UNIVERSITY OF CAPE COAST

POLLINATION ECOLOGY OF SHEA (*VITELLARIA PARADOXA* C.F. GAERTN.) IN THE GUINEA SAVANNA ZONE OF GHANA

LATIF IDDRISU NASARE

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BY

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Thesis submitted to the Department of Conservation Biology and Entomology
of the School of Biological Sciences, University of Cape Coast, in partial
fulfilment of the requirements for the award of Doctor of Philosophy degree in
Entomology

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DECLARATION

Candidate's Declaration

I hereby declare that this thesis is the result of my own original research and that no part of it has been presented for another degree in this university or elsewhere.

Candidate's Signature: .... Date: ....

Name: Latif Iddrisu Nasare

Supervisors' Declaration

We hereby declare that the preparation and presentation of the thesis were supervised in accordance with the guidelines on supervision of thesis laid down by the University of Cape Coast.

Principal Supervisor's Signature: .... Date: ....

Name: Prof. Peter Kofi Kwapong

Co-Supervisor's Signature: Jane Stout Date: ....

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ABSTRACT

Vitellaria paradoxa (shea) is an economic tree endemic to Sub-Saharan Africa. Shea fruit contributes to food security, while the edible fat from shea kernel is used industrially in cosmetic, pharmaceutical and confectionary products. However, optimum fruit yield is limited by inadequate pollination services. This study investigated floral phenology and explored managed bee (*Apis mellifera*) for enhanced pollination in shea parklands of six sites in three regions (Upper West, Upper East and North East) from August 2020 to December 2021. The study specifically sought to establish the relationship between climatic conditions and floral phenology, and the effect of apiary on shea flower visitors and fruit yield at four distances (100, 500, 1000 and 4000m) from the apiary. Alternative floral resources visited by shea pollinators (bees) were also surveyed monthly for one year. Shea flowering was significantly associated with soil moisture and temperature but the onset of flowering and morphometric traits of floral parts varied significantly between regions. Tree proximity to apiary had a positive effect on fruit set but not fruit weight and size. Presence of apiary did not have any effect on diversity and flower visitation frequency of other bees. Similarly, weather conditions had a minimal effect on flower visitor composition. Alternative forage survey identified 32 woody plants, 75% of which were visited by shea primary pollinators. The study concluded that beekeeping in shea parklands had some positive effects on pollination and fruit set. However, further studies are required to determine the optimal hive density per acreage of shea parkland and the long-term effects of beekeeping on other florivorous insects.

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DEDICATION

Dedicated to my dear wife, Inaas B. Saato and son, Imaan Yenliwiisi Nasare

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LIST OF ABBREVIATIONS

API	African Pollinator Initiative
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change
NE	North East
SSA	Sub Saharan Africa
UE	Upper East
UW	Upper West

CHAPTER ONE

INTRODUCTION

1.0 Background to the Study

Insect pollination is an essential ecosystem service required for the reproductive success of an estimated 94 % of tropical plants (Ollerton, Winfree, & Tarrant, 2011). Two thirds of food crop species are insect pollinator-dependent (Klein et al., 2007a). Although other animals aid in pollination, insect pollinators such as bees, flies, butterflies, moths, and beetles are the pollinators of most plants. Fruit/seed set is reduced when insect mediated pollination is not achieved in entomophilous plants (Delaney et al., 2020; Holland et al., 2020; Reilly et al., 2020).

The economic value of insect pollination is estimated at US$ 577 billion annually, constituting 9.5% of the monetary value of global food crops (Gallai, Salles, Settele, & Vaissière, 2009). Pollination does not only contribute to the quantity of world food production but also contributes to human nutrition (Eilers, Kremen, Greenleaf, Garber, & Klein, 2011), enhanced commercial value and shelf life of fruits, nuts and oils produced (Bartomeus et al., 2014; Burns & Stanley, 2022; Khalifa et al., 2021).

Despite the ecological and economic value of pollination, pollinator populations are reported to be in decline due to human-induced habitat degradation and climate change (Brown et al., 2016; Dibble, Drummond, & Stack, 2020; Dicks et al., 2021; Ganuza et al., 2022; Goulson, Nicholls, Botías, & Rotheray, 2015; IPBES, 2016). Ghazoul (2015) assumes that pollinator decline is limited to honeybees and bumble bees, but it is evident that pollinator diversity and distribution patterns have changed over time

(Ollerton, 2017). A decline in pollinator population will have implications on biodiversity, food security, and the resilience of ecosystems to climate change (Potts et al., 2010a; Vanbergen et al., 2013).

The impact of pollinator decline is predicted to be more severe on insect pollinated crops in agricultural landscapes due to limited floral diversity and nesting sites (Ferreira, Boscolo, & Viana, 2013; Ricketts, 2004). This could be the case for insect pollinated tree crops in Sub-Saharan Africa (SSA), as indigenous economic trees are retained and managed in cultivated landscapes under which annual food crops are cultivated (Ræbild, Hansen, & Kambou, 2012; Baffa, 2015). This traditional agroforestry system has led to the formation of extensive parklands often termed agroforestry parklands. Parklands are a major land use in arid and semi-arid regions of Sub-Saharan Africa (Bayala et al., 2015).

In the parklands of the Sudano- Sahalian zone, *Vitellaria paradoxa* (shea) is reported among the most dominant tree species (Agossou, Jakob, Wiegand, & Sinsin, 2008; Aleza et al., 2015; Chimsah, Nyarko, & Abubakari, 2013; Masters, Yidana, & Lovett, 2004; Tom-Dery, Hinneh, & Asante, 2013). *Vitellaria paradoxa* is native to about 21 countries in Sub-Saharan Africa, extending from Senegal in the West to Sudan in the East and onto the foothills of Ethiopia (Hall, Aebischer, Tomlinson, Osei-Amaning, & Hin- dle, 1996). In Ghana, *V. paradoxa* is recorded as the most abundant tree species in Northern Ghana, predominantly occurring in the Guinea and Sudan Savanna zones (Chimsah et al., 2013).

Vitellaria paradoxa provides valuable non-timber forest products such as food, oil, fuel, and medicine. The edible fruits of *V. paradoxa* are rich in sugars and ascorbic acid which contributes to food security, especially in the early rainy season (Karambiri, Elias, Vinceti, & Grosse, 2017; Maranz, Wiesman, Bisgaard, & Bianchi, 2004). The oil extracted from shea kernel (shea butter) is used as a major cooking oil across Africa (Gwali et al., 2011). Shea butter is also used internationally in the confectionery, cosmetic and pharmaceutical industries (Alander, 2004; Davrieux et al., 2010). Although protected primarily for its economic benefits, shea also offers several environmental benefits in parkland, including soil regeneration and carbon sequestration (Luedeling & Neufeldt, 2012).

1.1 Statement of the Problem

The West African Sudanian Savannah zone earns about US$150 million annually from shea exports (Glew & Lovett, 2014). Ghana exports about 9400 tons of shea annually and is the fourth largest shea producer (USAID, 2018). Shea income accounts for about 12% of household income in rural areas (Pouliot, 2012). Shea is one of the few crop industries that contribute directly to the economic empowerment of women, as women are the key players in the processing and marketing of shea butter (Mohammed, Baah-Ennumh, & Abdulai, 2016).

The price per tonne of shea butter is expected to increase due to increasing industrial demand in the cosmetics industry (Simmons, 2014; USAID, 2018). This economic outlook has led to an upsurge in the number of development projects supporting aspects of the shea value chain (Boffa, 2015). Increasing demand coupled with the wide geographic distribution in Africa is seen as an opportunity for economic empowerment and poverty alleviation in SSA.

Notwithstanding the prospects, the supply of shea nuts/butter to meet increasing demand is being threatened by anthropogenic disturbances in shea parklands (Boffa, 2015; Elias, 2015; Lovett & Haq, 2000b). Landuse change has gradually led to the elimination of natural areas that provide safe sites for regeneration and subsequent recruitment of saplings in cultivated lands (Tom-Dery, Sakyi, & Bayor, 2015). The decline in alternative tree species for fuel, construction, and carvings has resulted in indiscriminate felling of shea trees. In addition to these, inadequate pollination services for optimum shea yield have been reported as a threat to yield sustainability (Delaney et al., 2020; Kwapong, 2014; Stout et al., 2018).

The flower structures and antheses of Vitellaria paradoxa are adapted to pollen outcrossing (Okullo, 2004; Yidana, 2004) and therefore depend largely on insect pollinators for pollen dissemination. Fruit yield is significantly influenced by access to insect pollination services (Lassen et al. 2016; Delaney et al. 2020).

Notwithstanding the high insect pollinator dependence of shea, human-induced degradation of shea parklands has had both direct and indirect impacts on pollinators (Lovett & Haq, 2000b; Kwapong, 2014; Delaney et al. 2020). Perennial bush fires of the savanna generate heat and smoke that tranquilizes bees and sometimes result in mortalities (Millogo-Rasolodimby, 1989).

The drive to increase agricultural productivity to achieve Sustainable Development Goal 2 (Zero Hunger) has led to a gradual transition in Ghana from subsistence farming to large-scale commercial farming (Jayne et al., 2016; Kwapong, Ankrah, Anaglo, & Vukey, 2021; Tanko, Ismaila, & Sadiq, 2019). However, agricultural extensification is associated with reduction in natural areas (Bessah, Enoch Abdullahi, Bala Agodzo, Okhimamhe, Boakye, & Ibrahim, 2019) that provide forage and nesting sites for insect pollinators. Agricultural intensification on the other hand exposes pollinators and other beneficial insects to toxic hazards. These disturbances have reduced pollinator population which is manifested in inadequate pollination services for optimum fruit yield of *V. paradoxa* (Delaney et al., 2020; Lassen, Nielsen, Lompo, Dupont, & Kjær, 2016).

Among measures to boost pollination services for shea are recommendations for the incorporation of beekeeping into shea parklands (Lassen et al., 2016; Nasare, Kwapong, & Doke, 2019; Stout et al., 2018). Despite the evidence of managed bees for improved pollination services elsewhere (Bosch, Osorio-Canadas, Sgolastra, & Vicens, 2021; Evans et al., 2021; Geslin et al., 2017; Stern et al., 2001), there is limited evidence to justify the adoption of this approach in shea parklands. Moreso, shea parklands are known to be complex landscapes (Bayala et al., 2015), therefore the response of other shea flower visitors to apiaries as well as the effects of weather conditions on shea pollinators need to be investigated. The present study sought to examine these aspects of the pollination ecology of *V. paradoxa* in Northern Ghana.

1.2 Research Objectives

1.2.1 General objective

The main objective of this study was to examine the effect of managed honey bees on shea pollination, and the diversity of other shea flower visitors and to identify alternative forage resources for shea pollinators in the Guinea Savanna.

1.2.2 Specific Objectives

The specific objectives were to:

1. examine floral phenology and morphology of shea.
2. investigate the effect of beekeeping on shea flower visitor composition.
3. examine the effect of beekeeping on fruit set and yield of shea.
4. assess the effect of weather conditions (Temperature, relative humidity and wind speed) on shea flower visitor diversity and visitation.
5. identify alternative floral resources foraged by shea pollinators.

1.2.2 Hypotheses

1. The floral phenology and morphology of shea does not differ between geographical locations in northern Ghana.
2. The presence of managed bee colonies in shea parkland does not affect shea flower visitor composition.
3. Managed bees on shea parkland does not affect shea fruit yield.
4. Pollinator diversity and foraging behaviour within shea parklands are not influenced by climatic factors.
5. Shea pollinators forage on other plants in the Guinea savanna.

1.3 Significance of the Study

Beekeeping is been recommended for improved pollination services in shea parklands, but there is no blueprint to guide the incorporation of managed bees into shea parklands. The outcome of this study would establish the relationship between beekeeping and the reproductive success of shea in Northern Ghana. This would serve as a practical guide to farmers, Foresters and Extension officers working in shea ecosystems. This would equally serve as a guide for environmental education and pollinator conservation.

In Ghana, rural populations of the five northern regions are most vulnerable to climate change, as rain-fed agriculture in arid and semi-arid areas is expected to be vulnerable to climate change (Altieri & Koohafkan, 2008). These vulnerabilities have drawn attention to supplementary food sources through animal-related production systems such as beekeeping (Duah, Segbefia, Adjaloo, & Fokuo, 2017). Civil society organisations are therefore increasingly providing incentives to farmers in beekeeping as a climate change adaptation strategy. Conservation of melliferous plants is required for successful beekeeping and honey yields. Information on melliferous plants of the savanna would be useful to beekeepers, Foresters and Non-Governmental Organisations in this endeavour.

Moreover, the flowering period (30-75 days) of shea is relatively short (Hall et al. 1996). Aside shea, pollinators depend on other plants which are still largely unknown in the Guinea Savanna. Wild pollinators rely on several plants which flower sequentially to provide forage all year round (Ockinger & Smith, 2007). Roulston and Goodell (2011) identified the availability of food resources as the most outstanding factor among other factors limiting bee population. Information on alternative forage for shea pollinators would be useful to farmers and ecologists in prioritising tree species for the restoration of savanna woodlands. This would equally contribute to SDG 15 in restoring degraded ecosystems.

Recent review of shea literature has identified pollination as an area with major knowledge gaps (Nguekeng, Hendre, Tchoundjeu, & Kalousová, 2021; Tom-Dery, Eller, Reisdorff, & Jensen, 2018). These gaps are equally evident in the scope and methodologies of existing studies. For instance, previous studies on shea pollinators have mainly focused on pollinator diversity and contribution to fruit yield (Kwapong, 2014; Lassen, Nielsen, Lompo, Dupont, & Kjær, 2018; Nasare et al., 2019; Nguemo, Mapongmetsem, Tchuenguem, Gounhagou, & Yougouda, 2014; Stout et al., 2018) without considering the effect of climate on insect pollinators. Savanna ecosystems are amongst the most climate-sensitive biomes(Bond, Midgley, & Woodward, 2003; Sala et al., 2000), therefore, an assessment of insect pollinators in savannah ecosystems without examining the effect of climate variability on pollinator foraging behaviour and diversity would overlook important aspects in the variability of the system. The outcome of this study would therefore contribute to the literature on the effect of climatic factors on shea pollinators.

1.4 Delimitations and Limitations

1.4.1 Delimitations

This research only considered the effect of managed, *Apis mellifera adansonii* colonies on the fruit yield of shea although there are many other bee species managed for pollination services. Secondly, this study only selected communities in the Upper West, Upper East, and North East Regions which all fall within the Guinea Savanna agro-ecological zone.

1.4.2 Limitations

In the experiment, pan traps could have been used to complement the sweep nets in examining pollinator response to climatic factors from a landscape context but this was not done due to financial constraints. Climate data could have been taken in-situ to monitor the effect of weather conditions on floral phenology but the study relied on data from the nearest weather station owing to logistical constraints and poor road network.

1.5 Definition of Key terms

Fruit set: this is a count of the number of shea fruits produced.

Insect-to-flower visit: this refers to an insect visit to the shea flower and coming in contact with the reproductive parts of the flower.

Managed pollination services: Colonized artificial beehives in agricultural fields to boost pollination.

Shea parkland: This is a discontinuous canopy cover of dispersed shea trees under which food crops are cultivated yearly.

Flower visitor: Any insect species that come in contact with flowers

1.6 General Methodology

1.6.1 Study Area

The study was conducted from August 2020 to July 2021 at six sites in the Guinea Savannah agro-ecological zone of Ghana (Figure 1.1). The Guinea Savanna is located between the Forest Savanna Transition and the Sudan Savanna zones. It includes the North, Northeast, Savannah, Upper West and Upper East Regions and the northern parts of the Oti and Bono East Regions of Ghana(Incoom, Adjei, & Odai, 2020). The area records a unimodal rainfall pattern where the wet season occurs from April to October and is followed by a dry season (Incoom et al., 2020).

The vegetation of the Guinea Savanna is predominantly grassland dotted with some indigenous woody species such as shea (*Vitellaria paradoxa*), baobab (*Adansonia digitata*), dawadawa (*Parkia biglobosa*), African mahogany (*Afzelia Africana*), ebony (*Diospyros mespiliformis*), Linnea (*Lannea acida*) among others (Tom-Dery et al., 2013; Yeboah, Nasare,

& Abunyewa, 2022). *Vitellaria paradoxa* is however the most abundant tree species in the area (Chimsah et al., 2013).

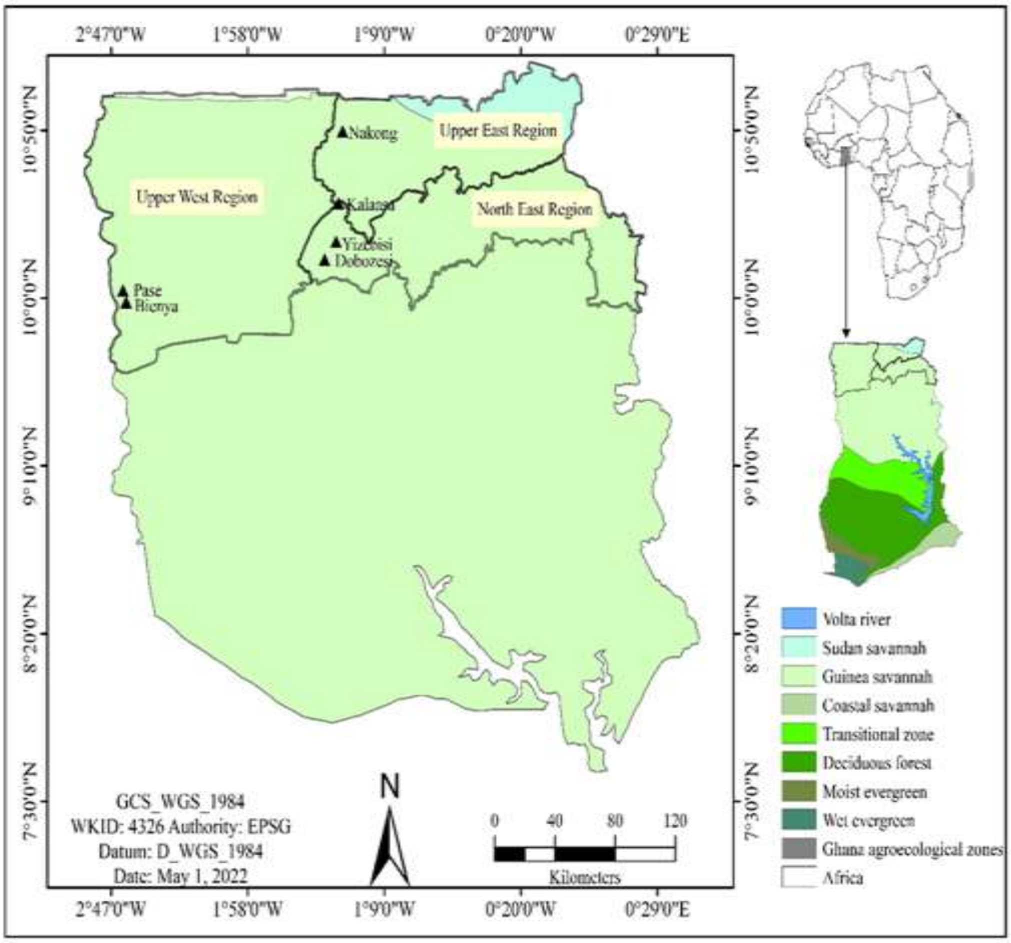

Figure 1. 1: Map showing the location of study sites

1.6.2 Experimental sites and Field Work

The study was conducted in shea parklands of six randomly selected communities that implemented the Agriculture and Natural Resources Management (AgNRM) beekeeping project in three regions (Upper West, Upper East and North East). In each community, an apiary of ten beehives was installed in July 2017 and communities that had apiaries with 6-8 colonised hives were randomly selected for the study. Thus, two sites per region (Figure 1).

In each site, four levels of proximity to the apiary were identified (100, 500, 1000 and 4000 m). Focal trees were randomly selected within each radius and three pollination treatments (open, bagged and hand pollination) were applied to three inflorescences of each focal tree. Data were collected on the number of flowering trees, climatic factors and morphometric traits of shea floral parts for geographic variation in floral phenology and morphology of shea. At the fructification stage, the number of fruit set per inflorescence was counted every fortnight and mature fruit and seed weight were taken to reveal the effect of beekeeping on fruit set and yield of shea. To examine the effect of beekeeping on other flower visitor diversity as well as the response of shea flower visitors to weather conditions, flower visitors were sampled every fortnight during peak flowering coupled with the observation of visitations to tagged inflorescences in 10 minutes periods per tree.

Insect flower visitors were also sampled once monthly from other plants in the savanna to reveal the alternative plants foraged by shea pollinators. All collected insect specimens were brought to the Insect Museum of the Department of Conservation Biology and Entomology of the University of Cape Coast for identification by a bee taxonomist.

1.6.3 Data analysis

Generalised Linear Mixed effect models (GLMMs) were used in predicting shea flowering based on the climatic factors whilst morphometric traits of shea flowers were compared between regions using an Analysis of Variance where significant means were separated with LSDs. GLMMs were again fitted for distance to apiary and pollination treatment effects on fruit set and yield. Flower visitor composition was compared between distance ranges to the apiary as well regions using Non-Metric Multidimension Scaling (NMDS). Again, GLMMs were used to predict insect visitation to shea flowers based on climatic factors. GLMMs were fitted using the lm4 and glmmTMB packages in R (Bates, Mächler, Bolker, & Walker, 2015; Brooks et al., 2017) whilst Vegan package was used for NMDS (Oksanen et al., 2022). All analysis were run in R Core Team (2021).

1.7 Linkage of Articles/Scientific Papers

This thesis is composed of manuscripts either published (1), submitted (2) to peer-reviewed journals or under review (3) as follows.

1. **Nasare, L.I.,** Stout, J., Lovett, P. and Kwapong, P.K. (2022). Determinants of shea (*Vitellaria paradoxa* C.F. Gaertn.) fruit yield: A review of research approaches and current knowledge. Scientific African. 17(2022) e01371**.** doi.org/10.1016/j.sciaf. 2022.e01371
2. **Nasare, L.I.,** and Kwapong, P.K. and Stout, J.C. (Manuscript submitted to Agroforestry Systems). Variation of shea (*Vitellaria paradoxa* subsp. paradoxa) floral phenology and morphology in Ghana.
3. **Nasare, L.I.,** Kwapong, P.K. and Stout, J.C. (Manuscript submitted to Journal of Applied Ecology). Influence of beekeeping on pollination and fruit yield of *Vitellaria paradoxa* in West African Agroforestry parklands.
4. **Nasare, L.I.,** Stout, J.C., Combey, R. and Kwapong, P.K. (Manuscript under review for Apidologie). Effect of proximity to managed bees on shea flower visitor diversity and visitation in Guinea savanna agro-ecological zone, Ghana.

5. **Nasare, L.I.,** Stout, J.C., Combey, R. and Kwapong, P.K. (Manuscript under review for Journal of Pollination Ecology). Influence of environmental factors on visitation and diversity of shea (*Vitellaria paradoxa*) flower visitors.
6. **Nasare, L.I.,** Stout, J.C., Combey, R. and Kwapong, P.K. (Manuscript under review for Journal of Apicultural Research). Alternative forage for shea (*Vitellaria paradoxa*) flower visitors in Northern Ghana.

1.8 Organisation of the Study

This thesis has been organised into nine chapters. Chapters one and two covered introductory overview of the study and general literature review of key concepts, respectively. Chapter three to eight were written as manuscripts based on the objectives of the study. Chapter three was a systematic literature review on determinants of shea fruit yield. Chapter four examined the geographic variation in floral phenology and morphology of shea in northern Ghana. Chapter five investigated the influence of beekeeping on pollination and shea fruit yield. Chapter six assessed the effect of proximity to beehives on shea flower visitor composition and abundance. Chapter seven examined the effect of climate on flower visitator diversity and visitation rate. Chapter eight identified alternative forage resources for shea flower visitors in the shea parkland. Chapter nine of the thesis was dedicated to summary, general conclusions and recommendations.

