Crescent, the dominant species foraged by the bees were indigenous (wild) plants: *Combretum molle*, *C. collium*, *Albizia* spp., *Piliostigma thonningii*, *Vitex doniana*, *Harrisonia abyssinica*, *Guizotia scabra*, *Ocimum tenuiflorum*, and *Acacia polycantha*. In Mid-north, the dominant species were cultivated crops (*Sesamum indica, Manihot esculenta, Helianthus annus, Cajanus cajan*) and indigenous (wild) plants *Guizotia scabra, Ocimum tenuiflorum, Vitex doniana, Combretum spp, Stachytarpheta jamaicensis, Triumfetta cordifolia, Urena lobata, Vernonia* spp.

In Kyoga plains, the dominant species were two cultivated crops (*Manihot esculenta* and *Zea mays*) and the weed *Bidens pilosa* dominant in two sites, while in all Kabarole (Western highlands) sites *Musa paradoxica* was the dominant species and also cultivated at all other sites.

Cover of bee plant forage species

After subjecting the data of land cover by bee forage plants to a two-way ANOVA, it is clear that the AEZ significantly (df = 3, $F = 60.537$, $P < 0.001$) influenced the honey bee forage species cover in areas that were sampled (Supplementary Table S1). The AEZ accounted for 95.32% of the observed variation. The site (apiary) location also significantly (df = 13, $F = 1.941$, $P < 0.05$) influenced the different honey bee forage species recorded (Table S1). However it only accounted for 3.05%, leaving a small residual contribution of 1.63%.

Having detected a large (95.32%) variation contributed by AEZs, the ANOVA results were subjected to Tukey HSD multiple range test to identify which AEZs were actually different from each other. Except for MN-LVC ($P > 0.05$) all the other pairwise comparisons between the AEZs returned highly significant ($P < 0.001$) differences, summarized in Table S2.

Honey production

A box plot of honey production per hive for the different AEZs (Figure 3) shows production differences per hive between AEZs WH-KP and MN-KP but no significant differences in all other pairs. Figure 3 also shows variations in honey production per hive from the average within the following AEZs: LVC, WH, and MN, except for KP where the production was around the mean. When the honey production data was subjected to a two-way ANOVA, the site (apiary) location significantly (df = 13, $F = 4.467$, $P < 0.001$) contributed to the observed variation in average honey harvested (Supplementary Table S3). Differences due to site (apiary) location accounted for 57.74% of the observed variation in honey harvests.

The AEZ was not a significant contributory factor to the variation of honey harvests (Supplementary Table S3); it however accounted for up to 29.32% of the observed variation and 12.93% was due to other unknown factors not explicitly included in the ANOVA terms. Out of the 136 pairwise comparisons between sites in the study, only 14 returned significant differences (Supplementary Table S4). The results also showed significant differences in honey production for sites from within and between different AEZs.

Discussion

A total of 75 plant species belonging to 31 plant families comprising shrubs, trees, weeds and grasses were identified as bee forage sources in this study. The most visited plants were in the family Fabaceae followed by family Asteraceae. Each study site had a considerable number of plants foraged on by the bees. This is similar to findings of Abdullahi et al. (2011), Dukku (2013) and Kangave (2015). Kangave (2015) identified 46 bee forage plants belonging to 20 plant families in Uganda. Abdullahi et al. (2011) and Dukku (2013) found the family Fabaceae as the most visited by the honey bee *Apis mellifera* in Nigeria.

The findings of our study show significant differences in dominance cover of the plant species foraged by the bees at both the apiary/site location and the AEZs (Table S1). Dominance cover of plant species here refers to dominant/prominent. This means that there are dissimilarities in dominance cover of bee forage plant species which may either be uniform, clumped or randomly dispersed and this is seen more at AEZ level. This large dissimilarity (95.32%) was apparent in three AEZs but not in Mid-North and Lake Victoria Crescent (Table S2) which was similar. The small residual contribution (1.63%) to the variations in dominance cover of the plant species foraged by the bees could be due to effects of land use (Kalema & Witkowski, 2012; Omer, Elhassan, & Mohammed, 2015) and environmental factors (Eilu, Hafashimana, & Kasenene, 2004). The findings of Kalema and Witkowski (2012) on species diversity response to three main land uses (grazing, cultivation, and charcoal production) in Nakasongola District, central Uganda, show that species diversity and richness in savannah is to a great extent influenced by land use and anthropogenic disturbances. According to Eilu et al. (2004) rainfall, soil pH and altitude are presumed to be important in influencing species diversity in Albertine Rift in western Uganda.