CHAPTER TWO

LITERATURE REVIEW

2.1 Origin and distribution of *V. paradoxa*

Vitellaria paradoxa is a tree plant of the family Sapotaceae, belonging to a monotypic genus (*Vitellaria)* with two reported sub-species; *V. paradoxa* subsp. *paradoxa* and *V. paradoxa* subsp. *nilotica* (FAO, 1988; White, 1983). It is endemic to 21 countries in Sudano-Sahelian zone of SSA, stretching from Senegal in West Africa to Uganda in the East (Bonkoungou, 2004; Hall et al., 1996). The endemism of the sub-species is known to be mutually exclusive where *V. paradoxa* subsp. *paradoxa* occurs in West and Central Africa whilst *V. paradoxa* subsp. *nilotica* occurs in East Africa (Hall et al., 1996). An estimated area of 3.41 million km^2 is known to be potentially suitable for *V. paradoxa* (Naughton, Lovett, & Mihelcic, 2015). *Vitellaria paradoxa* generally thrives in arid and semi-arid regions with mean annual rainfall of 500 – 1000 mm and a dry period of 5 – 8 months in a year(Glèlè Kakaï et al., 2011).

2.2 Shea agroforestry parklands

Farming systems in SSA are traditionally characterised by the deliberate retention of indigenous economic trees on farmlands under which annual crops are cultivated (Boffa, 2015). This is sustained by an alternate cultivation system, in which fallow periods are allowed for regeneration of seedlings, followed by a successive cultivation period (Boffa, 2015). The most frequently retained species in semi-arid regions include *Parkia biglobosa, Diospyros mespiliformis, Azadirachta indica, Daniellia oliveri, Hannoa undulata, Pericopsis laxiflora, Sterculia setigera, Lannea acida, Vitex* *doniana* among others (Chimsah et al., 2013). The density of a tree species on the farmland is often an indication of its socio-economic importance.

Although many indigenous plants are retained on farmlands, shea is one of the most managed species in traditional Agroforestry over the last 1000 years (Neumann et al., 1998) and has become the most abundant species in many of its native growing areas (Aleza et al., 2015; Chimsah et al., 2013; Lovett & Haq, 2000a). In Benin, shea constitutes about 70% of overall tree density in its naturally occurring regions (Aleza et al., 2015). In northern Ghana, Lovett and Haq (2000b) reported shea constitutes 34 – 79% of woody species in cultivated lands. Recent inventory in Ghana, indicates shea makes 62% of tree density in cultivated lands and 40% in fallow lands (Chimsah et al., 2013). In Burkina Faso, shea is reported as the most abundant indigenous economic species (Fischer, Kleinn, Fehrmann, Fuchs, & Panferov, 2011). These shea dominant landscapes are often termed as “shea parklands” or “agroforestry parklands”. Shea parklands have become common tree management system in the Sahelian regions of SSA (Bayala, Jean, & Zewge, 2008).

Although trees with desired traits are often recruited and managed on farmlands, the specific traits considered for retention differ between farmers as well as regions. In Uganda, the most important traits considered are the oil yield of the nuts and taste of the fruits produced along with other minor traits such as size of fruit and nuts (Gwali et al., 2012). In the case of northern Ghana, tree health, competitive effects on annual crops, size and taste of fruit are among the key traits considered (Lovett & Haq, 2000b) whilst in Burkina

Faso, productivity of the tree, shading effects and spacing are the major traits considered (Elias, 2013).

2.3 Floral phenology and morphology of shea

2.3.1 Floral phenology of shea

Phenology is the study of biological events and their timing of occurrence in reference to biotic and abiotic factors as well as the interrelation between phases of the same or different species (Chuine & Beaubien, 2001; Gordo & Sanz, 2010). Ecosystems generally undergo changes in response to changing climate. The West African savannas for instance have gone through considerable changes since the severe droughts of the 1970s. Plants therefore develop adaptive mechanisms to withstand the changes, which tends to shift phenological phases of their development (De Bie, Ketner, Paasse, & Geerling, 1998). Phenological events in plants are generally influenced by short term variation in climatic factors such as rainfall and humidity (Anderson, Nordheim, Moermond, Bi, & Boesch, 2005; Barrett & Brown, 2021). According to Oni et al. (2014) flowering of most savanna tree species starts in the late dry season and extends into the raining season.

Vitellaria paradoxa flowering is triggered by the change in moisture stress especially when relative humidity drops to the lowest and just begins to rise (Kelly, Poudyal, & Bouvet, 2018; Okullo, 2004). Flowering often occurs when the combination of climatic factors creates the driest conditions of the year. However, the exact month of *Vitellaria paradoxa* flower initiation differ between countries and agro-ecological zones. In Uganda, shea flowering is reported to occur from January to February (Okullo, Hall, & Obua, 2004) whilst in Ghana, flowering occurs from December to March (Yidana, 2004).

Similarly in some parts of Mali flowering commences in December (Kelly et al., 2018). This variation is influenced by abiotic conditions of the shea parklands (Kelly & Senou, 2017; Nguemo et al., 2014).

2.3.2 Floral morphology of *V. paradoxa*

Flowers of *V. paradoxa* are produced on dense fascicles at the distal ends of leafless branches (Stout et al., 2018). Nguemo al.(2014) observed six morphological phases from bud formation to anthesis of *V. paradoxa*. The first morphological phase is the formation of thick spherical buds at the distal ends of twigs. An estimated 60% of buds formed at this stage fall off the plant partly due to biting and sucking insect attacks. The second morphophase of the bud is characterised by the lengthening of the peduncle and increased size of the bud which spans one week. Even at this stage the calyx is still wrapped together with a greenish colour. The third stage of bud development is characterised by expansion of the bud resulting in an increased flower size. Flower anthesis occurs at the fourth stage with the emergence of the pistil from the flower bud. The fifth stage is characterised by the opening of the petals at the upper ends which forms a tube with a small opening containing eight cogwheel petaloid (Nguemo et al., 2014). The sixth and final stage coincides with the falling of some floral parts.

On average, each fascicle contains 50 creamy bisexual florets (Guira as cited in Lassen et al. 2016) but Stout et al. (2018) reported 31 florets per fascicle. The flowers are actinomorphic with an estimated diameter of 15mm containing 8 – 10 creamy petals and one style, but some flowers may have two styles (Hall et al., 1996). The style length ranges from 1.3 to 3.86 cm whilst the petal length ranges from 0.8 to 1.4 cm (Nguemo et al., 2014; Okullo, 2004). The stamens and staminodes occur in an alternating pattern where the staminodes bend towards the ovary. This provides protection for the nectar produced by the glandular hairs that are arranged to surround the ovary. Shea is protogynous such that the stigma protrudes the flower buds before bud bursts to expose anthers (Hall et al., 1996; Stout et al., 2018; Lassen et al., 2016).

Flower anthesis in shea is observed to occur at night where most floral buds open from 7 – 9 pm(Nguemo et al., 2014). The timing of anthesis is important in pollination as stigmas are often most receptive during anthesis (Kengue as cited in Nguemo et al. 2014). Aside anthesis, receptive flowers of *V. paradoxa* open daily during the morning hours to allow flower visitors to access nectar (Stout et al., 2018; Lassen et al., 2016). Shea produces relatively low volumes of nectar with strong honey scent as an olfactory cue for the attraction of insects and birds(Millogo-Rasolodimby, 1989). The pollen grain of shea measures 54 µm in its polar axis and 36 µm in equatorial axis having a spherical shape in the polar view and a prolate shape in equatorial view (Adekanmbi &Ogundipe, 2009).

2.4 *Vitellaria paradoxa* pollination and fructification

According to Ward, Dick, Gribel, & Lowe (2005) most tropical trees are self- incompatible and therefore relies on insects for pollen transfer. Genetic assessment of inbreeding in *V. paradoxa* revealed inbreeding coefficients close to zero an indication of weak selfing or non-occurrence of selfing (Kelly, Hardy, & Bouvet, 2004). This together with the protogynous flower development affirms the assertion that *V. paradoxa* is outcrossing. More especially within flower-self-fertilization is impossible because stigmas become receptive long before anthers mature. Notwithstanding, the occurrence of several flowers on the same fascicle where flowers mature at different periods can give a room for within- inflorescence self-pollination (Stout et al., 2018). Basga (2018) posits *V. paradoxa* exhibits both allogamous and autogamous mating systems. Many authors also posit *V. paradoxa* is perhaps also wind pollinated (Basga, 2018; Lassen et al., 2016; Okullo, 2004).

Insect visitors of shea are primarily found in the orders Hymenoptera, Coleoptera, Dictyoptera, Hemiptera, Diptera, Orthoptera and Lepidoptera (Stout et al., 2018; Nguemo et al., 2014; Okullo, 2004). In Cameroun, seven insect orders belonging to 46 genera/ species were identified as flower visitors of shea (Nguemo et al., 2014). Despite the reported diversity, bees are known to be the primary pollinators (Delaney et al., 2020; Basga, 2018; Stout et al. 2018; Lassen et al., 2016; Nguemo et al., 2014; Kwapong, 2014; Okullo, 2004). According to Stout et al. (2018), an estimated 88.2% of insects foraging on shea flowers are bees (*Apis mellifera adansonii*, *Ceratina moerenhouti*, *Compsomelissa nigrinervis, Hypotrigona gribodoi*, *Meliponula ferruginea and Meliponula beccari*).

Fruits are formed after fertilisation, where each fertilised ovary develops into a single fruit containing a seed. However, in some cases, a fruit may contain 2 fruits (Lassen et al., 2016). According to Elias (2015) in some rare cases a fruit may have 2 – 4 seeds. The fresh weight of the fruit ranges from 10 – 39.58 g, and the epicarp and mesocarp constitutes about 33 – 75% of the fresh fruit weight (Maranz & Wiesman, 2003).

2.5 Effect of abiotic factors on pollinators

Globally, insect pollinator decline is driven by natural and anthropogenic disturbances ranging from pollinator habitat fragmentation, parasites and diseases to climate change (Goulson et al., 2015; IPBES, 2016). Optimum crop yield is attained in landscapes with large pollinator population (Garibaldi et al., 2016) but anthropogenic activities in agricultural landscapes are reducing pollinator population (Ferreira et al., 2013; Ricketts, 2004). This raises further concerns on the sustainability of indigenous tree plants retained in agroforestry parklands.

Although shea parklands have been formed through long history of tree retention and management, these habitats are being degraded from multiple stressors such as agricultural extensification and intensification, unsustainable fuelwood collection and climate change (Boffa, 2015; Gaisberger et al., 2017). In Burkina Faso, Lamien et al. (2007) attributed the poor yield of shea in highland areas to cotton production which is associated with extensive use of pesticides. Again, the gradual loss of tree cover in these already harsh climates would eventually result in pollinator population declines since habitat degradation is often associated with pollinator declines (Kennedy et al., 2013). The effect of tree cover loss on shea pollinators was evident in the study of Delaney et al. (2020) where insect pollinator diversity and visitation rates were significantly reduced in shea parklands with low indigenous tree diversity.

Aside anthropogenic disturbances, climatic conditions are known to influence pollinator abundance and activity in shea parklands. The weather conditions, especially temperature, rainfall and humidity were found to have an influence on the occurrence of peak foraging period of pollinator species. The foraging population of *A. florea* was significantly influenced by the relative humidity of the early hours of the day (Nguemo et al., 2014). The interaction between climatic variables influences foraging activities, for instance, Iwamma as cited in Abrol et al. (2019) found interaction between temperature and light intensity to influence flight activity of *Tetragonis caangustica*. Also, flight activity of *Megachile lanata* is controlled by the interaction between light intensity and solar radiations. Morning activity of honeybees is also known to be directly correlated with nectar flow but in evening periods activity is correlated with photoperiod.

2.6 Managed bees for pollination services

Introduction of managed pollinators into agricultural landscapes is essential for high insect pollinator dependent crops in monocultural cropping systems, landscapes with reduced pollinator population, crops grown in enclosures (greenhouses) and seasonal crops preceding the annual activity of insect pollinators (Da Silva, 2018; Kambach, Guerra, Beck, Hensen, & Schleuning, 2013; Klein et al., 2007b). For every crop plant, the insect species with the highest pollination efficiency is preferred. This is determined based on the frequency of pollinator visits, the intra-floral foraging behaviour of the pollinator and ability to transport viable pollen grains to a receptive stigma (Sigrist & Sazima, 2015). Native pollinators are often recommended for their high pollination efficiency compared to introduced species (Freitas & Paxton, 1998). More importantly, native pollinators are well adapted to local climatic conditions (de Oliveira, Savoie, & Vincent, 1991).

The honeybee is the most widely used for managed pollination services due to its high pollination efficiency and polylectic foraging behaviour (Toni, Djossa, Yédomonhan, Zannou, & Mensah, 2018). The large body size of honeybee tends to facilitate pollen transport than smaller bees (Willmer & Finlayson, 2014). Notwithstanding the efficiency of honey bees, other social and solitary bees are equally efficient in pollination (Layek, Kundu, Bisui, & Karmakar, 2021; Viana et al., 2014). For instance, the pollination efficiency of a single visit by solitary bee (*L. funebre*) to watermelon flower is higher than that of managed honey bee (Layek et al., 2021). Native stingless bees can therefore be used to compliment pollination services of honeybee.

Despite the general assertion that managed pollinators can be used for improved pollination services, authors still disagree on the exact radius at which bee hives should be placed to exploit floral resources (Abrol et al., 2019). In savannas, the foraging radius is estimated to range from 1 to 4 km (Guinko as cited in Lassen et al., 2016). Variation is due to the fact that foraging distance is highly influenced by weather conditions, the floral resource in need and the surrounding supplies (Visscher & Seeley, 1982).

Experimental studies in shea parklands of Burkina Faso revealed a positive influence of *Apis mellifera* colony presence on the pollination and yield of shea (Lassen et al., 2014). Aside honeybees, presence of stingless bee nests on the trunk of shea tree equally had a positive effect on percentage fertilization and mature fruit set per inflorescence. Host trees of stingless bees produced 0.24 mature fruits per inflorescence whilst trees without stingless bee nest produced 0.4 fruits per fascicle (Lassen et al., 2014). However, the positive effect of stingless beehives on fruit seed set does not extend beyond the host tree. This affirms the fact that honeybees are good flyers and are capable of foraging at relatively longer distances extending the pollination effect beyond the immediate range of the hive compared to other bees (Pahl, Zhu, Tautz, & Zhang, 2011).

CHAPTER THREE

DETERMINANTS OF SHEA (*VITELLARIA PARADOXA* C.F. GAERTN.) FRUIT YIELD: A REVIEW OF RESEARCH APPROACHES AND CURRENT KNOWLEDGE

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3.1 Abstract

Vitellaria paradoxa (shea) has interannual variability in fruit yield patterns, which results in unpredictable export volumes. Research on factors accounting for this inconsistency is needed to manage tree stands for optimum yield, but existing studies on the topic have shown conflicting results. In order to synthesize research approaches used in examining determinants of shea reproductive success, and to identify research gaps, we reviewed the existing literature on the subject available in Scopus and Google Scholar from 2000 to 2021. Out of 119 primary research articles identified in our literature search, 40 articles met our predefined inclusion criteria. Geographically, most studies (75%) were conducted in West Africa, and six times as many studies used quantitative approaches compared with either qualitative or mixed method approaches. Fruiting emerged as the most studied aspect of shea reproductive biology (73% of studies), whereas less is known on floral biology and pollination. All studies that assessed the effect of agro-ecology, seasonality, pollination, and altitude reported significant effect of these factors on fruit yield. However, there were divergent outcomes on land use/management, dendrometry and parkland tree diversity on fruit yield. The majority of the studies examined single factor effects on yield for one flowering/fruiting season, which is a major weakness of the existing research. We recommended several strategies to improve the reliability of future studies on determinants of shea reproductive success, such as designing multi-factorial experiments to cater for extraneous variables, profiling land use history of the shea parkland and conducting experiments for multiple seasons.

3.2 Introduction

Traditional farming systems in SSA are characterised by the retention of indigenous economic trees in farmlands under which annual crops are cultivated (Boffa 2015). Tree populations are sustained in this system by alternating periods of cultivation with bush fallows to enable regeneration of saplings (Boffa, 2015). This traditional agroforestry practice has led to the formation of extensive parklands dominated by shea (*Vitellaria paradoxa*), commonly termed "shea parklands" or "agroforestry parklands" in parts of Northern Ghana and Southern Burkina Faso (Bayala, Bazié, & Sanou, 2013; Chimsah et al., 2013; Fischer et al., 2011).

Vitellaria is a monotypic genus of the family Sapotaceae with two subspecies; *Vitellaria paradoxa* subsp. *paradoxa* and *Vitellaria paradoxa* subsp. *nilotica* (Hall et al. 1996; Okullo et al. 2004). It is a tree of wide economic importance. The fruits are eaten as a dessert or whole meal in the shea belt of Africa (Karambiri et al., 2017; Maranz et al., 2004). The edible fat (shea butter) extracted from shea kernel is not only a major cooking oil for an estimated 80 million people in SSA (Naughton et al., 2015), but traditionally, the butter is used in African rituals such as funerals, marriages, coronations and rainmaking (Gwali et al. 2011; Souberou et al. 2015). Apart from local uses, shea butter is an industrial raw material in confectionery, cosmetic and pharmaceutical industries (Davrieux et al., 2010; Glew & Lovett, 2014; Lovett, 2005). Increasing industrial uses has increased demand and export earnings from shea (Lovett, 2013; Munialo, Nyawade, & Oluoch-Kosura, 2019).

Notwithstanding this demand, shea export volumes are unpredictable due to interannual variability in fruit yield patterns. According to Boffa (2015), inconsistent productivity patterns equally affect stakeholder perception on sustainability of the shea industry. Interannual variability in productivity is attributed to abiotic conditions such as land use, climate, aspect, topography and edaphic conditions of shea parklands (Nafan et al. 2008; Adande et al.

2015; Akpona et al. 2015; Aleza et al. 2018; Bondé et al. 2019). Among biotic factors, dendrometry (dimension of an individual tree including height, diameter, stem diameter and crown area) have been widely reported to influence shea fruit productivity (Lamien et al. 2007; Akpona et al. 2015; Bondé et al. 2019). According to Byakagaba, Eilu, & Mwavu (2012) , Fruit yield variability in shea have also been attributed to masting, but other authors attribute variability in fruit set to pollinator activity (Okullo 2004; Lassen et al. 2016). *Vitellaria paradoxa* dependence on insect pollination is evident in its breeding system (Okullo et al. 2004a; Yidana 2004). The flowering system is protogynous and largely dependent on insects for pollination services (Basga, 2018; Delaney et al., 2020; Kwapong, 2014; Nasare et al., 2019; Nguemo et al., 2014).

Despite the influence of these biotic and abiotic factors on fruit production, literature has focused extensively on socio-economics and other aspects with limited information on determinants of reproductive success (Kwapong, 2014; Nguekeng et al., 2021). Understanding the reproductive biology is essential to the management of natural stands and domestication for optimum fruit yield but existing ecological studies are equally shrouded in methodological inadequacies. For instance, literature identifies several biotic and abiotic factors to influence shea yield (Glèlè Kakaï et al., 2011) but most studies were designed for single factor effects on fruit yield. Moreover, interaction effect between these biotic and abiotic forces is poorly understood (Bondé, Ouédraogo, Traoré, et al., 2019). Reviews on shea so far have also been generic (Boffa 2015; Tom-Dery et al. 2018; Seghieri 2019; Nguekeng et al. 2021) providing limited information on reproductive biology.

In this study, we examined the existing literature on reproductive biology of shea with a special focus on the determinants of shea fruit yield through a literature review. More specifically, for every study reviewed, the following questions were asked: (i) which country was the study conducted, (ii) which methodological approaches were used, (iii) which aspect of reproductive biology was studied (iv) what is the taxonomic composition of shea flower visitors identified, (v) which determinant(s) of fruit set were studied. These questions were aimed at characterizing our current knowledge on reproductive biology of *V. paradoxa*, and how the existing knowledge was derived to identify relevant research gaps for future studies

3.3 Materials and methods

We searched Scopus database and Google scholar for studies that examined aspects of shea reproductive biology. Scopus is one of the largest journals indexing database with peer-reviewed articles published in credible journals. Google scholar was searched for its ability to reveal data from all countries better than other databases that are skewed towards research from specific regions (Lundin, Rundlöf, Smith, Fries, & Bommarco, 2015). Scopus database was searched in August, 2021 using the search string **“**(Pollination* or flower* or fruit* or fruit set* or fruit yield*) AND (*Vitellaria paradoxa* or shea)” covering papers from year 2000 to 2020 written in English. We also searched Google scholar in August 2021 using the following key phrases: “*Vitellaria paradoxa* flowering and fruiting”, “*Vitellaria paradoxa* pollination”, “*Vitellaria paradoxa* pollinators”.

The databases revealed 234 publications that included, book chapters, conference proceedings, original research articles, literature reviews, and duplicates. For an article to be eligible for inclusion in this review, it had to be a primary research article that examined either an aspect of flowering/floral structures, fruiting/fruit yield, or pollination/pollinators of shea or a combination of these aspects. Each eligible article was reviewed following a standard protocol developed for the review, and included the country and sub-region where the study was conducted. We also identified the research approach used in the study as “quantitative”, “qualitative” or “mixed methods”. We noted the aspect of reproductive biology studied either as “floral biology” (flower phenology and/or morphology), “fructification” (fruiting phenology, yield, or fruit/seed traits), or “pollination” (breeding systems, pollination, flower visitors/pollinators of shea). For experimental studies, we noted the number of flowering/fruiting seasons the study was conducted as “one season”, “two seasons”, “three seasons”, “four seasons” or “five seasons”.

For studies that examined floral biology of *V. paradoxa*, we further identified the aspect of floral biology studied either as “flowering phenology” (start of flowering, length of flowering, active flowering phase, and end of flowering); “density of flowering” (number of flowering trees, number of opened flower buds, number of flowering branches/trees); or “flower morphology” (measured parameters of floral parts). Moreover, for pollination studies we identified the aspect of pollination studied either as “mating system”, “pollination success” (degree of pollen limitation/sufficiency), “pollinator diversity” (pollinators/flower visitors of shea, or their foraging behaviour). Pollinators were classified based on Wurz, Grass, & Tscharntke (2021) either as “bees” (honeybees, stingless bees or other bees), “non-bee insects" (wasps, butterflies, beetles, flies and bugs), or "vertebrate pollinators" (mammals and birds).

Furthermore, the determinant(s) of fructification examined in each study were extracted and categorised either as "Land use/management", "altitude", "edaphic conditions", "aspect", "agro-ecology/climate", "seasonality", "dendrometry", "pollination", "insect pest", "parasitic plants", "pruning" or "tree population/diversity". The proxies for fruit yield estimation were also studied and categorised either as "number of fruits/nuts" (a count of the number of fruits/nuts produced per plot/tree/branch/inflorescence), "weight of fruits/nuts" (the weight of the fruits/nuts produced per plot/tree/ branch/inflorescence), "size of fruits/nuts" (length or diameter of fruit/nut), "composition of fruit pulp/kernel fat" (Total Soluble Solids of pulp, fruit sweetness, stearic acid content, kernel fat content, carbohydrates, crude protein, crude fat, or crude fibre), "phenotypic characters" (shape or colour of nut/fruit), "fruiting density" (number of fruit bearing trees/branches), or fruiting phenology (start of fruiting, time of fruit maturity, length of fruiting). Detailed list of articles included in the review can be found in appendix A.

3.4 Results and Discussion

3.4.1 Overview of research distribution and methods

3.4.1.1 Temporal and geographical distribution of studies

The search yielded 234 articles which were reduced to 130 after removal of duplicates. This was further reduced to 119 primary research articles after exclusion of all other publication types (book chapters, conference proceedings, thesis, and literature reviews) except primary research articles. Forty (40) articles finally met our eligibility criteria for classification in this study.

More than one third of all the studies (35%) were published in the last three years. The highest peak in studies was recorded in 2018 (Figure 3.1). Geographically the studies were conducted in twelve countries, but more than half (58 %) were conducted in three countries (Burkina Faso, Ghana, and Uganda). From a sub-regional perspective, 75% of the studies were conducted in West Africa. There was one transboundary study conducted in Ghana and Burkina Faso, and two interregional studies conducted in selected countries of West, Central and East Africa (Figure 3.2).

The predominance of studies in West Africa is likely to be an outcome of the endemism of *Vitellaria paradoxa* subspecies paradoxa in West Africa. The West African subspecies (paradoxa) is superior to the East African subspecies (nilotica) in fruit nutrients and kernel fat composition (Allal et al., 2013; Maranz et al., 2004; Maranz, Wiesman, & Garti, 2003). Locally stearic acid content (measure of fat hardness) influences packaging, kernel fat extracted from paradoxa is moulded in various solid shapes for sale but fat extracted from nilotica is semi liquid packaged in bottles due to extremely low stearic acid contents. Aside local packaging, industrial usage of shea fat in pharmaceutical and confectionery industries require the fat to remain solid at room temperature. Kernel fat of paradoxa subspecies has a relatively higher melting point which is most preferred for chocolates, margarines, ointments and cosmetic products (Maranz et al., 2003).

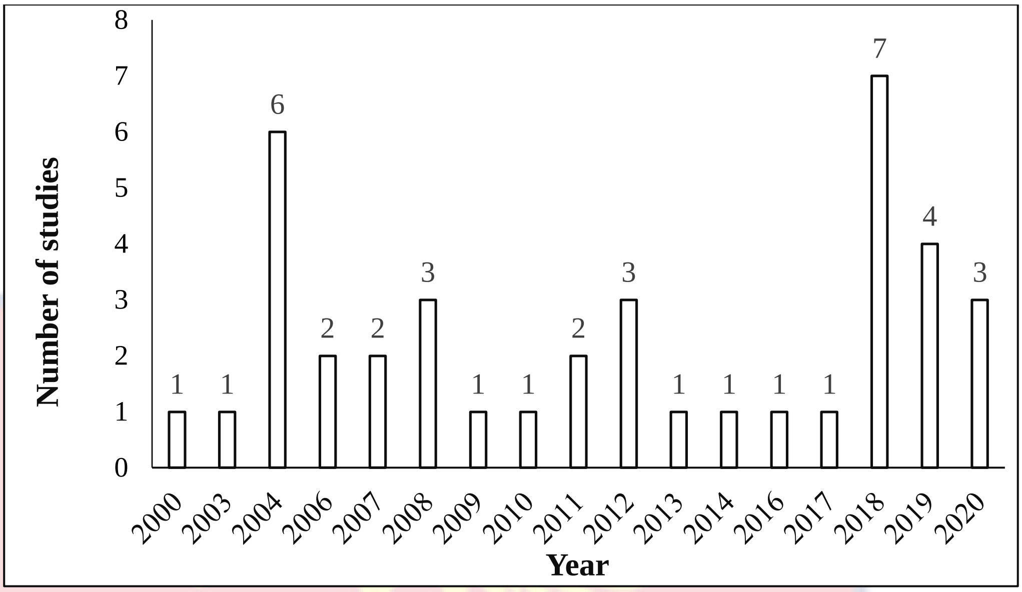

Figure 3. 1: Research on reproductive biology of shea over time

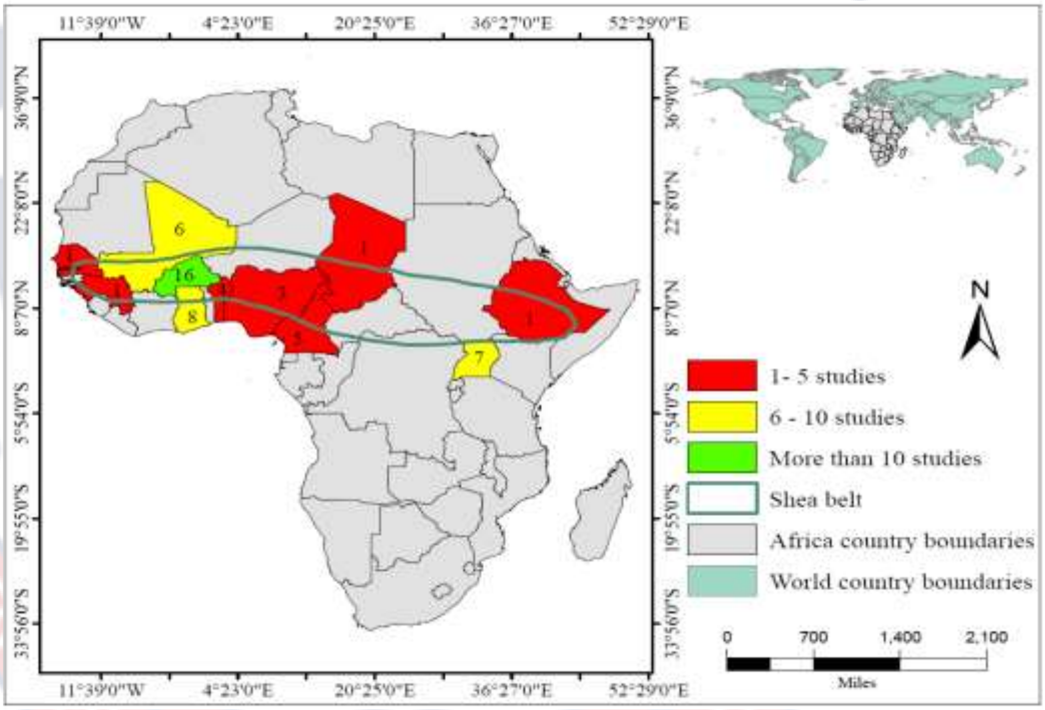

Figure 3. 2: Geographical distribution of studies on reproductive biology of Shea

The dominance of West Africa in studies can also be explained by the fact that West African countries (Burkina Faso, Ghana, Mali, and Benin) are the leading exporters of shea nut/butter (Lovett, 2013; Munialo, Nyawade, & Oluoch-Kosura, 2019) . The research in these countries was largely funded by major importers, which is supported by the fact that most of the research recorded in this study were funded by the European Union. Europe is the lead importer of shea nuts/butter (Lovett, 2013) and perhaps funds research in major exporting countries to boost supply.

Notwithstanding, the skewed geographical distribution of studies towards West Africa is a source of concern, considering the wide geographical coverage of the shea belt. The wide coverage of the shea belt is an opportunity for economic development of SSA but under representation of some regions in research could hamper this potential. However, under representation of some countries in research might also be attributed to the limitation of our search scope. The search was limited to articles documented in English, which excludes articles from Francophone countries. Notwithstanding, Burkina Faso being a Francophone country, the country dominated in the research documented in English. Perhaps because shea is a major export commodity in Burkina Faso (Rousseau, Gautier, & Wardell, 2015).

3.4.2 Methodological Approaches used

The number of studies that used quantitative approach was six times (n=31) the number of studies with qualitative (n = 4) and mixed method approaches (n = 5). Among quantitative studies, experimental research designs were frequently used in assessing the effect of biotic and abiotic factors on reproductive success. The few studies that employed qualitative approaches used interviews, focus group discussions, and questionnaires in reporting indigenous knowledge systems on reproductive biology of shea (Bortei Borketey-La, Kwapong, Botchey, Vanderpuije, & Borketey-La, 2019; Elias, 2015; Gwali et al., 2012; Okullo, Obua, & Okello, 2004).

The limited number of studies examining indigenous knowledge systems is a source of concern, as traditional knowledge is essential to shea conservation and management. This is supported by the long history of shea tree protection via customary laws and beliefs which demonstrates the efficacy of traditional systems. Indigenous knowledge from farmers indicated factors such as rainfall, soil physical properties, fires, mistletoe infestation, and traditional beliefs influence shea fruit yield (Aleza et al., 2018; Elias, 2015; Gwali et al., 2011, 2012). Aside traditional religious beliefs, all other biotic and abiotic factors identified by farmers were equally identified in experimental studies. This reveals that farmers have a rich understanding of various biotic and abiotic factors influencing shea fruit yield that can be incorporated into modern technologies to improve shea productivity.

3.4.3 Number of flowering/fruiting seasons experiment was conducted

More than half of the experimental studies (64%, n = 23) were conducted for one flowering/fruiting season. Two studies were conducted beyond three flowering/fruiting seasons. The longest study duration was for five seasons. The dominance of one flowering/fruiting season studies is problematic as seasonality has been reported to have significant effect on shea yield (Byakagaba et al. 2012; Aleza et al. 2018; Bondé et al. 2018, 2019; Kelly et al. 2019). Therefore, fruit production data of one flowering/fruiting season could be confounded in seasonality, multiple year comparison of fruit data is required to develop accurate production models. Three to five years of fruit production data is recommended for a good estimation of production patterns of fruit trees (Kouyate et al. but see Bondé et al. 2019).

3.4.4 Aspect of *Vitellaria paradoxa* reproductive biology studied

The most studied aspect of reproductive biology was fructification (n = 35), examined in almost two third (73%) of all studies. On the other hand, floral biology (n =5) and pollination (n =7) were least studied, examined in a quarter of studies on reproductive biology. Fructification, being the most studied aspect of shea reproductive biology confirms the assertion that shea fruits/nuts are the most valuable products of the plant (Gwali et al., 2012). Perhaps the fact that fruit/nut is the most prioritised by the shea industry, available research grants were skewed towards studies on fructification. Low awareness on relevance of other aspects of reproductive biology have also contributed to under representation in research. For instance, shea fruit yield is highly dependent on insect pollination (Nasare et al., 2019), but stakeholders of the shea industry have very limited knowledge on pollination (Bortei Borketey-La et al., 2019). Limited knowledge on pollination was reported among cocoa farmers as well (Frimpong-Anin, Kwapong, Gordon, & Pollinator, 2013). In Africa, there are major research gaps on pollination, pointing to limited knowledge on the concept (African Pollinator Initiative, 2004; Gemmill-Herren et al., 2014).

3.5 Floral biology of *Vitellaria paradoxa*

Among the three aspects of floral biology (flowering phenology, flowering density and floral morphology), flowering phenology was the most studied aspect (n =4) whilst flower density and floral morphology had 2 and 1 studies respectively. All studies that examined flowering phenology detected variation in the onset of flowering and length of flowering period between agro-ecological zones as well as sites (Kelly, Gourlet-Fleury, & Bouvet, 2007;

Kelly et al., 2018; Nguemo et al., 2014). *Vitellaria paradoxa* flowering is triggered by change in temperature and moisture stress especially when relative humidity drops to the lowest and just begins to rise (Nguemo et al., 2014; Okullo, et al., 2004). Shea flowering therefore occurs when the combination of climatic factors creates the driest conditions of the year.

Although the influence of climate on flowering has been established, the exact timing of shea flowering differs between countries. For instance, in Uganda, flowering commences in January (Okullo et al., 2004) whilst flowering in Ghana can commence in November or December (Yidana 2004; Stout et al. 2018). Peak flowering occurs in December in the Guinian zone of Cameroon but peak flowering in the Sahel zone occurs in March (Nguemo et al. 2014.). Peak flowering generally corresponds to the month of low humidity but the exact level of humidity required is specific to agro-ecological zone or site. Just as authors disagree on onset of flowering, there are divergent findings on the length of flowering. For instance, Kelly et al. (2018), reported a variation in the length of flowering phase between sites, but Nguemo et al. (2014) indicated the length of flowering period does not vary between sites.

Aside from climate and seasonality, land use practices influence flowering density such that trees in farm and fallow lands record higher percentage flowering than trees in forest stands (Kelly et al., 2007). Another reported driver of flowering phenology is the age of the tree where large sized trees have high flowering intensity and frequency of flowering between years (Okullo, et al., 2004) but the data supporting this, are not consistent as Kelly et al. (2007) did not record any effect of tree size on flowering. In one study Lamien et al. (2004) examined the impact of parasitic plants on flowering but the findings did not reveal any significant effect of mistletoe infestation on flowering.

It is evident that flowering phenology of shea cannot be attributed to one factor but a possible interactive effect of several factors specific to a stand or ecological zone. These ambiguities call for further research to comprehend the flowering phenology of shea. Fire for instance is known to affect shea flowering based on indigenous knowledge (Gwali et al., 2012) but our literature search did not reveal any experimental study on fire effect. Fire injuries can damage cambial, vascular and resource acquisition tissues of the plant (Bär, Michaletz, & Mayr, 2019). Therefore, plant response to fire stress can retard flower and fruit production.

Detailed knowledge on the influence of climate variability on flowering phenology is particularly important in predicting the effect of climate change on flower initiation. An observation of temporal flowering patterns of forest herbs revealed a shift to earlier flowering dates for most plants in response to increasing mean annual air temperature in Western Carpathians (Kubov, Schieber, & Janík, 2022). Again in the Czech Republic, on the onset of winter, oilseed rape (*Brassica napus*) flowering was found to be influenced by temperature (Hájková et al., 2021).

Flowers of *Vitellaria paradoxa* are produced on dense fascicles at the distal ends of leafless branches. On the average, each fascicle consists of 31 hermaphroditic florets (Stout et al. 2018). The flowers are actinomorphic having an estimated diameter of 15mm containing 8 – 10 creamy petals and one style, but some flowers may have two styles (Hall et al. 1996). Mean style length ranges from 3.86 to 13 cm (Nguemo et al., 2014; Okullo, 2004). The flower has a petal length of 8-14 cm which correlates positively with flower diameter (Okullo, 2004). The stamens and staminodes occur in an alternating pattern where the staminodes bend towards the ovary (Nguemo et al., 2014). Shea produces relatively low volumes of nectar at the base of the flower (Stout et al. 2018) but generates a strong honey scent as an olfactory cue for pollinator attraction. The pollen grain measures 54 µm in its polar axis and 36 µm in equatorial axis with a spherical shape in the polar view and a prolate shape in equatorial view (Adekanmbi & Ogundipe, 2009).

Although the floral morphology has been described, there are some variations in floral traits described by various authors. For instance, Okullo (2004) reported a mean style length of 13 cm but Nguemo et al. (2014) recorded 3.86 cm. This perhaps demonstrates differences in floral morphology between subspecies or sites. A detailed understanding of flower morphology would help explain the variability in fruit yield patterns as ecological evidence indicate flowering plants have co-evolved with pollinators. Flower size, arrangement of floral parts as well as visual and olfactory cues influence pollinator attraction (Martins, Gabriela, & Camargo, 2021). Perhaps our limited understanding of floral morphology accounts for the absence of information on pollination efficiency of shea flower visitors aside the study of Lassen et al. (2016).

Moreover, the quantity and quality of floral rewards especially nectar and pollen determine insect visitation in other plants (Brzosko et al., 2021; Lawson & Rands, 2019) but there is limited information on biochemical composition of shea flower nectar as well as the influence of nectar composition on pollinator attraction. These unexamined aspects of floral morphology limit our interpretation of shea pollination studies. Also, there is a high flower abortion (60%) attributed to insect pest damage and other factors (Nguemo et al., 2014) but there is no study on flower pest of shea except Lamien et al. (2008) who identified insect pests of shea flowers.

3.6 Pollination of *Vitellaria paradoxa*

Mating systems of *V. paradoxa* was the most studied aspect of pollination (n = 6) whereas pollination success and pollinator diversity were examined in 4 and 5 studies respectively. All studies on pollination success reported significant positive effect of insect pollination on yield and three out of the four studies reported shea to be pollen deficient. Thus, flowers that received supplemented pollen via hand pollination produced significantly larger number of fruits than those pollinated by natural agents only. In terms of pollinator/flower visitor diversity, the honey bee (*Apis mellifera*) was the most frequently reported flower visitor (n = 6). Seventeen other bee species, predominantly stingless bees, have been reported as flower visitors of shea. Thirteen identified species and nine unidentified non-bee insects have also been reported as flower visitors. Aside insects, vertebrate groups (birds and bats), have been observed foraging on shea flowers (Table 3.1).

Notwithstanding the paucity of information on shea pollination, all studies on mating systems indicate shea is outcrossing and exhibits a protogynous flower development (Okullo 2004; Yidana 2004). All studies that examined pollination success (Nguemo et al. 2014; Lassen et al. 2016; Delaney et al. 2020) revealed shea is pollen limited except Stout et al.(2018). It is most probable the findings of Stout et al. (2018) were influenced by the wide geographic scope which introduced extraneous variables.

Table 3. 1: Vitellaria paradoxa flower visitors/pollinators

Flower visitor group	Order	Linnean /common name	No. of studies	Studies
Bees	Hymenoptera	*Apis mellifera*	6	Delaney et al. 2020; Basga, 2018; Dodiomon & Koffi, 2011; Stout et al. 2018; Lassen et al. 2016; Nguemo et al. 2014
		Xylocopa olivaceae	1	Basga et al. 2018
		Xylocopa spp.	2	Nguemo et al. 2014; Kwapong, 2014
		Ceratina moerenhouti	1	Stout et al. 2018
		Ceratina sp	1	Nguemo et al. 2014
		Hypotrigona spp.	2	Lassen et al. 2016; Kwapong, 2014
		Hypotrigona gribodoi	1	Stout et al. 2018
		Hypotrigona ruspoli	1	Delaney et al. 2020
		Meliponula ferruginea	2	Stout et al. 2018; Kwapong, 2014
		Meliponula beccari	2	Stout et al. 2018; Kwapong, 2014,
		Braunsapis sp.	1	Delaney et al. 2020
		Liotrigona cf. bottegoi	1	Lassen et al. 2016
		Compsomelissa borneri	1	Stout et al. 2018
		Compsomelissa igrinervis	1	Lassen et al. 2016
		Amegilla calens	1	Stout et al. 2018
		Lipotriches natalensis	1	Stout et al. 2018
		Lassioglossum duponti	1	Stout et al. 2018
		Lassioglossum sp	2	Delaney et al. 2020; Basga et al. 2018
Non-bees	Hymenoptera	Unidentified	3	Kwapong, 2014
		Belonogaster juncea	2	Basga et al. 2018; Nguemo et al. 2014
		Philanthus sp	2	Basga et al. 2018; Nguemo et al. 2014
		Unidentified	3	Stout et al. 2018; Lassen et al. 2016
		Palthotyreus tarsatus	2	Basga et al. 2018; Nguemo et al. 2014
		Camponotus sp	1	Nguemo et al. 2014
		Camponotus brutus	1	Nguemo et al. 2014
		Crematogaster sp	1	Nguemo et al. 2014
		Polyrachis sp	1	Nguemo et al. 2014
		Paratrechina longicornis	1	Nguemo et al. 2014
		Pseudoanthidium	1	Stout et al. 2018

		truncatum		
	Orthoptera	Unidentified	1	Nguemo et al. 2014
	Coleoptera	Unidentified	5	Basga et al. 2018; Stout et al. 2018; Lassen et al. 2016; Nguemo et al. 2014; Okullo, 2004
	Diptera	*Musca domestica*	5	Basga et al. 2018; Stout et al., 2018; Lassen et al. 2016; Nguemo et al., 2014
		Calliphora sp.	2	Basga et al. 2014; Nguemo et al. 2014
		Unidentified	1	Nguemo et al., 2014
		Unidentified	1	Nguemo et al. 2014
		Unidentified	1	Nguemo et al. 2014
	Lepidoptera	Unidentified	5	Stout et al. 2018; Lassen et al. 2016; Okullo, 2004; Nguemo et al. 2014
		Junonia oenone	1	Nguemo et al. 2014
	Hemiptera	Unidentified	3	Stout et al. 2018; Okullo, 2004; Nguemo et al. 2014
	Dictyoptera	unidentified	1	Nguemo et al. 2014; Okullo, 2004
Vertebrate		Birds (unidentified)	3	Kwapong, 2014
	Columbiformes	doves	2	Okullo, 2004; Lassen et al. 2018
	Passeriformes	sunbirds	2	Okullo, 2004; Lassen et al. 2018
	Chiroptera	bats	1	Okullo, 2004

Pollination deficit is attributed to habitat degradation emanating from indiscriminate tree felling, pesticide use, and landuse change. Delaney et al. (2020) demonstrated the conservation of other indigenous tree species in shea parkland enhances pollinator diversity and activity. Moreso, the incorporation of honey beekeeping into shea parkland management have been recommended (Lassen et al. 2016; Stout et al. 2018). However, there is little evidence for the positive influence of managed bees on pollination success, except Lassen et al. (2016) who reported a positive effect of bees on fruiting. Moreover, the effect of abiotic factors (climate, landuse, soil tillage) on pollinator activities in shea parklands remains a grey area for research. Aside insects, vertebrates such as bats and sunbirds are frequently reported as shea flower visitors but the pollination efficiency of these vertebrates have also received little research attention.

Furthermore, pollinator conservation remains challenging given the high level of pesticide use. Pesticides are applied to legumes and cereals intercropped with shea, potentially exposing pollinators to a range of toxic hazards. Therefore, understanding of the effect of these pesticides on pollinators is required to optimise pollination and pest control in shea parklands. Lastly, pollination studies have concentrated mainly on diurnal insects, but Nguemo et al. (2014) reported that shea nectaries are opened at night prompting a possibility of flower visit by nocturnal insects. A comprehensive pollinator conservation and enhancement plan would also require information on alternative plants that sustain pollinators when shea is not in flower.

3.7 Fructification of *V. paradoxa*

3.7.1 Determinants of *V. paradoxa* fruit yield

Agro-ecology/climate (n =18) and land use/land management (n=9) were the most studied determinants of fruit yield. All studies that examined Agro-ecology/climate, seasonality, altitude, pollination, and aspect reported significant positive effects on fruit yield (Figure 3.3).

3.7.1.1 *Agro- ecology/climate*

All eighteen studies that assessed the effect of agro-ecology/climate on fruit production reported significant effects. In Nigeria, trees in the Northern Guinea savanna zone were found to exert comparatively higher efforts towards nut size and weight whilst trees in Southern Guinean Savanna invest more on fruit pulp(Ugese, , Baiyeri, & Mbah, 2010). Similarly, in Benin, fruit production increased along a south-north gradient where trees in the Sudanian zone produced higher fruit set than trees in Sudano-Guinean zone (Glèlè Kakaï et al., 2011).