Table 1. The 75 honey bee forage plants species in the study areas

Family	Species name	Plant form	Bees seen collecting	Flowering time
Acanthaceae	*Asystasia gangetica*	Shrub	N + P	Rainy
Anacardiaceae	*Lannea barteri*	Tree	N + P	
	Mangifera indica	Tree	N + P	Drought
	Rhus natalensis	Shrub	N + P	
Apocynaceae	*Carissa edulis*	Shrub	N	Rainy
	Thevetia peruviana	Shrub/tree	N	Rainy and drought
Arecaceae	*Borasus aethpicum*	Palm tree	P	
Asteraceae	*Bidens pilosa*	Herb	N + P	Rainy
	Bidens steppia	Herb	N + P	Rainy
	Conyza sumatrensis	Herb	N + P	Rainy
	Galinsoga parviflora	Herb	N + P	Rainy
	Guizotia scabra	Perennial/herb	N + P	Rainy
	Heliathus annuus	Herb	N + P	Rainy
	Tithonia diversifolia	Shrub	N + P	Rainy
	Vernonia adoensis	Shrub	N + P	Drought
	Vernonia sp.	Shrub	N + P	Drought
Bignoniaceae	*Jacaranda nimonsifolia*	Tree	N + P	Rainy and drought
	Markhamia lutea	Tree	N + P	Rainy and drought
Casuarinaceae	*Casuarina equisetifolia*	Tree	P	
Celastraceae	*Maytenus senegalensis*	Shrub/tree	N + P	
Cleomaceae	*Cleome gynandra*	Herb	P	Rainy
Combretaceae	*Combretum collinum*	Tree	N + P	Drought
	Combretum molle	Tree	N + P	Drought
Cucurbitaceae	*Cucurbita ficifolia*	Climber	N + P	Rainy and drought
	Cucurbita maxima	Climber	N + P	Rainy and drought
Ebenaceae	*Euclea divinorum*	Shrub	N + P	
Euphorbiaceae	*Bridelia micrantha*	Tree	N + P	Rainy and drought
	Flueggea virosa	Shrub	N + P	Rainy and drought
	Manihot esculenta	Shrub	N + P	Rainy and drought
Fabaceae	*Acacia brevispica*	Shrub	N + P	Drought
	Acacia hockii	Shrub	N + P	Drought
	Acacia polycantha	Tree	N + P	Drought
	Albizia coriaria	Tree	N + P	Drought
	Albizia ferruginea	Tree	N + P	Drought
	Albizia grandibracteata	Tree	N + P	Drought
	Bauhinia purpurea	Shrub	N + P	Drought
	Caesalpinia decapetala	Shrub	P	Rainy
	Caesalpinia pulcherrima	Shrub/tree	N + P	Rainy and drought
	Cajanus cajan	Shrub	N + P	Rainy
	Calliandra calothyrsus	Tree	N + P	Rainy and drought
	Crotalaria cleomifalia	Shrub	N + P	
	Delonix regia	Tree	N + P	Drought
	Erythrina abyssinica	Tree	N + P	Drought
	Piliostigma thonningii	Shrub	N + P	Rainy
	Tamarindus indica	Tree	N + P	Drought
Lamiaceae	*Hoslundia opposita*	Shrub	N + P	Rainy
	Hyptis sauveolens	Shrub	N + P	Rainy
	Leonotis ocymifolia	Woody herb	N	Rainy
	Ocimum gratissimum	Herb	N + P	Rainy
	Ocimum tenuiflorum	Herb	N + P	Rainy
Loganiaceae	*Strychnos innocua*	Shrub/tree	N + P	
Malvaceae	*Sida acuta*	Woody herb	N + P	Rainy
	Urena lobata	Woody herb	N + P	Rainy