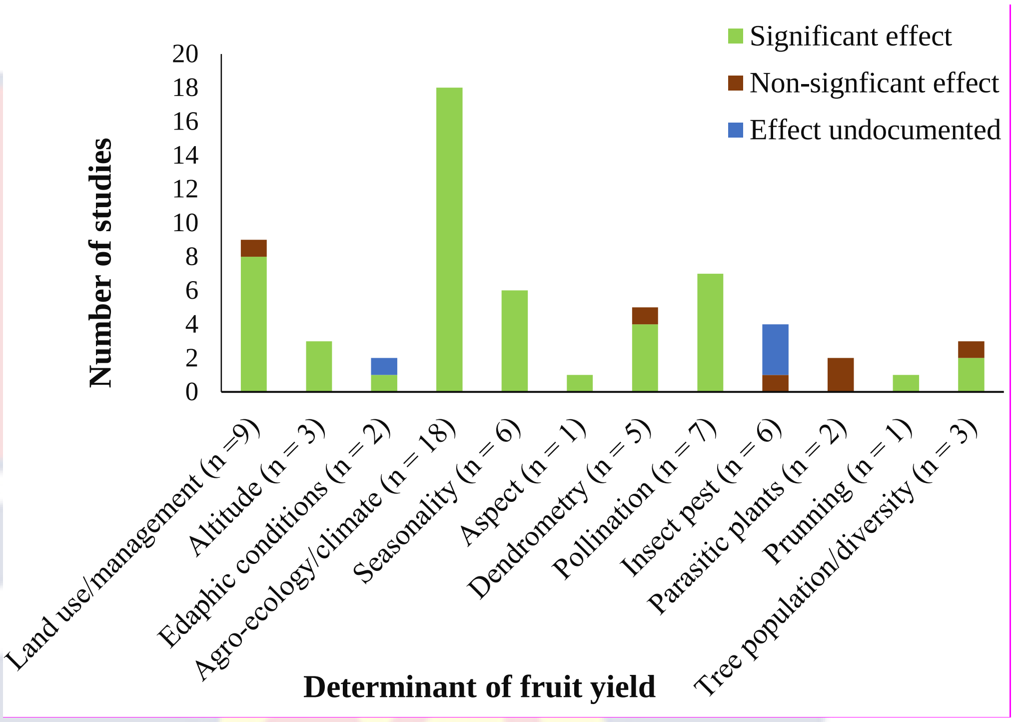

Figure 3. 3: Determinants of *V. paradoxa* fructification and their effects on fruit yield

Variation in kernel fat and fruit pulp composition were also reported along climatic gradients when fruits were sampled across the shea belt (Allal et al., 2013; Maranz & Wiesman, 2003; Maranz et al., 2004). Many authors sceptically attribute variation in fruit yield and seed traits to genetic make-up of the plant but Maranz and Wiesman (2003) posit that the differences cannot entirely be explained by genetics. Despite the high DNA polymorphism in shea (Abdulai, Krutovsky, & Finkeldey, 2017), trees in drier savannas are consistently associated with higher mean kernel fat and seed length, whilst trees in relatively humid savannas have higher mean Total Soluble Solids in pulp with heavier seeds (Maranz & Wiesman, 2003). This is noted as an adaptation mechanism where trees in drier savannas invest in seed fat to enhance seedling germination and establishment. Seed reserves such as fat content, soluble sugar, and proteins are known to correlate positively with percentage germination percentage and germination rates (Zhao, Zhang, Yan, Qiu, & Baskin, 2018).

The variation in fruit yield patterns between ecological zones implies that domestication efforts should be targeted at developing ideotypes specific to agro-ecological zone. Although fruit yield variability between agro-ecological zones have been studied extensively, the effect of long-term climatic variability on fruit productivity and kernel fat have received little research attention. This aspect however needs to be investigated to comprehend the effect of climate change on fruit set and kernel fat composition.

3.7.1.2 *Landuse/land management*

All studies that assessed the effect of land use/ management on fruit set reported significant effects (Byakagaba et al., 2012; Houehanou et al., 2013; Akpona et al., 2015; Aleza et al., 2018; Bondé et al., 2019; Delaney et al., 2020)**,** except Kelly et al. (2019). Aside the absence of competition in cultivated lands, fertilisation and soil tillage enhances soil moisture and nutrient availability for trees in agroforestry parklands. In addition, the limited plant biomass in cultivated lands reduce fire intensity (Hall et al., 1996). Plant ability to mobilise resources for leafing and fruiting is retarded by response to fire stress. This effect is severe in uncultivated lands with high fuel load. High fruit set among trees in cultivated land is also attributed to the careful selection of trees of desirable traits (Lovett & Haq, 2000b). Other authors (Akpona et al.

2015; Delaney et al. 2020) alluded to high frugivory in fallow lands and wild bushes to account for reduced fruit yield in uncultivated lands. However, the impact of frugivory on fruit set is still an area that requires further investigation.

3.7.1.3 *Dendrometry*

All studies on dendrometry (Lamien et al. 2007; Byakagaba et al. 2012; Akpona et al. 2015; Bondé et al. 2018) reported significant relationships between various dendrometric parameters and fruit set, except Aleza et al. (2018). Stem diameter, crown area, tree height, crown shape, crown height and number of branches were frequently used as predictors but Bondé, Ouédraogo, Ouédraogo, Thiombiano, & Boussim (2019) and Byakagaba et al. (2012) posit that Diamter at Breast Height (DBH) is the most precise predictor of shea fruit yield. High precision in DBH as a predictor might not only be an outcome of a perfect relationship between DBH and fruit yield, but accuracy of DBH measurements. DBH is the easiest and most accurately measured parameter in most tree plants (Kuyah & Rosenstock, 2015). Measurements of other dendrometric parameters such as tree height, crown height and crown area are prone to biases emanating from the operator especially when more than one individual is involved in data collection.

On the contrary, Lamien et al. (2007) did not find DBH to be a good predictor of yield but rather identified crown attributes and number of shoots as key predictors of fruit yield. Byagakaba et al. (2012) also found trees that have multiple branches at the first forking of the stem to have lower fruit yield compared to trees with few branches at first forking of the stem. This is attributed to light capture for photosynthesis where denser crowns limit sunlight paneteration to lower crown layers. This phenoemenoen is consistent with Lamien et al. (2007) observation of increasing fruit set from lower to upper crown layers.

The variations in accuracy of dendrometeric predictors of yield might be emanating from methodological differences. For instance, studies that used total number of fruit set per tree for yield estimation had a better chance of obtaining accurate relationships compared to branch sampling for yield estimation. Branch sampling is prone to errors when a smaller sample size is used because Okullo (2004) reported a variation in fruit set beween branches which limite the accuracy of extrapolations made from sampling. Studies that resorted to fruit traits (weight, size or shape) as response variables are also prone to errors since fruit traits can be influenced by genetic makeup of plant. We recommend total number/weight of fruit/nut per tree for future research on dendrometric parameters and fruit yield.

3.7.1.4 *Seasonality*

Interannual variation in fruit set patterns is reported in all studies that compared fruit yield between years (Byakagaba et al. 2012; Aleza et al. 2018; Bondé et al. 2018, 2019; Kelly et al. 2019). Fruit yield varies significantly between years such that high fruiting years often alternate with low fruiting years (Lamien et al., 2007). Climatic factors particularly rainfall pattern is known to account for this where years of high rainfall precede years of good fruit production (Okullo 2004; Kelly et al. 2019). However, the evidence supporting the influence of rainfall is not consistent (Bonde et al. 2019).

Another factor that has been attributed to seasonal variation in fruit set patterns is carbohydrate reserve allocation and utilisation. Flowering and fruiting in deciduous plants are known to rely on reserve metabolites, therefore carbohydrate reserves decrease significantly in years of high fruit production. This creates a deficit which results in low fruit production in the following year (Monselise & Goldschmidt, 1982). Notwithstanding the overwhelming consensus on this hypothesis (Lamien et al. 2007; Bondé et al. 2019; Kelly et al. 2019), Boffa (2015) posits the sequence of alternation between good, and bad fruit production can be disrupted by climatic and pathological events. This is confirmed by the assertion of Dodiomon and Koffi (2011) that a year of good fruit production occurs in every five years, indicating an irregularity in the pattern of fruit yield alternation.

The uncertainty on reasons accounting for the variability can be attributed to the absence of long-term studies on the effect of seasonality. The longest study duration was five years (Bondé, Ouédraogo, Traoré, et al., 2019). Another research gap is inadequate information on the relationship between plant metabolite reserves and fruit production. This is still an untested hypothesis deduced from the fruit production patterns of other woody plants.

3.7.1.5 *Insect pests*

Three studies examined damage caused by fruit borers whilst one study assessed the effect of defoliators on fruit yield. *Salebria sp*. (Lepidoptera: Pyralidae), *Nephopterix* sp and two other unidentified species have been reported as shea fruit borers (Dwomoh 2004; Lamien et al., 2008). Seven fruit fly species have also been identified as fruit pest of shea but *Ceratitis silvestrii* and *Bactrocera dorsalis* are the flies of economic importance (Zida, Nacro, Dabiré, Ouédraogo, & Somda, 2020). The genus *Ceratitis* is endemic to Africa but *Bactrocera* is exotic and poses a threat as Badii et al. (2015) identified shea to have higher infestation index among indigenous tree hosts of *B. dorsalis* in Northern Ghana.

Insect pest infestation results in substantial shea fruit losses. Physiological disorders caused by *Nephopterix* sp accounts for 16% of fruit losses (Dwomoh, 2004) and *Salebria* sp infestation damages 4 – 15% of shea fruits (Lamien et al. 2007). The average fruit damage caused by fruit flies ranges from 2.08 to 16.23% in the early part of the fruiting season and 39 to 66.61% in the mid fruiting season (Zida et al., 2020). An observation of phenological phases also revealed that flowering and fruiting are the most susceptible to insect attacks (Zida et al., 2020). Notwithstanding the economic importance of fruit borers, defoliation by edible caterpillar, *Cirina butyrospermi* have no effect on shea fruit yield (Payne et al., 2020). Defoliation perhaps results in an enhanced annual crop yield in shea agroforestry parklands.

In terms of pest ecology, Lamien et al. (2008) observed infestation rates to be higher among tree stands close to natural areas due to large host plant range. This implies interplanting shea in mixed stand plantation might increase pest prevalence. Crown height was found to influence fruit infestation by *Salebria* sp, and *Nephropterix* sp. (Dwomoh 2004; Lamien et al. 2008). *Salebria* sp infestation rates are highest in the upper crown layers whilst *Nephropterix* sp infestation rates are highest in the lower crown layers. Fruit borers therefore exhibit species specific niche preferences within the host which should be considered in developing management and control strategies for insect pest of shea.

3.7.1.6 *Other determinants of fruit yield*

Other abiotic factors identified in the literature include edaphic conditions, altitude and aspect. Soil properties influence fruit production where trees growing in lixisols have higher fruit set than trees growing in other soils (Aleza et al., 2018). Indigenous knowledge also revealed that trees growing in gravel soils tend to fruit more than trees in other soils (Okullo et al., 2004b). Notwithstanding, Sanou et al. (2006) did not record any effect of soil drainage on fruit traits. The effect of soil parent material on fruit yield needs to be investigated further to understand how various soil orders influence productivity.

All studies that examined the influence of altitude recorded significant effects on fruit yield as well (Lamien et al.2007; Lovett & Haq, 2000; Nafan et al. 2008). Trees growing in higher elevations record higher fruit sets than trees in lowland areas. Furthermore, the aspect in which the tree grows with respect to the crown orientation influences fruit set (Lamien et al., 2007). North-East portions of shea tree crown tend to have lower fruiting density compared to South-West and South-East portions. The Sudan and Sahelian zones where shea occurs are characterised by winds blowing from North-East to South-East directions from November to March (FAO, 1988). These strong sand carrying winds coincide with the flowering and fruiting season which obstruct pollinators and exacerbate the abscission of buds, flowers and fruits.

Other biotic determinants identified in literature include parkland tree population/diversity and mistletoe infestation. Two studies reported positive effect of shea parkland tree diversity/population on fruit productivity(Bondé et al., 2019; Delaney et al., 2020). This is attributed to microclimate amelioration, where the vegetation serves as wind break reducing flower and fruit abortion. Diverse shea parklands are also associated with high pollinator diversity which enhances fruit yield. On the contrary Sanou et al. (2006) did not find any influence of shea parkland tree density on fruit traits.

According to Asare, Avicor, Dogbatse, & Anyon (2019) over 50% of shea trees are infested with mistletoes but experimental studies did not record any significant effect of mistletoe infestation on shea fruit yield (Lamien et al. 2004; Houehanou et al. 2013). Notwithstanding, physiological impact of infestation on the host plant may have indirect effects on productivity. The accumulated impact of these hemiparasites on plant growth and physiology needs to be investigated. One study examined the effect of pruning on fruit characteristics but findings were not consistent. Nevertheless, pruning can be used for rejuvenating old trees since the study revealed total crown pruning enhances recovery of leaf biomass and fruit production (Bayala et al., 2008).

3.8 Number of fruit yield determinants examined in a study

More than half of the studies (55%) examined one determinant effect on fruit yield, followed by three determinants effect (22%). Experiments that examined four determinants constituted 6% of studies (Figure 3.4). Most studies have been designed for one determinant effect on fruit yield (n=22), which presents a limitation to research on shea reproductive biology. Several biotic and abiotic factors influence shea yield because the shea parkland is a complex landscape shaped by land use/land management history (Bayala et al., 2015). In Burkina Faso for instance, stand characteristics varied between farmlands based on management practices employed by land users (Elias, 2013).

Moreso, farmers recruit trees on farmland based on fruit/seed traits, and the traits of preference differ between farmers (Elias, 2015). This anthropic selection together with land use history creates a complex set of conditions unique to a stand, which makes it difficult to isolate the effect of a single biotic or abiotic factor on productivity. Ouvrard and Jacquemart (2019) equally emphasised this point when methods used to investigate oil seed rape dependence on pollination were reviewed.

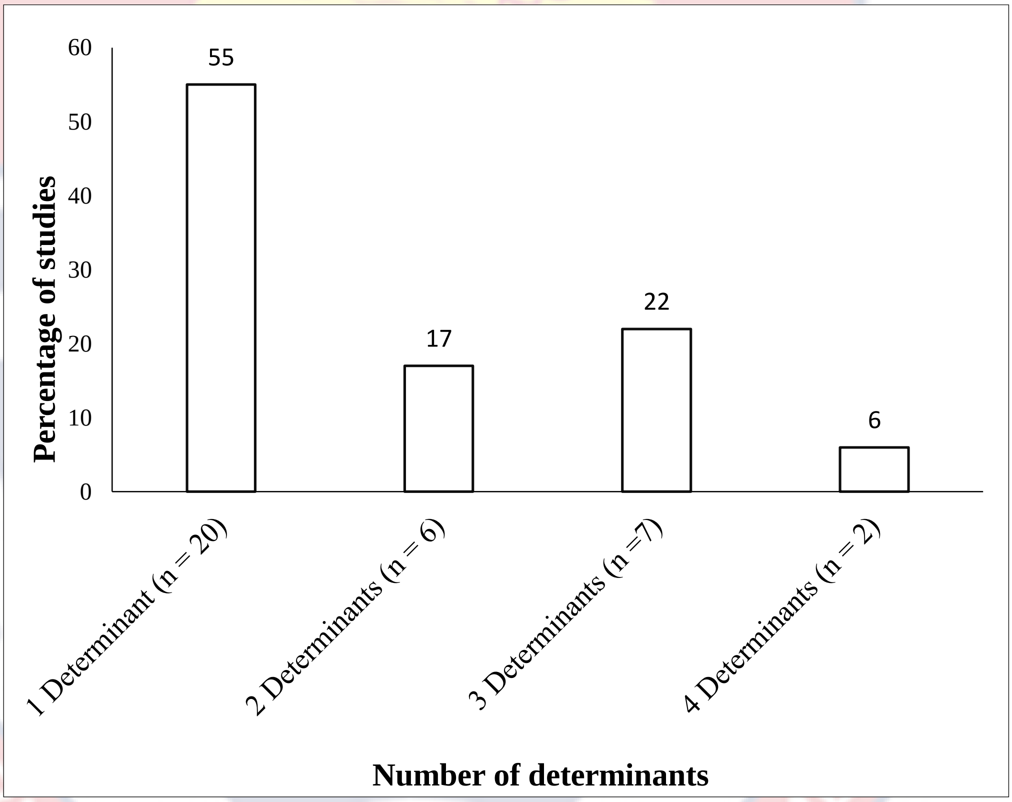

Figure 3.4: Number of fruit yield determinants studied

3.9 *Vitellaria paradoxa* fruit yield estimation

About one third of the studies (35%) used number of fruits/nuts as a proxy for fruit yield estimation. Fruiting density (4%) and phenotypic characters of fruits/nuts (4%) were the least used proxies for yield estimation (Figure 3.5). Number of fruits/nuts and weight of fruits/nuts being the most used proxies is probably because these proxies are equally used in economic valuation of fruits/nuts and easily understood by stakeholders of the industry.

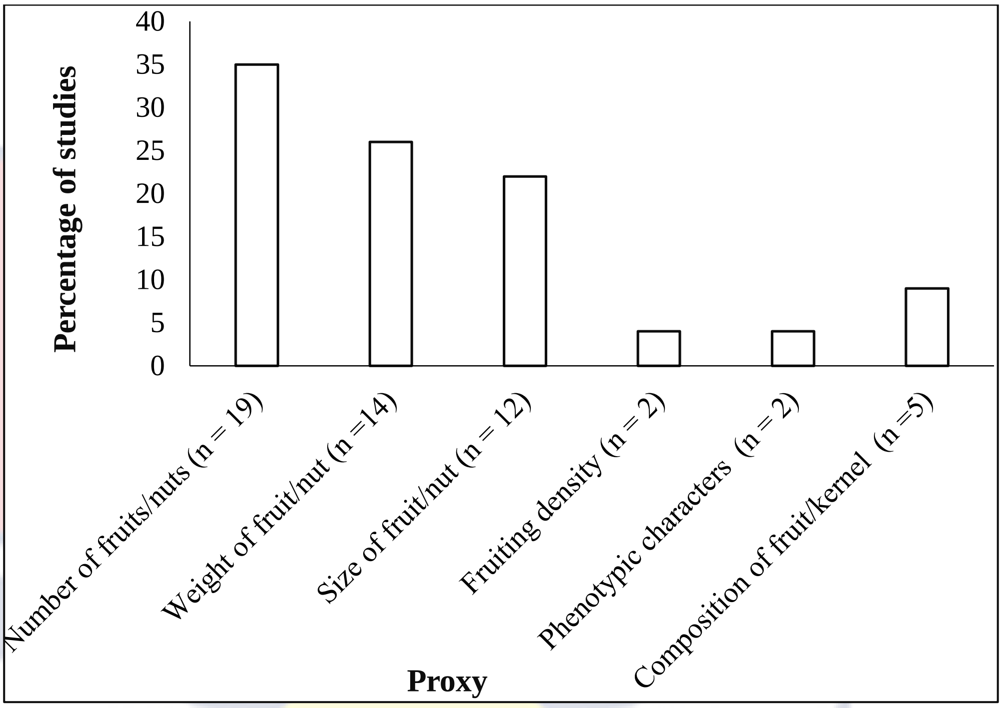

Figure 3. 5: Proxies used for shea fruit yield estimation

More so these proxies are easy to measure and less expensive compared to proxies such as kernel fat composition that requires complex and expensive laboratory analysis. However, composition of fruit/kernel should be considered in shea research as it is the only proxy providing information on fruit/kernel fat quality. This proxy could aid in grading shea butter to maximise trade benefits to both suppliers and consumers. The high diversity of proxies used in fruit yield estimation does not permit fair comparison of findings between studies. This poses a limitation in building data for future studies.

3.10 Conclusion

There is an increasing research effort on reproductive biology of shea, but the research is skewed towards West Africa, particularly Burkina Faso and

Ghana. Floral biology and pollination were understudied compared to fructification. The literature revealed several biotic and abiotic factors influencing yield, but authors presented divergent views on the effect of these factors on fruit yield. All studies that examined effect of Agro-ecology/climate, seasonality, altitude and pollination reported significant effects on shea yield but there were varied reports on the effect of dendrometry, land use, insect pests, and parkland tree diversity. Number and weight of fruits/nuts have been the most used proxies for shea fruit yield estimation. However, there are knowledge gaps in the existing literature. The dominance of one factor studies introduces confounders as it is difficult to isolate the effect of a single factor in shea parklands. The interaction effects of these factors are less understood. We recommend future studies to consider multi-factorial designs to account for several factors and identify interaction effects. Finally, the paucity of information on floral biology and pollination ecology of shea limits our understanding of the reproductive success since these precede fructification. We recommend increased research efforts in these aspects to enhance a comprehensive understanding of the reproductive biology of shea.

CHAPTER FOUR

VARIATION OF SHEA (VITELLARIA PARADOXA SUBSP. PARADOXA) FLORAL PHENOLOGY AND MORPHOLOGY IN GHANA

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Supervised and assisted in review and editing of manuscript.

Stout J.C. **(Co-Supervisor)**

Supervised and assisted in design, review and editing of manuscript.

4.1 Abstract

Vitellaria paradoxa is a multipurpose tree endemic to the Sudano-Sahalian zone of Africa. The fat extracted from shea seed is of cultural, nutritional and industrial significance, but seed production is largely dependent on insect pollinators. Pollination success and seed production can be influenced by the timing of flowering and floral display. This study investigated the spatial variation in floral phenology and its association with environmental cues, and tested geographic differentiation of floral traits in six

sites across three regions of Ghana. There was a variation in the timing of flowering between regions in the same agro-ecological zone. Flowering started in the Upper West over a month earlier than Upper East and North East Regions. The onset of flowering was significantly associated with soil moisture and soil temperature. All morphometric traits of floral parts (pedicel diameter, pedicel length, petal length, filament length and style length) differed significantly between regions. The study recommended that, large geographic variation in floral phenology and morphology should be considered in germplasm collection for tree improvement and domestication.

4.2 Introduction

Environmental conditions and biotic interactions act as evolutionary drivers of floral phenological and morphological traits. Thus, plants have evolved to avoid flowering during adverse environmental conditions, and to match their flowering time with favourable conditions for fruiting and seedling establishment (Fogelström, 2019; Miller-Rushing, Abraham, Høye, Inouye, & Post, 2010). Similarly, plant reproductive success can be enhanced when flowering, fruiting and seed production is asynchronous with antagonists (competitors, herbivores and seed-predators) (Fogelström, 2019), but synchronised with mutualists (pollinators and seed dispersers) (Miller-Rushing et al., 2010). The timing of flowering is genetically controlled (Craine, Wolkovich, & Towne, 2012), but can be influenced by climatic factors (including photoperiod, air temperature, soil moisture, precipitation and relative humidity) (Chauhan, Ryan, Chandra, & Sadras, 2019; Jarrod, Vivekananda, Shahbaz, Alessandro, & Mario, 2021; Kubov et al., 2022). Thus, short term climatic variability can influence the timing of flowering

(Anderson et al. 2005; Barrett and Brown 2021). This can result in a shift in flowering phenology, potentially resulting in a mismatch between flowering period and pollinator activity(Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Forrest & Miller-rushing, 2010).

Phenological mismatches are being exacerbated by climate change, with studies showing earlier flowering in a range of species in response to increasing mean annual air temperature (Kubov et al., 2022). However, evidence for complete temporal mismatches between plants and their pollinators is scarce, as often the factors influencing the timing of flowering also influence pollinator activity and behaviour (Renner and Zohner 2018).

In addition to flowering timing, flower morphology and flower rewards also affect pollinator activity and behaviour, and thus pollination efficiency (Martins et al., 2021; Rossi, Fisogni, Nepi, Quaranta, & Galloni, 2014). Floral traits (including colour, size, shape and scent of flowers, as well as the quantity and quality of nectar and pollen rewards) influence the foraging behaviour of flower visitors (Proctor et al. 1996; Parachnowitsch and Caruso 2008; Linglind et al. 2017), including the time they spend searching for and handling floral rewards, which can in turn influence pollination success (Fisogni et al. 2011; Rossi et al., 2014).

Aside floral rewards, the density of flowers produced at the community or individual level influences pollinator attraction (Lázaro, Jakobsson, & Totland, 2013). Rathcke and Lacey (1985) theorized that a functional relationship exists between flower density and insect visitation where floral density increases with increasing insect visits until a maximum is attained then declines at saturation of pollinators. Primarily, a larger number of flowers increases visual conspicuousness of the flower, which increases the insect attraction. Flower number was found to be significantly associated with pollinator visitation rates where plants with more flowers attracted more pollinators (Eckhart, 1991).

Although there have been many studies on floral phenology and morphology, these have focused extensively on temperate herbaceous plants, whilst less is known about woody tropical plants. Phenological studies are particularly important for plants in arid and semi-arid regions of Sub-Saharan Africa as savanna biomes are known to be sensitive to climatic changes (Bond et al., 2003; Sala et al., 2000).