Family	Species name	Plant form	Bees seen collecting	Flowering time
	Grewia mollis	Shrub	N+P	Rainy
Meliaceae	*Azadirachta indica*	Tree	N+P	Rainy
Moringaceae	*Moringa oleifera*	Tree	N+P	Rainy
Musaceae	*Musa paradoxica*	Perennial herb	N+P	Rainy and drought
Myrtaceae	*Callistemon citrinus*	Tree/shrub	N+P	Rainy and drought
	Eucalyptus sp.	Tree	N+P	Rainy and drought
	Syzygium cumini	Tree	N+P	Rainy
Passifloraceae	*Passiflora edulis*	Climber	N+P	Rainy
Pedaliaceae	*Sesamum indica*	Herb	N+P	Rainy
Poaceae	*Zea mays*	Annual grass	P	Rainy
Rubiaceae	*Vangueria apiculata*	Shrub	N+P	Drought
Rutaceae	*Citrus aurantifolia*	Shrub/tree	N+P	Drought
	Clausena anisata	Shrub/tree	N+P	Rainy
	Zanthoxylum chalybeum	Shrub/tree	N+P	Drought
Simaroubaceae	*Harrisonia abyssinica*	Shrub/tree	N+P	Drought
Solanaceae	*Brugmansia hybrid*	Shrub	N+P	Rainy
	Brugmansia suaveolens	Shrub	N+P	Rainy
	Solanum incanum	Herb	P	Rainy
Tiliaceae	*Triumfetta cordifolia*	Woody herb	N+P	Rainy
Verbenaceae	*Stachytarpheta jamaicensis*	Herb	N	Rainy and drought
	Vitex doniana	Tree	N+P	Drought
Vitaceae	*Cyphostemma adenocaule*	Climber	N+P	Rainy

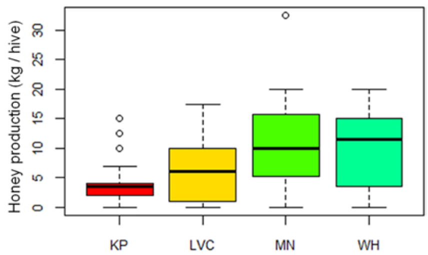

Figure 3. Box plot of honey production per hive for the different agro ecological zones. KP-Kyoga Plains, LVC-Lake Victoria Crescent, MN-Mid-North, and WH-Western Highlands.

Our study shows significant differences in average honey harvested at the site (apiary) location (Table S3); the dissimilarity (57.74%) was actually contributed by 14 apiary sites (Table S4) within and between different AEZs. The significant difference in production between apiaries of Lake Victoria Crescent and Mid-North AEZ (nak5-lira3, nak2-lira4, nak3-lira4, nak5-lira1, nak5-lira3, and nak5-lira2) (Table S4) is probably not caused by bee forage; the two AEZs had similar bee forage cover (Table S2); nak2 and nak3 apiary sites had higher production than lira4 site while nak5 had no production as compared to sites lira1-3. This finding shows that other factors are the possible causes for the differences in average honey production per hive in Lake Victoria Crescent and Mid-North AEZ which we attribute to honey bee pests, viruses and management. Our findings agree in part with work done in Uganda by Amulen et al. (2017), Kajobe et al. (2016) and Kasangaki et al. (2018). Kasangaki et al. (2018) reports Mid-North AEZ as having the strongest colonies with high productivity compared to Lake Victoria Crescent AEZ (an area with pastoral livestock production). Amulen et al. (2017) reported a zero detection of pesticides in MN AEZ, which according to the authors could result in the high honey production. The significant difference in honey production between sites of Kyoga Plains and Lake Victoria Crescent (tor4-nak5) (Table S4) reflect 0.0 kg of honey harvested at nak5 and an average of 6.87 kg per hive harvested at tor4, which we attribute to differences in forage cover, poor apiary management practices and pests observed at nak5. Kajobe et al. (2016) showed pests strongly affecting honey bee colonies and productivity in Uganda.

We found production differences between sites of Western Highlands and Lake Victoria Crescent (Table S4, nak5-kab2 and nak5-kab3); there was higher average honey yield per hive for kab2 and kab3 (19 and 14 kg/hive) respectively with no production at nak5. This finding is attributed to other factors (poor apiary management practices and pests observed) at site nak5 and high elevation at kab2 and kab3; the forage cover of the two AEZs, Western Highlands and Lake Victoria Crescent were significantly different (Table S2). This finding in part agrees with the findings of Asensio et al. (2016) who found high productivity of apiaries associated with elevation.

Conclusion

Bee forage plants are an important consideration for beekeepers. The honey production differences found between sites of different AEZs KP and LVC is attributed to differences in forage cover. The observed average honey production differences per hive in sites of AEZ with similar bee forage cover is attributed to other site (apiary) factors, e.g. honey bee pests, viruses, and management as the possible causes for the differences in average honey production. We suggest that where an apiary is located locally, and how colonies are maintained, probably more influences the amount of honey harvested than the studied agroecological zones. Therefore we conclude that beekeeping can be done anywhere in Uganda as long as good forages are provided and other factors, such as pests, are managed according to good apicultural practice.

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Supplementary material

Supplementary material is included for this article at: http://dx.doi.org/10.1080/0005772X.2019.1608892.

Disclosure statement

No potential conflicts of interest are reported by the authors.

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