Shea is endemic to arid and semi-arid regions of Sub-Saharan Africa (Hall et al. 1996). The species is generally undomesticated but retained and managed on farmlands for multiple reasons, including its contribution to carbon sequestration and soil rejuvenation (Chimsah et al., 2013), medicinal use of its leaves and stem bark (Gwali et al., 2012), the local and international use of the fat extracted from shea kernel (Glew and Lovett, 2014; Lovett, 2005), and because the edible fruits are rich in vitamins and sugar (Nguekeng et al., 2021). Owing to the high economic value of the fruit, shea research has been overly focused on fruiting, with limited knowledge on floral phenology and morphology (Nasare et al., 2022).

Existing data indicate that floral phenology is influenced by land use and parkland management practices (Kelly et al., 2007, 2018; Okullo, Hall, et al., 2004). There is also a variation in the timing of shea flowering across agro-ecological zones of the shea belt (Kelly et al., 2018; Nguemo et al., 2014). Despite this variability, less is known on the specific climatic factors influencing flowering, except Okullo (2004) and Nguemo et al. (2014) who examined the effects of a few climatic factors (relative humidity, temperature and precipitation) on flowering in Uganda and Cameroon.

Identifying the proximate environmental cues to floral phenology is a fundamental step to predicting the effect of climate change on shea productivity. Moreso, existing literature revealed a variability in shea floral density (Okullo, 2004; Stout et al., 2018) but differences in study years do not permit fair comparison of floral density between ecological zones nor sites. The floral morphology of the shea subspecies (nilotica) endemic to East Africa has been documented (Okullo 2004) whilst little is still known on the morphometric traits of West African subspecies (paradoxa).

Understanding the floral phenology and morphology of shea is also essential to domestication and stand management for optimum fruit yield as it influences plant pollinator interactions and fruit set (Okullo et al. 2004a). Moreso, domestication and tree improvement would require a detailed understanding of the variability in morphological traits in developing ideotypes for specific regions. This study hypothesised a geographic variability in floral phenology and morphology of shea. The study specifically aimed to: i) examine the geographic differentiation in onset of shea flowering ii) identify the climatic factors related to shea flowering, and iii) examine the geographic differentiation in floral density and morphometric traits.

4.3 Materials and Methods

4.3.1 Study Area

The study was conducted in the Guinea savanna zone of Ghana for a 12-month period from August 2020 to July 2021. The Guinea Savanna is located between the Forest Savanna Transition and Sudan Savanna zones. It covers the entire Northern, North East, Savanna, Upper West and Upper East Regions as well as the northern parts of Oti and Bono East Regions of Ghana (Incoom et al., 2020).

The area records a monomodal rainfall pattern which varies significantly between years (Incoom et al., 2020). The wet season commences in April and ends in October with a mean annual rainfall of 1,034 mm (Savanna Agriculture Research Institute, 2015) Maximum mean monthly temperatures are recorded in March/April whilst the minimum temperatures are recorded in December. Mean monthly temperatures range between 27 and 36 °C (Darko, Adjei, Obuobie, Asmah, & Trolle, 2019; Ghansah et al., 2018).

The vegetation density is shaped by the land use and management of the area. It is dominated by cultivated landscapes but periods of cultivation alternates with bush fallows creating mosaics of semi-natural vegetation patches in some areas. However, the natural vegetation of the area is composed of grasses dotted with indigenous woody species (Darko et al., 2019). The most frequently occurring woody plants of the zone include shea (*Vitellaria paradoxa),* baobab (*Adansonia digitata),* dawadawa (*Parkia biglobosa),* African mahogany (*Afzelia Africana),* ebony *(Diospyros mespiliformis),* Linnea *(Lannea acida*), acacia (*Faidherbia albida*) among others (Yeboah et al., 2022). These economic trees are equally retained and managed in farmlands for multiple uses. Herbaceous plants and grasses such as *Tridax procumbens, Andropogon pseudapricus, Panicum maximu,* *Pennisetum purpureu, Boerhavi diffusa* are the most common in the area (Ziblim, Abudul-Rasheed, & Aikins, 2015).

4.3.2 Experimental Design

The study was conducted in six shea parkland sites across three regions (Figure 1). In each region, two sites were selected at minimum distance of 4 km and a maximum of 25 km apart, to minimize variability in climatic conditions within region. Experimental sites were located in young fallows (lands that were uncultivated for 2-5 years) based on land use history obtained from farmers.

4.3.3 Tree selection

A random point was located in each site and all trees of a predetermined size class (DBH; 25-30 cm, Height ≥ 10 m and crown area ≥ 20 m^2) within a 500 m radius of the focal point were identified and coded to constitute a population. This size class was used because it is reported to be the most abundant in the Guinea savanna zone (Tom-Dery et al., 2015), and was selected to standardise samples and to limit the effect of tree age and size on flowering. Twenty focal trees were randomly selected per site from the population of each site using a random number generator and numbered chronologically per site with tags. Five secondary branches (branches extending from the second forking of the stem) were randomly tagged across the crown of each focal tree for the observation of phenological events.

4.3.4 Phenological parameters recorded

Flowering phenology was observed weekly from October 2020 to May 2021 on the following phenological parameters;

i) The onset of flowering: the date on which the first open flower(s) were observed on a focal tree.

ii) Weekly number of trees in flower: the number of trees that have commenced flowering from the 20 focal trees within a site

iii) Days to 50% flowering: the difference between the date on which half of the focal trees commenced flowering and the date of flowering onset in a site.

iv) Floral density: this was measured on three parameters;

  a) Flowering ability of a tree; measured on a binary scale either as 0 (if the individual tree did not produce any flower) or 1 (if the individual tree produced flowers) as used in Kelly et al. (2007).

  b) Flowering ability of a branch: this was also measured on a binary scale either as 0 (if the individual branch did not flowered) or 1 (if the individual branch flowered).

  c) Number of flowers/buds per inflorescence: the number of flowers/buds initiated per inflorescence was counted in three randomly selected inflorescences per tree during peak flowering (having 50% of branches flowering).

4.3.5 Morphometric traits of floral parts

Three inflorescences were randomly sampled from independent branches of each focal tree in peak flowering and transported in an ice-chest to the Laboratory for the measurement of floral traits. Three flowers were then plucked from each inflorescence across three lateral positions of the inflorescence based on Guitián et al. (1997). For each flower, the morphometric traits of floral parts (pedicel length, pedicel diameter, petal-limb length, filament length, and style length) were measured with callipers (Figure 4.1. a). For filament length, three independent filaments were measured per flower and averaged. Pedicel diameter was measured on the lower and upper ends of the pedicel and averaged (Figure 4.1. b and c).

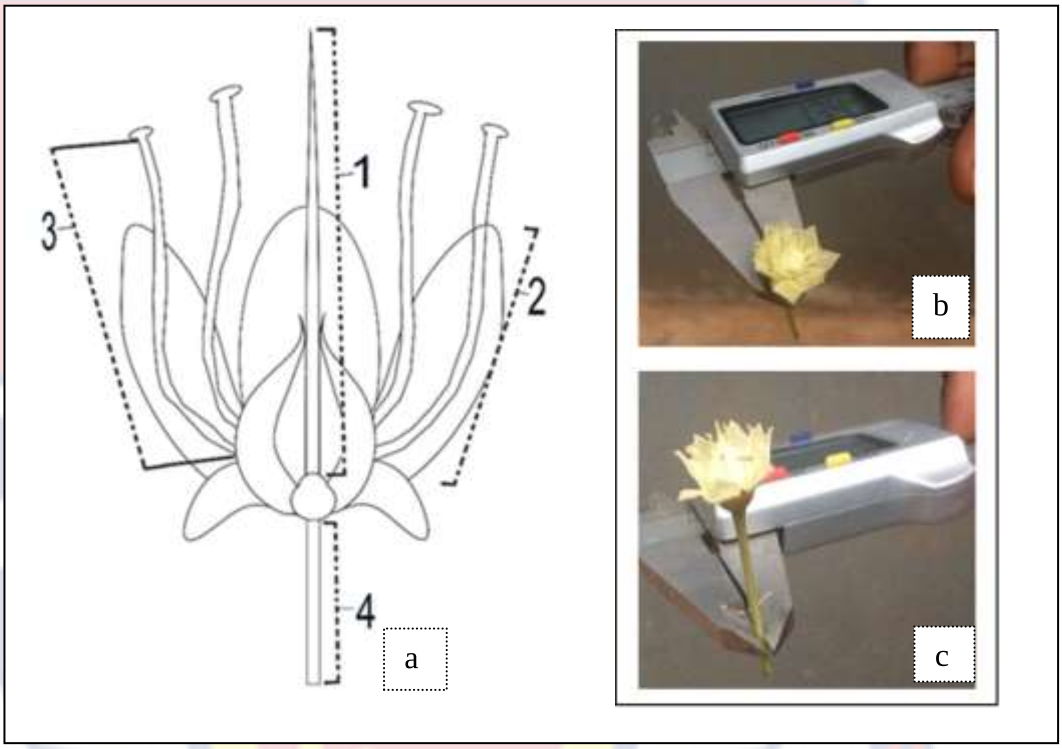

Figure 4.1: Morphometric traits of shea floral parts. The numerals/alphabets correspond to measured floral parts: (a.1) style length, (a. 2) Petal length, (a. 3) Filament length, (a. 4) Pedicel length, (b) pedicel diameter at the upper end, b. pedicel diameter at the lower end.

4.3.6 Climatic factors

Daily weather data of each region were collected from the nearest weather station to experimental site from Trans-African Hydrometeorological Observatory (TAHMO). Weather stations were located within a 30 km radius of experimental sites. The climatic variables examined were, average air temperature, maximum air temperature, minimum air temperature, soil moisture, soil temperature, relative humidity and wind speed. The weekly and monthly means were calculated for each climatic variable.

4.3.7 Data analysis

Generalised Linear Mixed-effect Models were used to model the weekly number of trees initiating flowers as a function of climatic parameters. GLMMs were used based on the multilevel structure of the data (climate being nested in the region) having repeated measures of a dependent variable (weekly number of trees in flower) in discrete scale. The model was built by inserting each climatic predictor variable (atmospheric temperature, minimum soil moisture, relative humidity, wind speed, maximum atmospheric temperature, minimum atmospheric temperature*)* as a fixed effect and region as a random factor using a Poisson distribution. Multicollinearity of the regression was checked with Variance Inflation Factor estimates. Climatic factors with VIF greater than 5 were tested for collinearity. Predictors that were correlated at Pearson r ≥ 0.7 (level of collinearity that can bias regression) were not combined in the same model based on Dormann et al. (2013) and Kath et al. (Jarrod et al., 2021). Model performance was assessed with the Akaike's Information Criteria (AIC). All models were fit using the lme4 and glmmTMB packages in R (Bates et al., 2015; Brooks et al., 2017).

A Kruskal Wallis test was used to compare the mean flowering ability of trees as well as branches between regions. Post hoc tests were conducted to separate significant means using Bonferroni corrections. Morphometric traits (pedicel length, pedicel diameter, petal-limb length, filament length and style length) were analysed by comparing the means between regions with a one-way ANOVA (α=0.005). Tukey test was used for post hoc multiple comparison of significant means. All analyses were done using the R Core Team (2021).

4.4.0 Results and Discussion

4.4.1 Geographic differentiation in floral phenology of *V. paradoxa*

4.4.1.1 Onset and rate of flowering

The onset of shea flowering varied between regions, where first flowering in Upper West (UW) region was recorded in late November, whilst first flowering in Upper East (UE) and North East (NE) regions were recorded in January and February respectively. However, the shea parklands in UW took the longest duration (21 days) to attain 50% flowering compared to UE and NE, which took 14 days (Table 4.1).

Variation in date of flowering onset between regions mirror previous phenological studies in which shea flowering varied between study sites (Kelly et al., 2007, 2018; Okullo et al., 2004a). However, differences recorded in previous studies were marked by agro-ecological zones, this study observed a variability in onset of flowering within the same agro-ecological zone.

Table 4. 1: Onset of flowering and number of days taken to 50% flowering

		First flower set		≥ 50% of trees flowering		
Region	**Site**	**Month**	**Week**	**Month**	**Week**	**Days to 50% flowering**
UW	Pase	Nov. 2020	3	December	2	21
	Bienya	Nov. 2020	3	December	2	21
UE	Kalaasa	Feb. 2021	1	February	3	14
	Nakong	Feb. 2021	3	March	1	14
NE	Yizibisi	Jan. 2021	4	February	2	14
	Dobozisi	Feb. 2021	1	February	3	14

This seems to suggest flowering is not an outcome of wider agro-ecological zone climatic effect but is influenced by local microclimatic conditions. The commencement of flowering in the month of November in

UW is similar to the onset of flowering in the Guinean zone of Cameroun whereas UE flowering onset in February can be likened to the Sudanian zone of Cameroun (Nguemo et al., 2014).

Shea flowering is known to occur along a South-North gradient, where flowering commences in relatively humid agro-ecological zones prior to less humid zones of most countries (Kelly et al., 2007, 2018; Nguemo et al., 2014). Although the current study was limited to one agro-ecological zone, the early flowering recorded in UW followed by NE and UE depicts this South-North gradient of flowering considering the geographical locations of study sites (Figure 1). The South- North gradient effect is not limited to flowering phenology, leaf morphology (Sanou, 2008), fruit productivity (Glèlè Kakaï et al., 2011) as well as fruit pulp and kernel fat composition of shea are all known to vary along this gradient in the shea belt (Allal et al. 2013; Maranz and Wiesman 2003; Maranz et al. 2004). This gradient effect on phenological events has equally been observed in *Adansonia digitata* (Oni, Attah, Awosan, & Sobola, 2016) and *Parkia biglobosa* (Oni, 2001) in SSA.

Although our findings portray the South-North gradient of flowering, there might also be a West-East gradient of flowering in the Guinea Savanna zone of Ghana. This is supported by the fact that UE and NE Regions are geographical closer to the Sudan Savanna zone (driest agro-ecological zone) of Ghana, therefore flowering commenced in the relatively humid parts (UW) of the ecological zone prior to less humid areas (UE). Lovett and Haq (2000a) also reported an increasing trend of shea seed characteristics along a Northeast gradient in Ghana.

The commencement of flowering in the early dry season (November) of the Guinea savanna, is inconsistent with Okullo (2004) who indicated shea flowering in Uganda occurs in the late dry season as an adaptation to avoid fire disruption of flowering and fruit formation. Flowering in UW commenced in the peak fire season, it is therefore possible that *paradoxa* sub-species is well adapted to fires compared to *nilotica* sub species. The dry season flowering of *V. paradoxa* confirms Oni et al. (2014), assertion that most tropical plants flower in the dry season prior to the onset of rains.

Notwithstanding, dry season flowering of shea is most likely to be an adaptation for optimum pollination services. Shea flower development and arrangement of floral structures depict a high dependence on insects for pollen transfer (Nasare et al. 2019; Okullo, 2004; Yidana, 2004). However, rainfall is known to have both direct and indirect impacts on plant-pollinator interactions (Lawson and Rands 2019). For instance, flowers produced in the rainy season risk nectar dilution, and loss of volatiles needed in pollinator attraction (Cnaani, Thomson, & Papaj, 2006). Loss of pollen viability, and reduced pollen adhesion to stigmatic surfaces are associated with wet season flowering (Fan et al. 2012).

As a mitigation strategy, plants flowering in the rainy season position their flowers to be downward-facing to reduce nectar dilution and pollen degradation (Whitney et al. 2011). Considering the upward-facing position of the shea flower, flowering in the rainy season would be a great disadvantage to pollination. Thus, flowering in the early dry season in Northern Ghana avoids an overlap of flowering with the rainy season, but to synchronise flowering with pollinator activity. Unlike shea, cocoa flowers in the rainy season as an adaptation to synchronise flowering with pollinator activity since the primary pollinators (biting midges and gall midges) are most abundant in the wet season (Adjaloo, Oduro, & Banful, 2012). The timing of flowering is a co-evolutionary process for enhanced reproductive success (Van Schaik, Terborgh, & Wright, 1993).

4.4.2 Climatic factors influencing flowering

Soil moisture (β = -58.558± 18.463, *p* = 0.001), and soil temperature (β = 0.262 ± 0.098, *p* = 0.007) significantly predicted the weekly number of trees in flower. The best model fit were soil moisture and soil temperature but not relative humidity, mean air temperature, minimum air temperature, maximum air temperature nor wind speed (Table 4.2). Air temperature was autocorrelated with soil temperature, min. air temperature, as well as max. air temperature (Appendix B). Therefore, no model was fitted combining two of these climatic variables in the same model. The model in which soil temperature was fitted with soil moisture, relative humidity and wind speed had the lowest AIC emerging as the best performing model for predicting shea flowering.

Table 4. 2: Relationship between climatic factors and shea flowering

				95% C. I ----------------------		
Climatic factors	**β**	*SEβ*	**Wald Chi-square**	**Lower**	**Upper**	***P* value**
(Intercept)	-2.438	2.835	-0.86	-8.00	3.12	0.389
Relative Humidity	1.473	1.616	0.91	-1.69	4.64	0.362
Soil moisture	-58.558	18.463	-3.17	-94.74	-22.37	0.0015 **
Soil temperature	0.262	0.098	2.68	0.07	0.45	0.0073 **
Wind Speed	0.125	0.701	0.18	-1.25	1.50	0.859

*β = Beta, SEβ =standard error of Beta, ** = significance at 1%.*

The annual weather data revealed similar patterns of relative humidity, soil moisture and soil temperature in all three regions. There were increasing and decreasing phases of climatic variables, marked by the wet and dry seasons of the Guinea savanna ecological zone. The dry season (October – February) was characterised by decreasing relative humidity and soil moisture with increasing soil temperature. Relative humidity (91.5 - 85.8%) and soil moisture peaked in September in all regions whilst the minimum occurred in February. On the other hand, soil temperature peaked (35.7 - 38.84 ºC) in March/April but the minimum was recorded in September for all regions (Figure 4.2).

Commencement of flowering in NE and UE regions in the month of least relative humidity and soil moisture (February) is consistent with the findings of Okullo (2004) that shea flowering commences when the interaction between climatic factors creates the driest conditions of the year. On the contrary, flowering in UW region commenced in November, approximately two months prior to the driest period of the region (Figure 4.2).

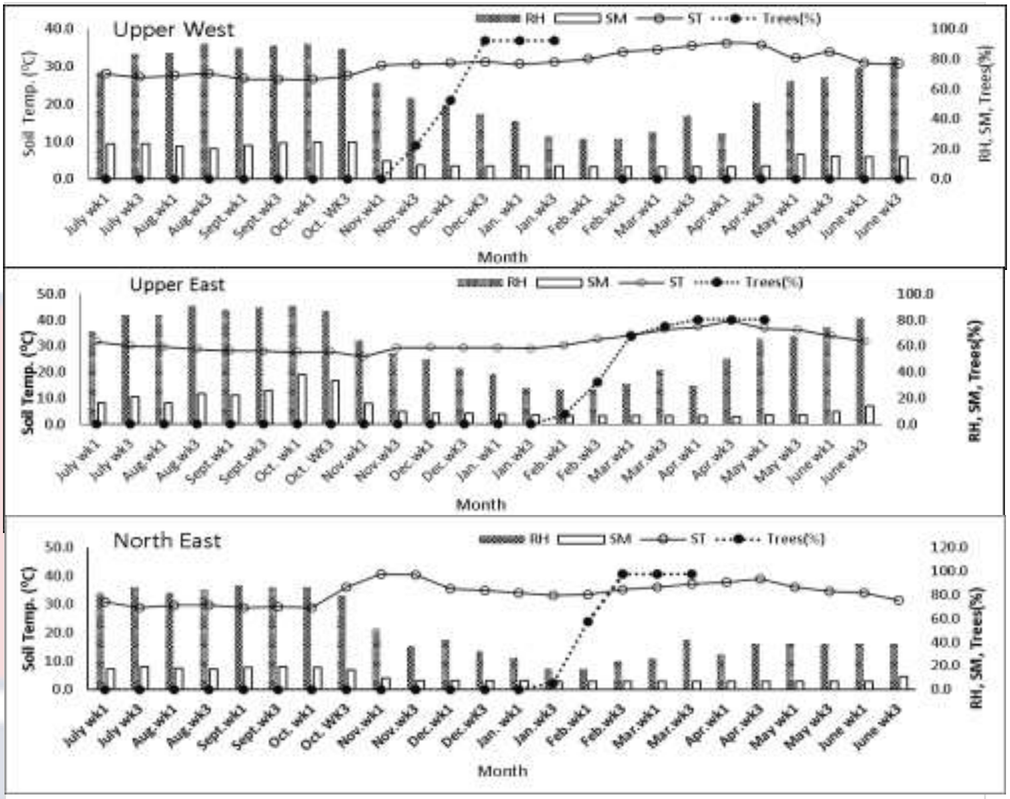

Figure 4. 2: Phenogram of *V. paradoxa* flowering and climatic conditions of Upper West, Upper East and North East regions of Ghana in 2020/2021 flowering season. RH =Relative humidity, SM = soil moisture and ST =soil temperature.

This is attributed to the unusual rise in soil temperature between October and November in UW. Climatic conditions of all three regions were characterised by a progressive increase in soil temperature by 1 - 2 ºC between successive months for most parts of the dry season (October to April). However, in the UW region, there was a 3 ºC increase in soil temperature from October to November. This increase was unusually higher than the monthly soil temperature increment (1- 2 ºC), which was associated with the onset of flowering.

Similarly, NE and UE recorded 3 and 4 ºC rise in temperature respectively from February to March (highest temperature difference between successive months). This also coincided with the onset of flowering. It is evident that flowering is influenced by unusual change in soil temperature in the dry season. This finding is in concordance with Barret and Brown's (2021) observation that flowering in tropical plants is triggered by short term variability in climatic events.

The climatic factors (soil moisture and temperature) that significantly predicted flowering in this study were different from those reported in previous studies. In Cameroun, relative humidity and temperature were identified as the climatic factors associated with flowering (Nguemo et al. 2014). Also, in Uganda maximum temperature and relative humidity significantly correlated with flowering (Okullo, Hall, et al., 2004). In this study neither relative humidity nor air temperature predicted flowering significantly but rather soil temperature and soil moisture. The reliability of soil moisture in predicting flowering was demonstrated in other plants. Models that included soil moisture as a predictor of flowering were able to explain 66 % of the variation in flowering compared to 24% when soil moisture was excluded (Chauhan et al., 2019).

Despite the accuracy of soil conditions in predicting shea flowering, none of the previous phenological studies included soil moisture nor soil temperature in phenological observations. Air temperature and relative humidity were the most used predictors, perhaps owing to easy availability of data compared to soil temperature and moisture data that sometime requires cumbersome and expensive procedures in measurements (McMaster & Wilhelm, 1998). Significant associations were recorded between air temperature and flowering in the previous studies because of the autocorrelation between air temperature and soil temperature. Therefore, air temperature served as proxy for soil temperature. However, it is evident in this study that, soil temperature enhances model performance better than air temperature.

The climatic factors associated with flowering are unique to each plant species, in central Himalayas, increasing soil moisture was found to be associated with flowering of *Rhododendron arboreum* (Tewari, Bhatt, & Mittal, 2016). Likewise, precipitation was found to be the most perfect external factor influencing early flowering of cocoa (Adjaloo et al. 2012). For winter oilseed rape (*Brassica napus*), temperature was the most accurate predicator of flowering onset (Hájková et al., 2021). Soil moisture stress seems to be the most significant trigger of shea flowering in Northern Ghana. However, the interpretation of our results is limited by the short duration (one year) of phenological observations. An observation of flowering patterns for longer periods are needed for a better understanding of the factors underlying observed flowering patterns. Notwithstanding, climatic factors identified to be associated with flowering in this study would guide future phenological studies to include soil moisture and temperature as predictors of flowering.

4.4.3 Geographic variation in the floral density of *V. paradoxa*

4.4.3.1 Flowering ability of trees and branches

The flowering ability of trees (number of trees that initiated flowers) did not vary significantly between regions (*H* (2) = 5.3041, *p* = 0.0705). Notwithstanding, the UE recorded a marginally lower percentage (80%) flowering compared to other regions (Figure 4.3a). However, the flowering ability of branches (number of tagged branches that initiated flowers) varied significantly (H (2) = 9.328, *p* = 0.009) between regions. Pairwise comparisons revealed a statistically significant difference between UE and NE (*p* = 0.011) but there was no significant difference between UW and NE (*P* = 0.976), nor UW and UE (*p* = 0.252) (Figure 4.3b).

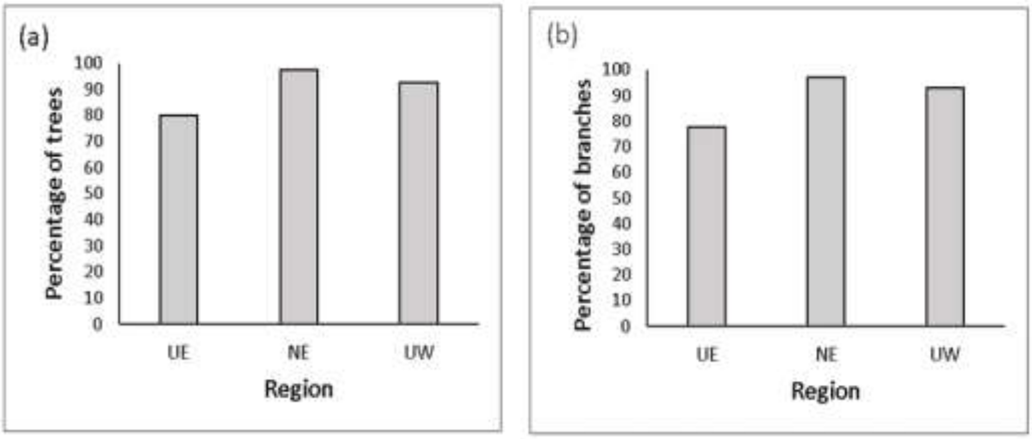

Figure 4. 3: Flowering ability of *V. paradoxa*, a = Percentage of trees that flowered, b = percentage of branches that flowered.

The percentage flowering ability of trees recorded in all regions are within the flowering range of 80 -100% recorded in northern Mali (Kelly et al. 2018). Insignificant differences in flowering ability of trees between regions can be attributed to the selection of a specific size class of trees in areas with similar land use history. This reduced the effect of land use and stand age which were previously reported to have significant effect on percentage flowering of trees (Kelly et al., 2007, 2018; Okullo, Hall, et al., 2004).

On the contrary, significant differences in percentage of flowering branches between regions might have been influenced by biotic factors particularly mistletoe infestation. Over 50% of shea trees are known to be infested with mistletoes in Northern Ghana (Asare et al. 2019). The severity of infestation varies between branches and this could have contributed to the variability in flowering. Mistletoes are xylem-tapping which are evergreen for most parts of the year, with higher transpiration rates. This lowers the water use efficiency of host with immediate impacts being felt in reduced growth vigour of branches above the point of attachment (Broshot & Tinnin, 1986).

This can retard the production of reproductive structures contributing to the variability in flowering of branches.

4.4.3.2 Number of buds/flowers initiated

The mean number of flowers initiated per inflorescence differed significantly between regions (H (2) = 19.93, *p* =0.001). Pairwise comparisons showed a significantly higher mean number of flowers (41.10) in UW compared to UE (*p* =0.001) and NE (*p* =0.001) which recorded 31.88 and 30.93 flowers respectively. However, there was no statistically significant difference (*p* = 0.901) between UE (31) and NE (Figure 4.4).

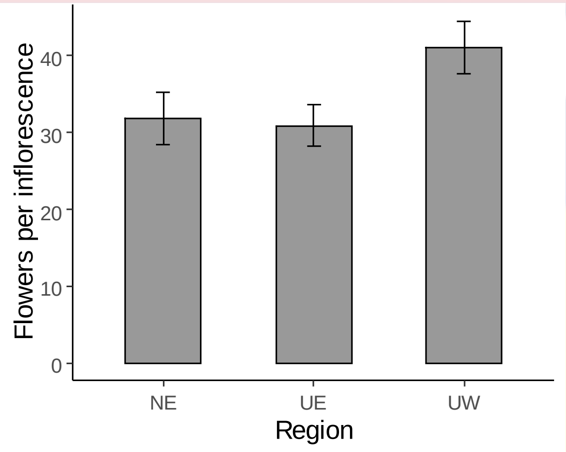

Figure 4. 4: Mean number of flowers ± S.E per inflorescence

The mean number of flowers per inflorescence recorded in this study is consistent with Okullo (2004) who indicated shea produces 20 to 100 flowers in a fascicle. The mean number of flowers recorded in UE and NE were similar to Stout et al. (2018) who previously reported an average of 31 flowers per inflorescence in Northern Ghana. The significantly larger number of flowers produced per inflorescence in the UW region can be attributed to high soil fertility in the area. The soils in UW were reported to contain higher amount of organic matter due to long fallow periods compared to other parts of Northern Ghana (Tetteh et al., 2016). The western highlands near Bole and

Wa were identified among the most favourable areas for yam cultivation, especially newly cleared farmlands (Lovett and Haq, 2000b).

The suitability of this area for yam is an indication of high soils fertility since yam has high soil nutrient demands. A comparison of soil physical and chemical properties reveals some variability between the three regions (Tetteh et al., 2016). Soils that are deficient in essential nutrients for flowering, particularly phosphorous, can limit flower production in plants. The soil properties play a significant role in plant growth and reproduction; therefore, variability in flowering can be explained by soil properties. Similarly, Kelly et al. (2007) detected a significant influence of soil conditions on flowering of tree stands in Mali

4.5 Geographic variation in morphometric traits of shea flowers

The one-way ANOVA revealed a statistically significant difference in mean pedicel diameter between regions ($F_{2,\ 536} = 5.22$, $p = 0.0057$). Tukey's HSD Test for multiple comparison of means showed a significantly (p = 0.001, 95% C.I. = 0.026, 0.157) larger mean pedicel diameter in UW (1.29 mm) compared to UE (1.21 mm). Pedicel diameter of UW was also marginally larger than that in NE (p = 0.313, 95% C.I. = -0.025, 0.106) (Figure 4.5a). The mean length of the pedicel also differed significantly between regions ($F_{2,\ 536}$ = 323.5, p = 0.00). The Tukey's HSD Test for multiple comparison of means showed a significantly larger pedicel length (20.1 mm) in UW compared to NE (p = 0.001, 95% C.I. = 1.252, 2.964) and UE (p = 0.00, 95% CI = 8.026, 9.743) that recorded 18 and 11.5 mm respectively. On the other hand, flower pedicels in NE were significantly longer than UE flowers (p = 0.001, 95% C.I. = -7.63, -5.919) (Figure 4.5b).

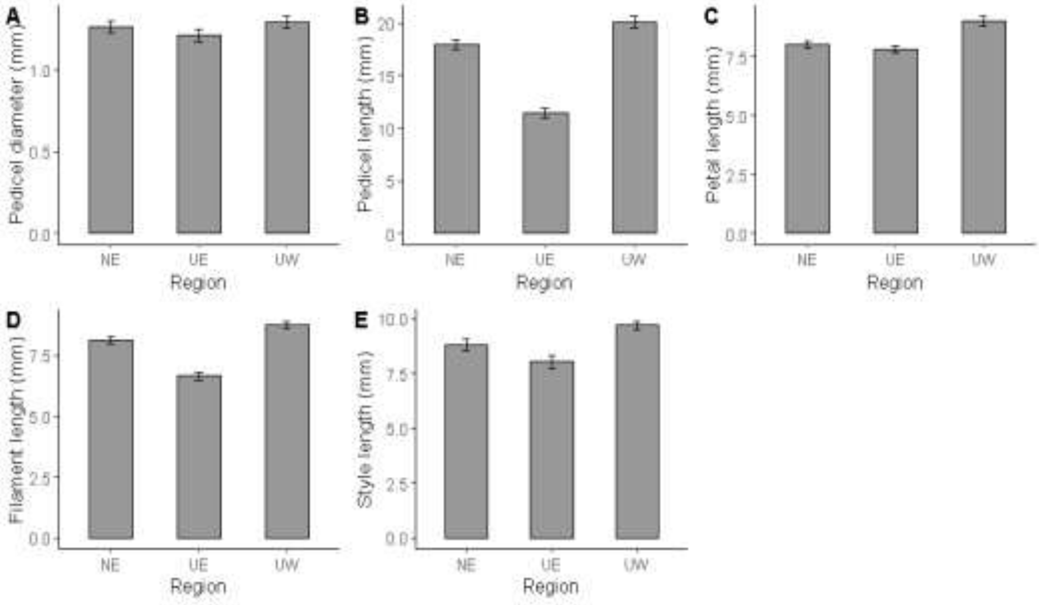

Figure 4. 5: Morphometric traits of *V. paradoxa* flowers

The mean petal length also varied significantly between regions ($F_{2, 536} = 58.63$, $p = 0.001$). Petals from UW were significantly longer (9.00 mm) than NE ($p = 0.001$, 95% C.I. = 0.712, 1.276) and UE ($p = 0.001$, 95% C.I. = 0.935, 1.497) that recorded 8.02 and 7.79 mm respectively. However, there was no statistically significant difference between mean petal length of flowers from UE and NE ($p = 0.131$, 95% C.I. = -0.505, 0.058) (Figure 4.5c). The mean filament length varied significantly between the three regions ($F_{2, 536} = 173.2$, $p = 0.001$). Multiple comparison of means showed a significantly longer filament (8.76 mm) in UW compared to NE ($p = 0.001$, 95% C.I.= 0.358, 0.902) and UE ($p = 0.001$, 95% C.I.= 1.829, 2.374) that had 8.12 and 6.65 mm respectively. However, filament length of NE was significantly longer than UE ($p = 0.001$, 95% C.I. = 1.744, -1.199) (Figure 4.5d).

Region had a statistically significant effect on style length ($F_{2,536} = 38.67$, $P = 0.000$). Tukey’s HSD test for multiple comparison of means revealed a significantly longer style in UW (9.71 mm) compared to NE ($p = 0.001$, 95% C.I.= 0.475, 1.342) and UE ($p = 0.00$, 95% C.I. = 1.619, 1.185) that had 8.05 and 8.88 mm respectively. Meanwhile, mean style length in NE was also significantly longer than UE (p = 0.001, 95% C.I.= -1.144, -0.277) (Figure 4.5e).

The morphometric traits of all floral parts recorded in this study were smaller than those reported in Uganda, except mean pedicel length of UW (20.1mm) which was slightly longer than mean (19.7mm) recorded in Uganda (Okullo 2004). This confirms Hall et al. (1996) assertion that flowers of *paradoxa* sub-species tend to be smaller than that of *nilotica* in terms of petal length, sepal length and style length. The longest mean style length (9.71 mm) recorded in this study is still shorter than the mean style length (2.89 mm) measured in Cameroon (Nguemo et al. 2014). Aside variation between studies, there was a significant variation in morphometric traits between the three regions of northern Ghana. Generally, the UW region recorded higher values for all floral traits measured.

Although flower development is known to be influenced by environmental factors, other studies have shown a large influence of selected genotypes on flowering (Craine et al. 2012). There is a high DNA polymorphism in shea (Abdulai et al., 2017) which could have accounted for this variability in floral traits. Just like many other ecological phenomena, phenology is known to be under strong genetic control (Craine et al. 2012), therefore the internal reproductive capacity of each plant might influence the floral traits portrayed. Secondly, genetic diversity of shea tree population in managed landscapes have been shaped by strong anthropic selection (Lovett and Haq, 2000b). The choice of tree traits for selection and retention in farmlands might differ between ethnic groups based on ethnobotanical knowledge. Considering the wide geographic distribution of our study sites, anthropic selection of traits unique to regions might have also contributed to this wide variation in floral traits.

4.6 Conclusion

The results show the onset of shea flowering is influenced by local microclimatic conditions and not only the wider climate of the agro-ecological zone. Soil temperature and soil moisture are the significant predictors of flowering. Flowering occurs in the early dry season as an adaptation to synchronise flowering with periods of high bee pollinator activity. Furthermore, the dry season flowering is to avoid nectar and pollen dilution by early rains. Despite the significant relationship between climatic factors and flowering, the effect on climate change on shea flowering is still far from understood, but a climate driven shift in timing of flowering could cause asynchrony of flowering and pollinator activity. We recommend longer periods of phenological observations to help understand this concept.

Floral density and morphology also varied significantly between regions in response to biotic and abiotic conditions. Floral traits could be genetically controlled as traits considered in tree selection and retention on farmlands differ between farmers based on their ethnobotanical knowledge. Our findings are significant to domestication and tree improvement strategies. The variability observed in floral phenology and morphology within the same agro-ecological zone implies germplasm collection for tree improvement should be targeted at improving ideotypes for specific geographic areas and not a wider agro-ecological zone.

CHAPTER FIVE

INFLUENCE OF BEEKEEPING ON POLLINATION AND FRUIT YIELD OF VITELLARIA PARADOXA IN WEST AFRICAN AGROFORESTRY PARKLANDS

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Conceptualisation, design of experiment, data collection, analysis and writing of manuscript.

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5.1 Abstract

Vitellaria paradoxa (shea) is a fruit tree of domestic and industrial importance in arid and semi-arid regions of Sub-Saharan Africa. Fruit set is largely dependent on insect pollination. Recent studies revealed reduced fruit set due to pollen deficit. Beekeeping is known to be an effective approach for enhanced pollination services in temperate climates but there is limited evidence to justify promotion of beekeeping for pollination in shea agroforestry parklands of West Africa and the tropics. The study investigated the effect of managed honey bee colonies (*Apis mellifera*) on fruit yield. Tree proximity to the apiary had a detectable effect on fruit set within a 500 m range of the apiary. Proximity of shea trees to apiary was significantly related to number of immature fruit set but not number of mature fruits. Fruit weight and size were not significantly related to distance from apiary nor pollination treatment. This implies that the introduction of beekeeping has the potential to address the shea pollination deficit at least within a 500 m range of the apiary. Further work is needed to determine the optimal hive density per acreage of shea parkland to maximise pollination services.

5.2 Introduction

Managed honey bees are increasingly being introduced into agricultural landscapes to enhance pollination services in many regions of the world (Bosch et al., 2021; Evans et al., 2021; Geslin et al., 2017; Stern et al., 2001). This is particularly important for insect pollinator dependent crops in monocultural landscapes and regions with reduced wild pollinator populations (Da Silva, 2018; Kambach et al., 2013; Klein et al., 2007b). Although several pollinator species can be managed for pollination services, social bees of the genus *Apis* are often kept for pollination services in agricultural landscapes, not only for their polylectic nature, but also the wide geographic distribution, long history of manipulation and management in artificial hives (Viana et al. 2014; Willmer & Finlayson 2014; Toni et al. 2018).

The positive effect of introduced bee colonies on pollination and fruit yield have been reported in temperate fruit trees such as apples, macadamia and strawberry (Abrol et al., 2019; Evans et al., 2021; Stern et al., 2001; Viana et al., 2014). Pollination and fruit yield of tropical plants such as watermelon is enhanced with managed bees (Layek et al., 2021). In India, the introduction of managed bee colonies increased watermelon yield by 46.32% and significantly enhanced fruit size and weight (Layek et al., 2021). In Brazil, introduced bee colonies increased apple fruit set (Stern et al., 2001). Notwithstanding the overwhelming evidence of managed bee effect on pollination and fruit set, studies on pollination do not represent continents and climatic regions evenly, especially Africa (Archer, Pirk, Carvalheiro, & Nicolson, 2014; Brom, Underhill, & Winter, 2022; Toni et al., 2018).

Despite the significance of managed bees in pollination enhancement, there are no justifications for introduced bees in landscapes with sufficient wild pollinator populations (Thomson, 2004). Indeed, globally it has been found that managed bees can supplement, not replace, pollination by wild insects (Garibaldi et al., 2013). Managed honeybee colonies are often introduced as a remedy to pollination deficit emanating from wild pollinator population declines (Belsky & Joshi, 2019; Garibaldi et al., 2016).

Globally, agriculture is a primary driver of pollinator population decline (IPBES, 2016) but the impact of agriculture on pollinators of economic trees might be severe in Sub-Saharan Africa. This is because indigenous trees are often integrated with annual food and fibre crops (Boffa 2015), which exposes pollinators to chemicals used in crop pest control (Connolly, 2013). Aside chemical hazards, agricultural extensification and intensification is degrading agroforestry parkland habitats (Boffa, 2015; Lompo et al., 2017; Lovett & Haq, 2000a), with direct impacts on nesting, foraging and breeding sites for wild pollinators. Delaney et al. (2020)

confirmed the negative effect of local tree diversity losses on pollinator populations and pollination success in Burkina Faso.

The impact of these anthropogenic disturbances on pollinators is being felt on the reduced fruit yield of major economic trees such as shea (Lassen et al., 2016; Nasare et al., 2019; Stout et al., 2018). Shea is the most abundant economic tree in Northern Ghana, Southern Burkina Faso and other parts of Sudano-Sahelian zone (Bayala et al., 2013; Chimsah et al., 2013; Fischer et al., 2011). The edible fat extracted from shea kernel is used locally and industrially contributing to poverty alleviation and food security (Marle, 2013; Munialo et al., 2019; Naughton et al., 2015).

Shea fruit set is largely dependent on insect pollinators, primarily *Apis mellifera andosonii* and stingless bee species (Nasare et al., 2019; Okullo, 2004; Yidana, 2004) but recent experimental studies show that shea is pollen limited (Delaney et al., 2020). Although managed bee colonies are used for enhanced pollination services in other regions of the world, this approach is less practiced in Africa (Toni et al., 2018). Important concepts such as bee colony quality, colony placement range and required colony densities, as well as economic viability of managed bees within the current entomofauna of Africa are still poorly understood (Toni et al., 2018).

The pollen deficit in shea is a well-identified problem (Delaney et al., 2020; Lassen et al., 2016), but other than Lassen et al. (2016) there are no studies exploring beekeeping for addressing shea pollen deficit. The study of Lassen et al. (2016) shows feral bee colonies within a range of 1000 m improve pollination. However, this is not an easy approach as feral bee colonies cannot be guaranteed within reasonable distances in all parklands.

Aside the difficulties associated with standardizing feral bee colony age, the geographic scope (one site) of their study limits the interpretation of findings as several abiotic factors are known to influence shea fruit set (Bondé, Ouédraogo, Traoré, et al., 2019). Studies on fruit productivity requires multiple sites to offset the effect of site conditions (Nasare, Stout, Lovett, & Kwapong, 2022).

Understanding the influence of managed bee colonies on fruit set is important in guiding farmers and other stakeholders on best approaches for managing bees in shea parklands. This study tested the null hypothesis that fruit yield of shea is not influenced by beekeeping. Specifically, the study examined: a) the effect of apiary on the percentage of inflorescences that bore fruits b) estimated the degree of pollen limitation across different distances away from apiaries and c) assessed the effect of apiaries on number of fruit set and fruit/seed traits.

5.3 Materials and methods

5.3.1 Study Area

The Experiment was conducted in the Guinea Savanna agro-ecological zone of Ghana during the 2020/2021 shea flowering and fruiting season. The Guinea Savanna is the largest agro-ecological zone in Ghana, stretching from Oti and Bono Regions in the South to Upper East and Upper West Regions in north (Incoom et al., 2020). The area records a monomodal rainfall with a mean annual rainfall of 1034 mm and a mean monthly temperature ranging from 27 to 35 °C (Darko et al., 2019; Ghansah et al., 2018). The Guinea savanna records a mean monthly minimum and maximum relative humidity of 53% and 80% respectively.

The vegetation is predominantly grassland interspersed with trees and shrubs (Darko et al., 2019). The most frequently recorded herbaceous plants and grasses include *Boerhavia diffusa*, *Andropogon pseudapricus*, *Tridax procumbens* and *Panicum maximu*, (Ziblim et al., 2015). Among common tree species in the area are baobab (*Adansonia digitata*), Linnea (*Lannea acida*), acacia (*Faidherbia albida*), dawadawa (*Parkia biglobosa*), and ebony (*Diopyros mespiliformis*).

5.3.2 Study plant (*Vitellaria paradoxa* C.F. Gaertn.)

Vitellaria paradoxa, commonly known as shea in English and Karite in French is a tree native to arid and semi-arid regions of Sudano-Sahelian zone of Africa. Shea is of the family Sapotaceae, with two subspecies (*nilotica* and *paradoxa*) but only the *paradoxa* subspecies occurs in Ghana. Shea occurs in four agro-ecological zones of Ghana but the Guinea savanna zone contains the largest shea population. The species is generally uncultivated, but saplings are selected, retained and managed on farmlands during land clearing under which annual crops are cultivated in a traditional agroforestry system. It is recorded as the most abundant economic tree in northern Ghana constituting about 62% of tree density in cultivated lands and 40% in fallow lands (Chimsah et al., 2013).

The tree attains a mean height of 10m at maturity but can reach 15m under favourable environmental conditions (Hall et al., 1996). According to Dalzeil as cited in Marle (2013), the shea tree has a life span of 200-300 years and a gestation period of about 15-20 years prior to flowering and fruiting. However, peak fruit production is only reached when trees are 50 – 100 years (Glèlè Kakaï et al., 2011). Shea flowering commences in the early dry season from November to May but the exact timing of flowering differs between regions. Fruiting occurs from March to August. Both fruit pulp and the seed are of economic importance.

5.3.3 Field layout and tree selection

The study was conducted in shea parklands of six selected sites in UW, UE and NE regions of Ghana. In each region, two replicate sites were selected ensuring a minimum distance of 4 km and a maximum of 25 km to minimize variability in climatic conditions between sites (Figure 1). Experimental sites were located in young fallows (shea parklands that were uncultivated for 2-5 years) that had established apiaries. The selected parklands had apiaries of ten empty beehives each installed in July 2017. Sites that had six to eight colonised hives as of October 2020 were selected for the study.

In the apiary-parkland, three distances (100, 500 and 1000m) away from the apiary were established. A control parkland was located at a distance of 3 to 4 km away from the apiary considering the design of Delaney et al. (2020). This was to limit the influence of external factors (semi- natural sites, feral bee colonies, human settlement, and climatic factors etc.) on pollinator abundance. This was done to minimize variability in environmental conditions between treatment and control parklands.

Five focal trees of a predetermined size class (DBH; 25-30 cm, Height ≥ 10 m and crown area ≥ 20 m^2) were randomly selected at each distance range and the control parkland. These DBH and height classes were selected because they contain the highest mature shea tree abundance in the Guinea savanna zone (Tom-Dery et al., 2015). This also standardized the samples to minimise tree effect on yield. Similarly in the control shea parkland, a predetermined point was identified and five focal trees of the pre-determined size class were selected within a 100 m radius.

5.3.4 Experimental Treatments

Three pollination treatments were applied to inflorescences of each focal tree and replicated three times in a tree. The pollination treatments were:

Open pollination ("open"): Tagged inflorescences that were left unmanipulated and exposed to all agents of pollination throughout the flowering period (Figure 5.1a)

Insect exclusion ("bagged"): inflorescences bagged at bud stage with a muslin net (net mesh size diameter of approximately 1mm) to prevent all insect pollinators from accessing the flowers throughout the flowering season. A binding wire (diameter ~ 0.61mm) was erected over the inflorescences before the net was wrapped to prevent wind from pushing net in close contact with flowers (Figure 5.1b).

Supplemental Hand pollination (hand): Pollen manually applied to protruding stigmas directly from the anthers of other neighbouring shea trees. Pollen was supplemented twice at an interval of two weeks during peak flowering (Figure 5.1c).

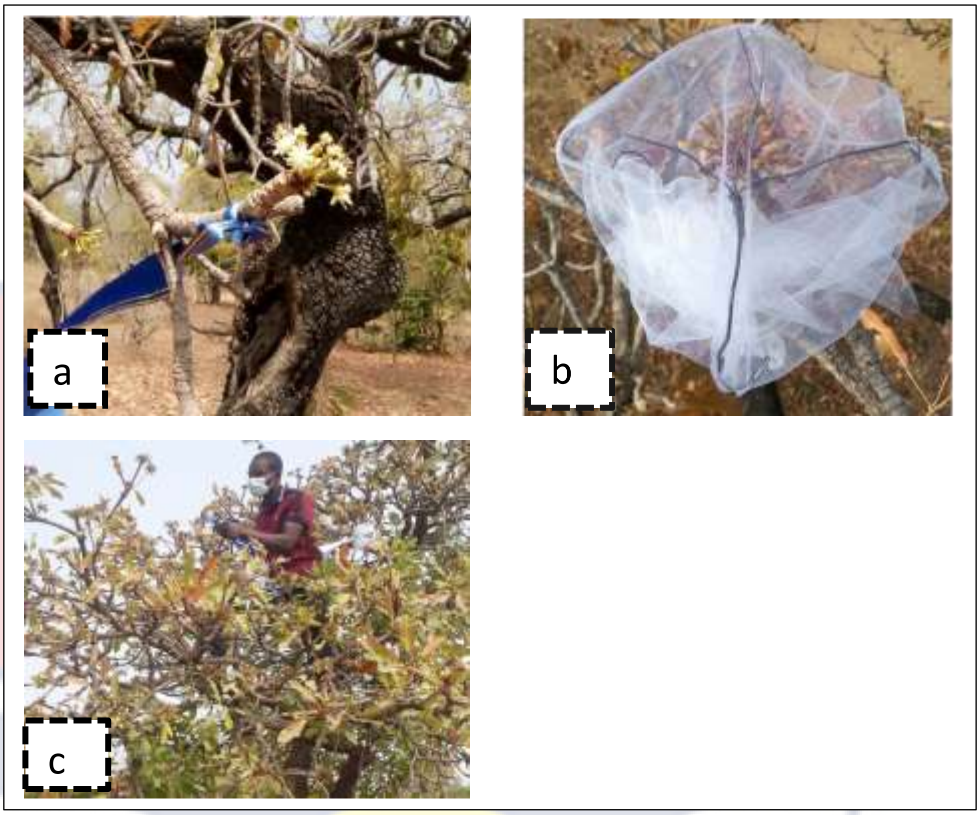

Figure 5. 1: Experimental Treatments applied to inflorescences. a = Open pollination, b= Insect exclusion, & c = pollen supplementation by hand

In the UW region, all treatments were applied in December/January, 2020/21 whist that of NE and UE were applied in February/March 2021. The timing of treatment application differed due to variation in timing of peak flowering. At the fructification stage, the number of fruit set per focal inflorescence was counted every fortnight till fruit maturity. Mature fruits were harvested and weighed prior to fruit fall. Fruit length and width were measured with a digital calliper, after which the fruit pulp was removed before nut weight and size were measured (Figure 5.2).

Figure 5. 2: Measurement of fruit/nut weight and size. a =Fruit weight, b = nut weight, c = fruit width, d = nut length.

5.3.5 Data Analysis

Linear mixed effect models were run for effect of distance and pollination treatment on various measures of pollination/fruit yield with appropriate distribution and link function. The study also ran separate models for fruit yield in the open pollination treatment only with distance as response variable. In all models, region was as a random effect to account for the nested effect of tree within a region. Hurdle models, were run for effect of treatment and distance on fruit set where the response variable (fruit set) was broken into presence/absence of fruit as well as the quantitative measure of non-zero values. Degree of pollen limitation was estimated by the difference in number of fruits per inflorescence between hand pollinated and open pollinated inflorescences (Table 5.1).

Table 5. 1. Mixed effects models used in fruit analysis. Hurdle models were used for all models investigating fruit set. D= Distance, PT =Pollination Treatment, I = Interaction

Model	**Dependent variable**	**Fixed effect 1**	**Fixed effect 2**	**Fixed effect 3**	**Random effect**	**Distribution**
Fruit set	*M1. Part 1*: Presence of mature fruit on inflorescence	D	PT	I	Region	Binomial (logit)
	M1. Part 2: Number of mature fruits in inflorescence that bore fruit	D			Region	Poisson (log link)
	M2. Part 1: Presence of mature fruit on open pollinated inflorescence	D	PT	I	Region	Binomial (logit)
	M2. Part 2: Number of mature fruits on open pollinated inflorescences that bore fruit	D	PT	I	Region	Poisson (log link)
Pollen deficit	Number of fruits produced in pollen supplemented inflorescences - fruits produced in open pollinated inflorescences	D			Region	Gaussian (log link)
Fruit/nut weight	Weight of fruit or nut	D	PT	I	Region	Gaussian (log link)
	Weight of fruit or nut on open pollinated flowers	D			Region	Gaussian (log link)
fruit/nut size	*M1*: Length of fruit or nut	D	PT	I	Region	Gaussian (Log link)
	M2: Length of fruit or nut on open pollinated flowers	D			Region	Gaussian (log link)
	M3: Width of fruit or nut	D	PT	I	Region	Gaussian (log link)
	M 4: width of fruit or nut on open pollinated flowers	D			Region	Gaussian (log link)

Data on proportion of inflorescences that bore fruits and number of fruit set per inflorescence were not normally distributed and statistical transformation was not useful to attain normality, therefore non-parametric test was performed using Kruskal Wallis test. Post hoc pairwise comparisons were performed with Mann-Whitney U-tests. On the other hand, fruit, nut weight and size were compared between distances using one-way Analysis of Variance. Post hoc pairwise comparisons were conducted using Bonferroni corrections. All models were run using the lme4 and glmmTMB packages (Bates et al., 2015; Brooks et al., 2017) in R Core Team (2021).

5.4. Results

5.4.1 Influence of beekeeping on number of fruit set

Inspection of both parts of the hurdle model showed the presence of immature fruit (fruit set recorded on the 4th week of fructification) on an inflorescence was significantly related to the interaction of distance and pollination treatment ($\beta = 0.25 \pm 0.13$, $p = 0.049$, Figure 5.3, Table 5.2). Similarly, number of fruits where present was significantly related to distance and pollination treatment interaction ($\beta = 0.11 \pm 0.032$, $p = 0.00046$).

In the open pollination treatment, the presence of immature fruit was not significantly related to distance but the number of fruits where present was significantly related to distance ($\beta = -0.280 \pm 0.035$, $p = 0.001$). Number of immature fruits ranged from 0 to 3 in the bagged pollination treatment whilst the open and hand treatments both had 0 – 9 (Appendix C).

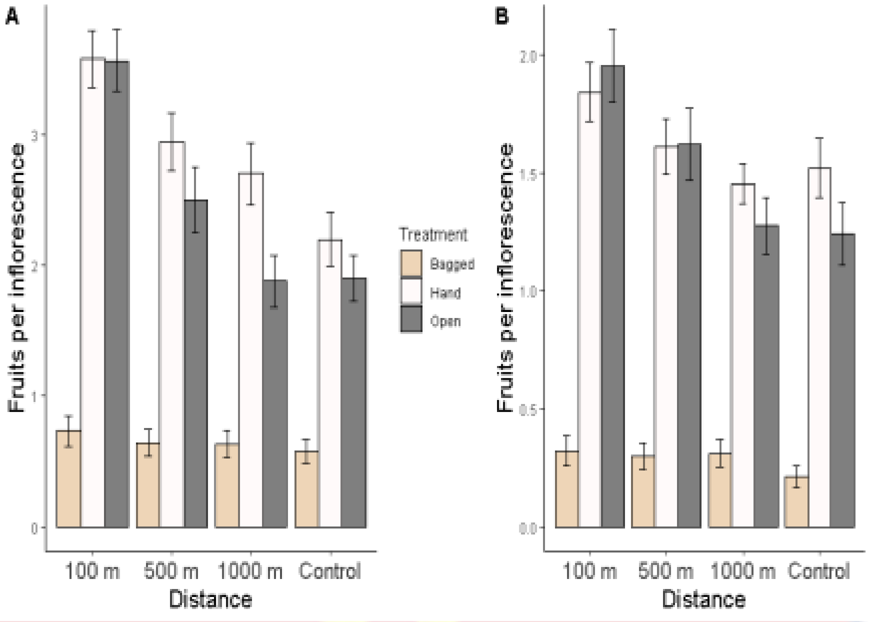

Figure 5. 3: Mean (± S.E) fruit set per inflorescence A) immure fruit set, B) mature fruit set

For mature fruits, the presence of a mature fruit on the inflorescence was neither significantly related to pollination treatment nor distance. However, the number of mature fruits where present, was significantly related to distance ($\beta = -0.33 \pm 0.052$, $p = 0.001$, Figure 5.3, Table 5.2). In the open pollination treatment, the presence of a mature fruit was not significantly related to distance, but where present, the number of fruits was significantly related to distance ($\beta = -0.14 \pm 0.048$, $p = 0.0029$, Figure 5.3, Table 5.2). Trees at 100 m to apiary produced significantly larger number of mature fruits compared to 1000 m ($p = 0.0053$) and the control ($p = 0.0039$). Similarly, 500 m had significantly larger number of fruits than 1000 m ($p = 0.001$) and control ($p = 0.010$). Number of mature fruits ranged from 0 to 3 in the bagged pollination treatment whilst the open and hand treatments had 0 – 5 and 0 – 6 respectively (Appendix C).

Table 5. 2: Summary of statistical analysis of fertilisation and fruit set according to pollination treatment, distance to apiary and the interaction of these factors. Significant factors are highlighted in bold and with an asterisk (*).

Response variable	Distance effect	Treatment effect	Interaction effect
M1. Part 1: Presence of immature fruit on inflorescence	$\boldsymbol{\beta = -0.27 \pm 0.14,\ p = 0.045*}$	$\boldsymbol{\beta = -1.89 \pm 0.34,\ p = 0.001*}$	$\boldsymbol{\beta = 0.25 \pm 0.13,\ p = 0.049*}$
M1. Part 2: Number of immature fruits where present	$\boldsymbol{\beta = -0.33 \pm 0.052,\ p = 0.001*}$	$\beta = 0.11 \pm 076$, $p = 0.14$	$\boldsymbol{\beta = 0.11 \pm 0.032,\ p = 0.005*}$
M2. Part 1: Presence of immature fruit in open treatment only	$\beta = 0.11 \pm 0.148$, $p = 0.46$		
M2. Part 2: Number of immature fruits in open treatment only	$\boldsymbol{\beta = -0.280 \pm 0.035,\ p = 0.001*}$		
M1. Part 1: Presence of mature fruit on inflorescence	$\beta = -0.086 \pm 0.16$, $p = 0.60$	$\beta = -4.88 \pm 4.06$, $p = 0.23$	$\beta = 0.024 \pm 1.37$, $p = 0.86$
M1. Part 2: Number of mature fruits where present	$\boldsymbol{\beta = -0.22 \pm 0.081,\ p = 0.0069*}$	$\beta = 0.07 \pm 0.12$, p = 0.51	$\beta = 0.07 \pm 0.048$, $p = 0.12$
M2. Part 1: Presence of mature fruit (open pollination only)	$\beta = 0.16 \pm 0.26$, $p = 0.53$		
M2. Part 2: Number of immature fruits (open pollination only)	$\boldsymbol{\beta = -0.14 \pm 0.048,\ p = 0.0029*}$		
Pollen deficit (Immature fruits)	$\boldsymbol{\beta = 0.39 \pm 0.57,\ p = 0.014*}$		
Pollen deficit (Immature fruits)	$\beta = 1.062 \pm 1.07$, $p = 0.32$		
M1: Weight of fruit	$\boldsymbol{\beta = 0.56 \pm 0.194,\ p = 0.0034*}$	$\beta = 0.64 \pm 0.36$, $p = 0.076$	$\beta = -0.000463 \pm 0.001$, $p = 0.73$
M2: Weight of seed	$\beta = -0.00549 \pm 0.014$, $p = 0.699$	$\beta = -0.004 \pm 0.031$, $p = 0.89$	$\beta = 0.0192 \pm 0.015$, $p = 0.200$
Fruit	$\boldsymbol{\beta = 0.812 \pm 0.226,\ p = 0.00032*}$	$\beta = 0.812 \pm 0.481$, $p = 0.091$	$\beta = 0.659 \pm 0.4924$, $p = 0.046$
Seed	$\beta = 0.795 \pm 0.236$, $p = 0.00075$	$\beta = 0.832 \pm 0.506$, $p = 0.101$	$\boldsymbol{\beta = 0.626 \pm 0.307,\ p = 0.0415*}$
Fruit	$\boldsymbol{\beta = 0.769 \pm 0.225,\ p = 0.00062*}$	$\beta = 0.848 \pm 0.492$, $p = 0.084$	$\boldsymbol{\beta = 0.579 \pm 0.295,\ p = 0.02559*}$
Seed	$\boldsymbol{\beta = 0.720 \pm 0.231,\ p = 0.00189*}$	$\beta = 0.77 \pm 0.475$, $p = 0.105$	$\beta = 0.485 \pm 0.291$, $p = 0.095$

[1] *Hurdle models were used to analyse fruit set, and so two significance values are generated, one for each part of the model.*

5.4.2 Influence of beekeeping on pollen limitation

The degree of pollen deficit was significantly related to distance for immature fruit set, with increased deficit further from apiaries (β = 0.39 ±

0.57, *p* = 0.014). However, for mature fruits, pollen deficit was not significantly related to distance (β = 1.062 ± 1.077, *p* = 0.32, Table 5.2).

5.4.3 Influence of beekeeping on fruit/seed traits

5.4.3.1 Fruit/seed weight

The mean weight of shea fruit was signficantly related to distance (β = 0.56 ± 0.194, *p* = 0.0034) but not the pollination treatment. However, this relationship was not consistent as there was no significant relation between distance and fruit weight in open pollinated flowers. Seed weight was not significantly related to distance nor pollination treatment (Figure 5.4, Table 5.2).

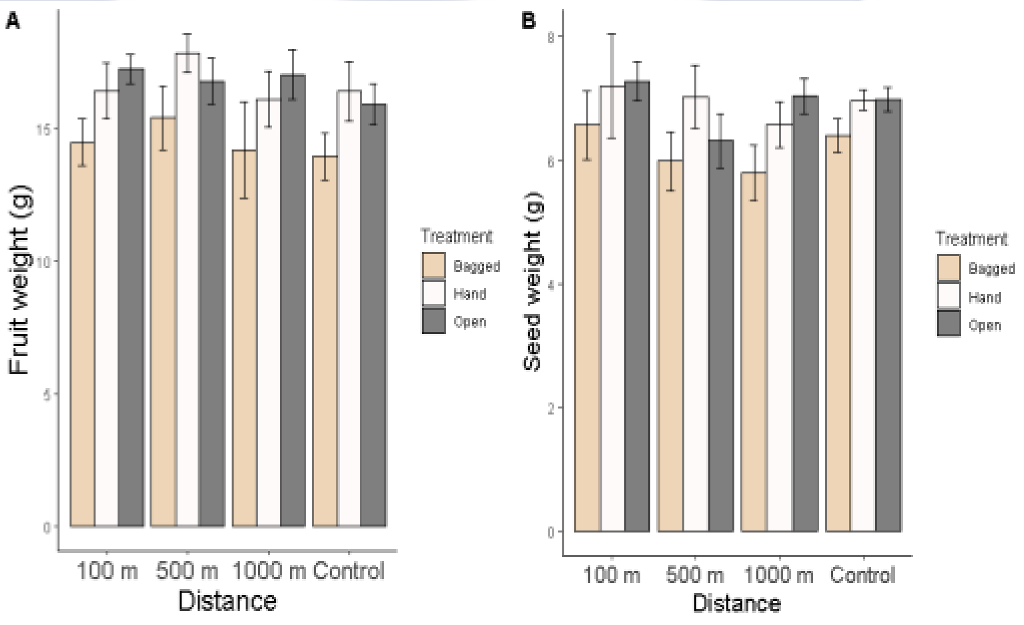

Figure 5. 4: Mean (± S.E) weight of shea; A) fruit, B) seed

5. 4.3.2 Fruit/seed size

Fruit length was significantly influenced by distance and pollination treatment interaction (β = 0.6588± 0.4924, *p* = 0.046). Meanwhile fruit length of the open pollinated flowers was not significantly related to distance (β = -0.0002765 ± 0.0003711, *p* = 0.456). Fruit width was also significantly influenced by distance and treatment interaction (β = 0.579 ± 0.2951, *p* = 0.02559) However, fruit width of the open pollinated flowers was not related to the distance. Similarly, seed length was significantly related to distance and pollination treatment interaction (β = 0.626± 0.307, *p* = 0.0415). However, seed length in the open pollinated treatment was not significantly related to distance. Seed width was significantly related to distance (β = 0.7200± 0.231, *p* = 0.00189) but not pollination treatment. However, seed width of the open pollinated was not significantly related to distance (Figure 5.5, Table 5.2).

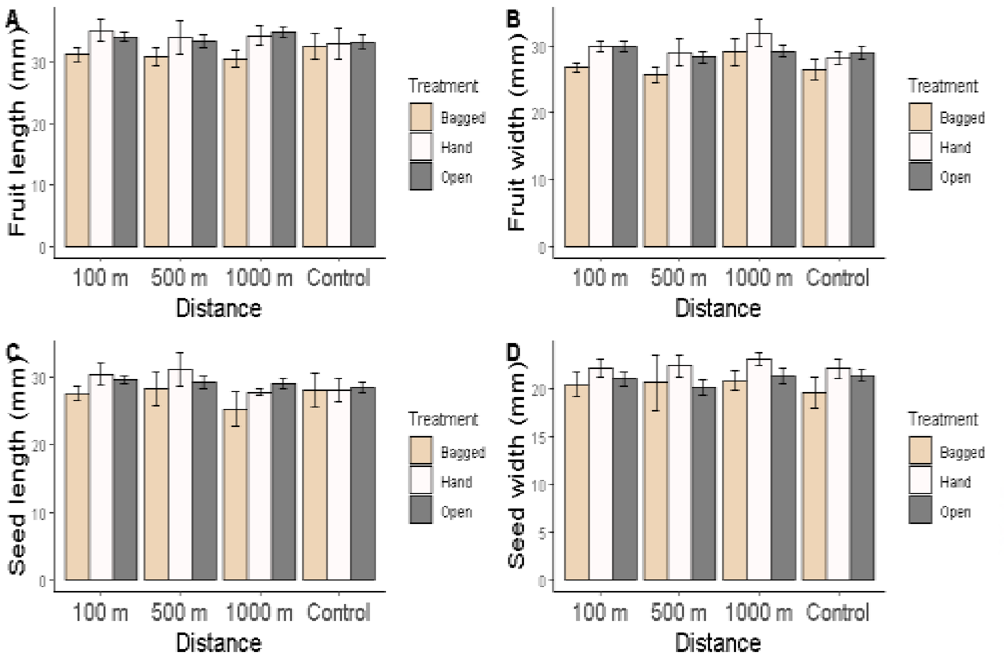

Figure 5. 5: Mean (± S.E) size of fruits and seeds. A) Fruit length, B) Fruit width, C) Seed length, D) Seed width

5.5 Discussion

5.5.1 Fruit set

The data suggests distance to apiary and pollination treatment interaction, determine the presence and number of immature fruits produced per inflorescence. Notwithstanding the positive effect of these factors on immature fruit set, distance to the apiary did not significantly influence the presence of a matured fruit on an inflorescence. This implies that, immature fruit may develop after fertilisation, but several biotic and abiotic factors including infestation by fruit pests (Dwomoh, 2004; Lamien et al., 2008; Zida et al., 2020), herbivory by small mammals and frugivorous birds (Delaney et al., 2020) and wind damage, could lead to premature fruit loss.

Despite the fact that presence of a mature fruit on an inflorescence is not explained by distance to apiary, in situations where fruit (s) is/are present, the number of fruits was significantly related to distance. Among open pollinated inflorescences, trees that were at closer proximity to the apiary (100 and 500 m) recorded significantly higher fruit set than trees at 1000 m and the control parkland. The implication of this finding is that the positive effect of colonies on number of matured fruit set is not felt beyond 500 m range of the apiary. Although honey bees are known to forage up to a distance of 10 km from the hive (Steffan-Dewenter & Kuhn, 2003), long distant flights are only done by a few “scout bees” within the colony (Chandler & Dunwell, 2008; Ramsay, 2005). In USA, the number of foraging bees was found to decrease exponentially with distance away from the hive with honey bees noted to forage within 800 m range of the apiary (Hagler, Mueller, Teuber, MacHtley, & Van Deynze, 2011). In the African Savannas, Guinko as cited in Lassen et al. (2016) proposed a mean honey bee foraging distance of 1 km.

Irrespective of the accuracy of these estimates, the fundamental principle in foraging economics is that the farther the distance of the forage resources from the colony, the more energy consumed in foraging (Esch & Burns, 1996). Considering the fact that shea trees bloom within a shorter time duration and being the most abundant species in the savanna, bees would find forage at closer proximity to their hives eliminating any justification for long distant flights. This perhaps accounted for the non-detectable effect of apiary effect on fruit set beyond 500 m. This can be supported by the fact that bee visits are known to correlate negatively with distance from beehives (Lee, Yoon, Lim, & KO, 2014).

The 500 m range of detectable positive effect on fruit set recorded in this study is relatively short when compared with Lassen et al. (2016) who reported positive effect of feral honey bee colonies within 1000m range. However, Lassen et al. (2016) did not find any positive effects in the second year of their experiment. One factor that might account for these differences is the confounding effect of stingless bee contribution to shea pollination. Stingless bees are known to compliment honeybees in shea pollination (Kwapong 2014; Lassen et al 2016) but our experiment did not control for stingless bee contribution to pollination success.

In Burkina Faso, host trees of stingless bee nests produced higher fruit set than non-host trees in the parkland (Lassen et al 2016). In Brazil, it has already been noted that, the supplementation of Africanised honey bee pollination with stingless bee hives increases apple fruit set than orchards with Africanised honey bee colonies only (Viana et al., 2014). This confounding effect of stingless bees might have influenced pollination and fruit set of shea. Future studies should control this factor and potentially explore the effect of meliponiculture on pollination and fruit set.

Furthermore, the density of flowering trees in a shea parkland could also influence foraging distance. Shea parklands with higher tree density might record shorter foraging ranges compared to parklands with dispersed tree population. Densely populated parklands would provide abundant floral resources within close proximity of the hive enhancing shorter foraging ranges than sparsely populated parklands. Many studies have shown positive effect of floral density on pollination and plant reproductive success (Dauber et al., 2010; Essenberg, 2012).

Aside this, diversity of alternative plants flowering simultaneously within the parkland could influence foraging behaviour as well as foraging distances. Delaney et al. (2020) reported a positive relationship between shea parkland tree diversity and pollinator visitation in Burkina Faso. These aspects may be explored further in future studies to better understand the role of these factors on pollination and fruit set.

A possible limitation to the interpretation of finding of this study could be the limited number of distance ranges established. Establishing several distance ranges at shorter intervals would be relevant in unveiling the optimum placement distances.

5.5.2 Pollen deficit

Distance to the apiary had a significant relationship with the degree of pollen deficit for immature fruit set but no relationship was detected for mature fruit set. This reiterates the fact that many other factors influence the sustenance of a fruit to maturity. Notwithstanding, there were no significant differences between hand and open pollinated inflorescences at 100 and 500 m, an indication that the presence of bee hives might have addressed pollen limitation within 500 m range of the apiary. However, this interpretation cannot be generalised as the study could not verify whether the hand pollinated inflorescences had received the adequate amount of pollen required for maximum fruit set. Ashman et al. (2004) point out that the lack of information on a plant's pollen requirements prior to pollen supplementation negates the assumption that hand pollination represents the maximum achievable fruit set. Also, the duration of stigma receptivity after anthesis is still poorly understood in shea and the study could not ascertain the level of stigmatic tissue receptivity during pollen supplementation.

Among other inaccuracies associated with pollen supplementation include variation in pollen quality between the supplemented and the control treatment, tendency of the plant to reallocate excess resources to other flowers other than the pollinated and most importantly, pollen limitation is estimated at population level and not an individual limitation (Ashman et al. 2004). This study was not immune to these factors which limits the interpretation of the variability in yield between hand pollinated flowers.

5.5.3 Fruit/seed traits

The data revealed that fruit/seed weight is not significantly related to pollination treatment nor distance. However, the bagged treatment recorded a marginally small fruit/seed weight compared to the open and hand pollinated flowers. The insignificant effect of pollination treatment on fruit weight has been reported in previous studies (Delaney et al., 2020; Lassen et al., 2016; Stout et al., 2018). Similarly, fruit/seed size (length and width) were not related to distance nor the pollination treatment. This indicates that pollination enhances fruit set but not fruit weight nor size. This trend was equally reported in watermelon where bee colony size correlated positively with fruit set but did not explain size nor weight of fruit (Lee et al., 2014). Therefore, shea fruit/seed weight and size are likely to be controlled by environmental conditions after fertilisation. It is therefore possible that biotic and abiotic conditions that control plant growth including climate, genetics and soil conditions determine fruit/seed weight and size properties.

Although pollination treatment did not affect fruit size and weight, the effect of pollination on seed viability have already been reported in Burkina Faso (Lassen et al., 2016). Therefore, effect of pollination on other fruit and seed quality parameters such as fruit pulp and kernel fat composition need to be examined to comprehend the influence of pollination on fruit pulp and fat quality. In some instances, pollination can influence seed production at the expense of fruit pulp. This was observed in water melon where multiple bee visits to pistillate flowers produced fruits with larger number of seeds compared to flowers that were hand pollinated once (Lee et al., 2014). Therefore, in commercial fruit crops like watermelon excessive bee visits to flowers might enhance seed production at the detriment of fruit quality.

5.7 Conclusion

By highlighting the importance of beekeeping for improved pollination of shea, this study contributes to arguments for integration of beekeeping into shea parkland management and adoption of bee-friendly agricultural practices to help conserve pollinators. This should be guided by placing bee colonies at effective distances for optimum pollination benefits. Notwithstanding, further studies are still required to estimate the optimal number of hives per shea parkland area for maximum pollination benefits.

CHAPTER SIX

EFFECT OF PROXIMITY TO MANAGED BEES ON SHEA FLOWER VISITOR DIVERSITY AND VISITATION RATE IN THE GUINEA SAVANNA AGRO-ECOLOGICAL ZONE, GHANA

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6.1 Abstract

The introduction of managed bees into agricultural landscapes is increasingly being adopted as an approach to supplementing insect pollination services. Although this approach is less practised in Africa, beekeeping is adopted as an alternative livelihood activity in rural areas. This study examined the effect of these aggregated honey bee colonies on the diversity and foraging behaviour of other flower visitors of *Vitellaria paradoxa*. Flower visitors were sampled from focal trees at four distance ranges from apiaries in six sites. Insect visitation to tagged inflorescences were also observed for 10-minute periods in the early morning hours 6:00 - 8:30 GMT during peak flowering. Proximity to the apiary was not significantly related to composition, richness nor abundance of other bee visitors of shea flowers. However, the frequency of *Apis mellifera* visitation was significantly predicted by distance to apiary (-0.23 ± 0.067, p = 0.001) whilst no significant relationships were found for other bees (0.010 ± 0.065, p = 0.87). The study concludes that presence of managed bee colonies in shea parklands has a minimal effect on other shea flower visitors. However, further studies are required to investigate the long-term effect of beekeeping on biodiversity of florivorous insects from a landscape perspective.

6.2 Introduction

Pollination is an essential ecosystem service required for the reproductive success of plants in both managed and natural systems (Appiah & Agyei Dwarko, 2013; Potts et al., 2010b). About 94% of tropical plants (Ollerton et al., 2011) and 75% of food crop species (Klein et al., 2007a) depend on some level of insect pollination for fruit/seed set. There are advocates for pollination to be valued as an agricultural input and not just an ecosystem service (Allsopp, de Lange, & Veldtman, 2008). Despite the relevance, pollination service is been threatened by declining pollinator populations, mainly attributed to anthropogenic disturbances (habitat fragmentation and degradation, agriculture, invasive species and fires) (Brown et al., 2016; Dibble et al., 2020; Dicks et al., 2021; Goulson et al., 2015; IPBES, 2016).

These disturbances have reduced pollinator population creating a pollination deficit with reduced fruit/seed yield of insect pollinated plants (Holland et al., 2020; Reilly et al., 2020). This could implications for food production and nutrition, as pollination deficits in major economic crops such as macadamia and shea are already reported in Africa (Delaney et al., 2020; Grass et al., 2018). Pollination deficit is reported for apples in Europe (Osterman, Theodorou, Radzevičiūtė, Schnitker, & Paxton, 2021) and custard apples in Australia (Pritchard & Edwards, 2006). Although major staple crops of the world (rice, wheat, barley and maize) are not insect pollinated (Richards, 2001), insect pollinated plants are rich sources of vitamins and proteins that contribute to human nutrition (Eilers et al., 2011). Pollination service declines therefore have implications on human nutrition. Pollination deficit will equally affect regeneration in natural ecosystems with cascading effects on biodiversity and ecosystem restoration (Biesmeijer et al., 2006; Christmann, 2019).

The decline in pollinator population coupled with increased cultivation of insect pollinator-dependent crops have heightened demand for insect pollination services (Aizen, Garibaldi, Cunningham, & Klein, 2008). Pollination service enhancement practices such as the establishment of wild flower stripes/bee reservoirs in cultivated landscapes (Donoso & Murua, 2021; Venturini, Drummond, Hoshide, Dibble, & Stack, 2017), restrictions on agrochemical use (Pisa et al., 2014), adoption of mechanised/hand pollination services (Gianni & Vania, 2018; Wurz et al., 2021) and introduction of managed bees in cultivated landscapes (Layek et al., 2021) are increasingly being adopted. Although all the practices have some positive effect on pollination enhancement, introduction of managed bees have become the most potent for mitigating pollination deficit (Bommarco et al., 2014; Carreck & Williams, 1998).

In many instances, social insects particularly, honeybees (*Apis mellifera*) are introduced or managed in native regions for pollination services (Viana et al., 2014; Willmer & Finlayson, 2014). Managed honeybees in agricultural landscapes have proven to be effective in mitigating fruit yield decline associated with pollination deficits in apple, oilseed rape, strawberry, watermelon, macadamia and pear (Abrol et al., 2019; Evans et al., 2021; Layek et al., 2021; Stern et al., 2001; Viana et al., 2014). Aside their pollination efficiency, beekeeping is known to be a viable economic activity for poverty alleviation, particularly in Sub-Saharan Africa (Dossou, Adanguidi, Aoudji, & Gbedomon, 2022; Duah et al., 2017). Beekeeping is increasingly being adopted in many parts of Ghana (Duah et al., 2017) as a double-edged sword to improve pollination services and livelihoods in rural areas.

In Agroforestry parklands of Northern Ghana, beekeeping was recommended as a viable option to enhancing pollination of *V. paradoxa* whilst producing honey to supplement household income (Stout et al., 2018). *Vitellaria paradoxa* is a high insect pollinator dependent species (Nasare et al., 2019) mainly pollinated by *Apis mellifera adansonii* and stingless bee species (Kwapong, 2014; Stout et al., 2018). Experimental studies have shown positive effect of bee colony proximity on shea fruit yield in Burkina Faso

(Lassen et al., 2016). This justifies calls for upscaling this approach to address pollen deficit for shea and other insect pollinated plants in parklands.

Notwithstanding the prospect of beekeeping in shea parklands, there are divergent reports on the effect of managed bees on native pollinator population and diversity in other regions (Mallinger, Gaines-Day, & Gratton, 2017; Paini, 2004). About 53% of studies elsewhere have shown negative effects on other wild pollinators, 28% had no effects whilst 14% reported mixed effects (Mallinger et al., 2017). Competition between managed pollinators and native wild species often results in suppression of wild bee population and richness when floral resources are finite (Angelella, McCullough, & O'Rourke, 2021; Aslan, Liang, Galindo, Hill, & Topete, 2016; Thomson, 2004; Wignall et al., 2020).

Resource competition can exacerbate niche overlaps which mainly affect wild pollinator population due to high managed bee densities (Herbertsson, Lindström, Rundlöf, Bommarco, & Smith, 2016; Thomson, 2016). Oligolectic bees are the most vulnerable as specialist foragers are unable to shift floral preferences to avoid competition with honey bees (Roubik & Villanueva-GutiÉrrez, 2009).

Aside direct effects, resource scarcity indirectly increases parasitism of solitary bees (Goodell, 2003), affects native bee colony fitness and performance (Elbgami, Kunin, Hughes, & Biesmeijer, 2014), and results in pathogen and parasite spill over (Dynes, Berry, Delaplane, Brosi, & De Roode, 2019; Fürst, McMahon, Osborne, Paxton, & Brown, 2014). Viruses and other honeybee pathogens are transmitted via pollen to native bees foraging on the same floral hosts (Fürst et al., 2014). In some instances, suppression of foraging activities of other native pollinators result in reduced fruit set (Angelella et al., 2021).

Notwithstanding reports on competitive effects, there are complementary effects of managed bees as well (Abrol et al., 2019; King, Serem, & Russo, 2018; Layek et al., 2021). The introduction of managed stingless bee colonies in watermelon field did not have any effect on the foraging activities of other native pollinators but contributed to improved fruit yield (Layek et al., 2021). In Kenya, honey bee fences did not show any negative effects on population and diversity of other native bees (King et al., 2018). More importantly, Cane & Tepedino (2017) posit there are limited convincing experimental studies demonstrating competitive interactions between honeybee and native bee species. This is mainly due to difficulties in having uniform landscapes with apiaries for replicated field trials, and the difficulties in excluding feral honeybees from experimental fields. Landscape management for instance was found to significantly influence functional diversity of pollinators even in the midst of managed bees (Roquer- et al., 2021).

This highlights the need for landscape specific studies on effect of managed bees on native pollinators. However, despite increasing adoption of beekeeping in SSA, less is still known about the impact of managed bees on other native bees of Africa (but see King et al. 2018). Understanding the effect of managed bees on other native pollinators is particularly important for shea parklands as the pollen deficit in shea (Delaney et al., 2020) has heightened efforts to improve pollination services concomitant with the upsurge in beekeeping as an alternative livelihood in Ghana (Duah et al., 2017). This would guide beekeeping in shea parklands to avoid potential unintended negative outcomes on other bee flower visitors of shea. We hypothesised proximity to apiary to have no effect on composition, diversity, and visitation rate of other shea flower visitors.

6.3.0 Materials and Methods

6.3.1 Study Area

The experiment was conducted in agroforestry parklands of six villages in three regions of northern Ghana from October 2020 to April 2021. The Guinea Savanna has a monomodal rainfall pattern, with the rainy season lasting from April to October, preceded by a dry season. The mean monthly temperature of the area ranges from 27 to 36 ℃ (Darko et al. 2019; Ghansah et al. 2018) but highest temperatures are recorded in the dry season.

The highest relative humidity is recorded in August – September in the rainy season whilst the least humidity is recorded in March-April in the dry season. The vegetation is predominantly grassland interspersed with perennial woody species where shea is the most common native tree species in all landuse (Chimsah et al., 2013). The landuse is characterised by alternating periods of cultivation and bush fallows. However, fallow lands are gradually shrinking due to agricultural extensification. There are also protected forest areas dotted across the Guinea savanna zone.

6.3.2 Site selection

The survey was conducted in shea parklands of communities that participated in the Agriculture and Natural Resources Management beekeeping project. The project was initiated in 2017 where apiaries of 10 beehives were installed in selected sites to provide alternative livelihoods to farmers and contribute to pollinator conservation in northern Ghana. In the current study we selected communities that had apiaries in shea parklands with 6-8 colonised beehives as at August 2020. For each site, shea trees were selected at three different radii away from the apiary (100, 500, and 1000m) and 4000m as control site. Five focal trees of a predetermined size class (DBH; 25-30 cm, Height ≥ 10 m and crown area ≥ 20 m^2) were randomly selected within each radius for flower visitor surveys.

6.3.3 Flower visitor survey

To understand how other flower visitors of shea responded to the apiaries, we observed and sampled flower visitors from focal trees during peak flowering (December to April) in all sites. The frequency of insect visits to five tagged inflorescences were recorded for 10 minutes on each tree in the early morning hours (6 to 8:00 am GMT) during each observation. Flower visitors of shea are most active during the early morning hours (Stout et al. 2018; Delaney et al. 2020). For observation of visitation episodes, flower visitors were categorised into two functional groups thus *Apis melifera* and all other bee visitors (non-Apis). Visitation episodes were therefore recorded separately for each functional group. Observations were done once every fortnight for three months.

Flower visitors were sampled with an extended handle sweep net for 10-minute periods on each tree between 6:00 to 8: 00 am GMT. Insect surveys were conducted once every fortnight during peak flowering. All sampled insect specimen were temporally stored in vials containing 70% ethanol and brought to Insect Museum of the Department of Conservation Biology and Entomology, University of Cape Coast for mounting and identification by a bee taxonomist. Specimens were identified to genus or species based on the available taxonomic keys.

6.3.4 Data analysis

To predict flower visitor community response to apiary proximity we ran a model using the Constrained Correspondence Analysis (CCA). This enables an assessment of data with several dimensions in one model. To visualize flower visitor communities in different distances and regions, an ordination (NMDS) was done using the function metaMDS in the vegan package (Oksanen et al., 2022). NMDS are suitable ordination methods for representing ecological communities without the linear constraints associated with other ordination methods (Jenerette et al., 2016). Other bee flower visitor abundance and richness were predicted using a GLMM in which distance was a fixed effect and region as a random effect.

For visitation, linear mixed effect models were run for the effect of distance on flower visitation frequency in separate models for *A. mellifera* and other bees. Linear Mixed effect models were run with the glmmTMB function in the glmmTMB package (Brooks et al., 2017). Model fittness was assesssed based on residual plots (Appendix D) using the DHARMa package in R programming(Hartig, 2022). All analysis were carried out in the R Core Team (2021).

6.4.0 Results

6.4.1 *Vitellaria paradoxa* flower visitor community structure

A total of 197 bee specimens were sampled from shea flowers representing 7 morphospecies; *Apis mellifera*, *Hypotrigona gribodoi*, *Xylocopa caffra*, *Thyreus ramosus*, *Lipotriches orientalis*, *Amegilla calens*, *and Lithurgus pullatus*. Specimens belonged to three families (Apidae, Halictidae, Megachilidae), however, majority (90%) of the specimens were from the family Apidae. The Constrained Correspondence Analysis did not show any significant effect of distance ($F_{3, 20}$ =1.153, p = 0.344) nor region ($F_{2, 20}$ =1.153, p = 0.427) on flower visitor community structure. The NMDS revealed significant overlap in the flower visitor community of the four distances as well as the three regions (Figure 6.1 and 6.2)

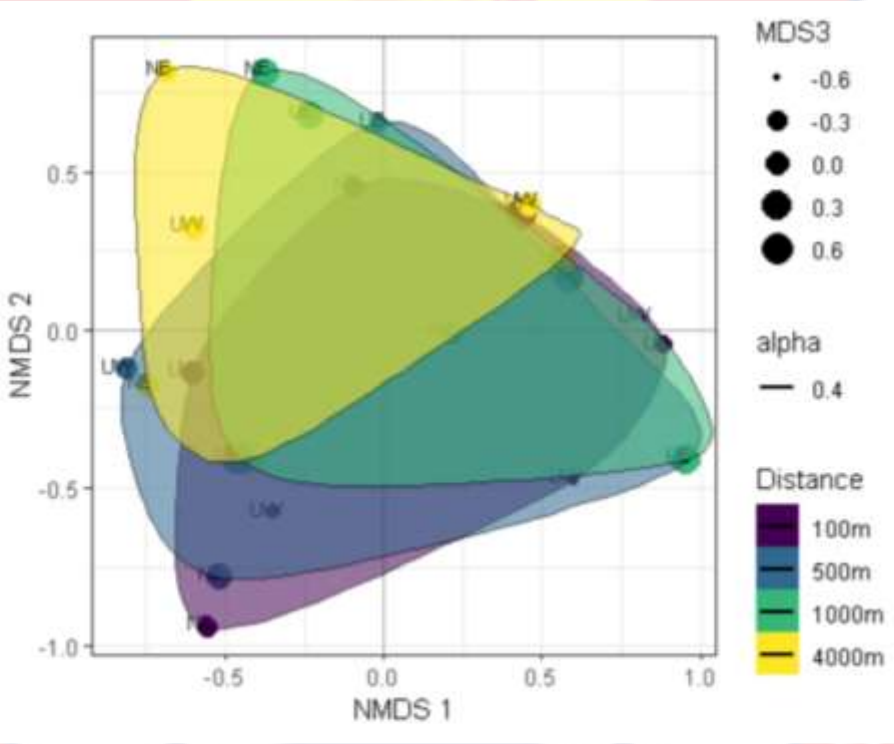

Figure 6. 1: A non-metric dimensional–scaling (NMDS) plot *V. paradoxa* flower visitor community structure of the four distances. UE =Upper East, UW= Upper West, NE = North East.

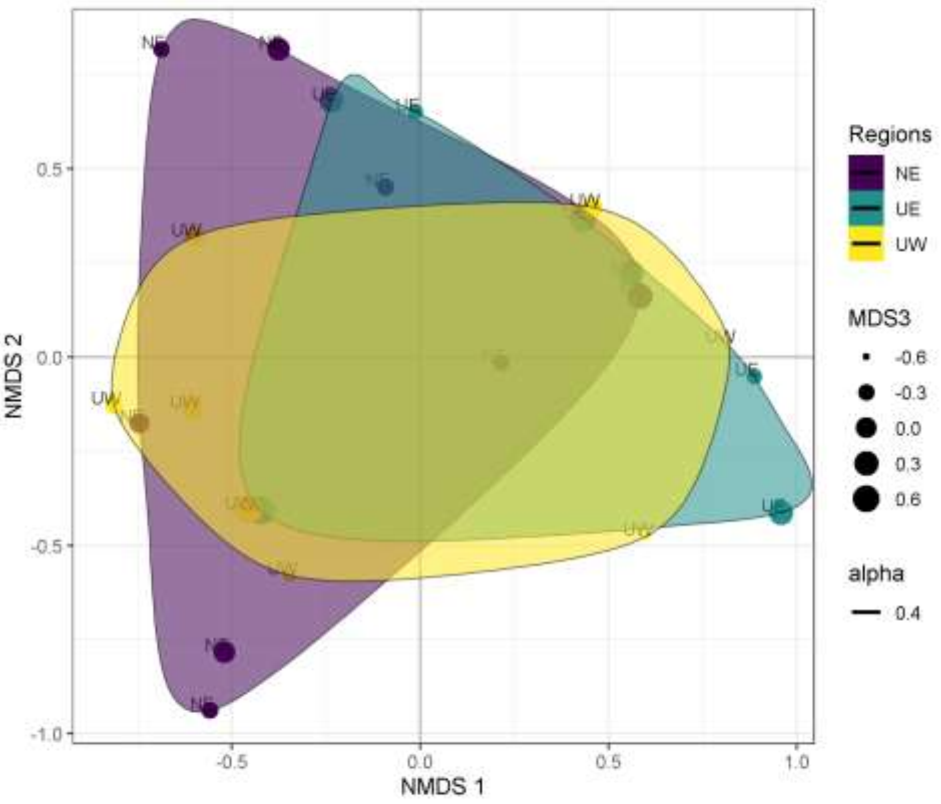

Figure 6. 2: A non-metric dimensional–scaling (NMDS) plot of flower visitor community structure of the three regions. UE =Upper East, UW= Upper West, NE = North East.

6.4.2 Effect of proximity to apiary on other bee flower visitor community structure and visitation

The richness of other bee flower visitors of shea was not predicted by distance (-0.036 ± 0.134, *p* = 0.787). Similarly other bee flower visitor abundance was not significantly influenced by the distance (0.02286 ± 0.10693, *p* = 0.831). Visualization of the NMDS plot showed an overlap of other bee flower visitor communities between distances (Figure 6.3). The stress of the ordination was estimated at 0.155 which represents a good ordination. The frequency of other bee visits was not significantly influenced by proximity to the apiary (0.010 + 0.065, *p* = 0.872).

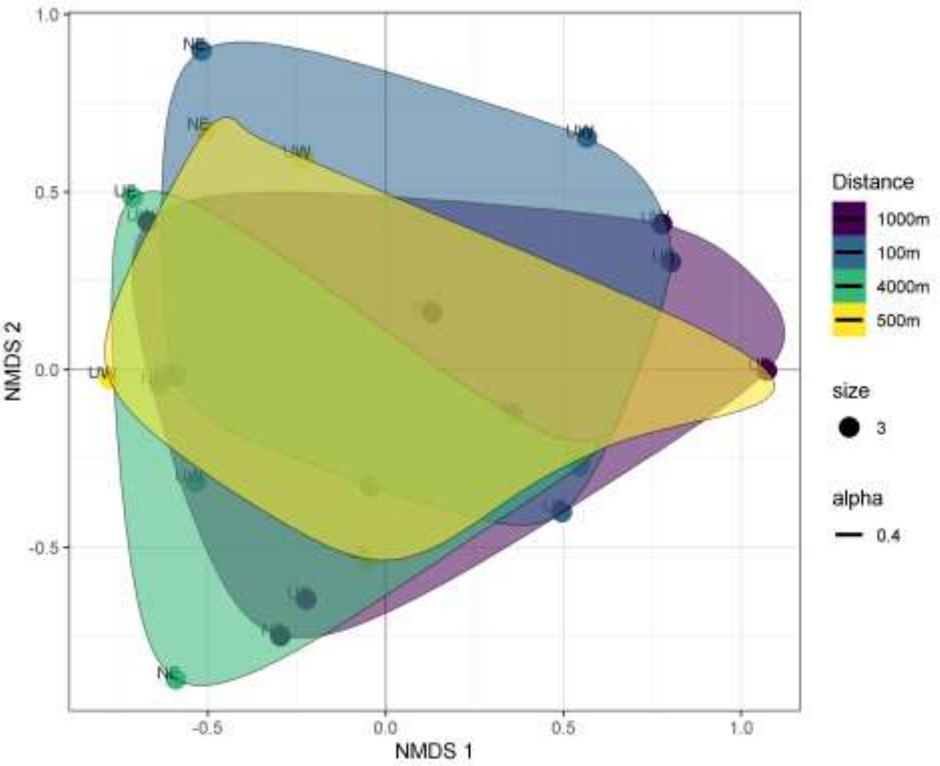

Figure 6. 3: A non-metric dimensional–scaling (NMDS) plot of other bee flower visitor community structure across four distances. UE =Upper East, UW= Upper West, NE = North East.

6.4.3 Effect of apiary proximity on *Apis mellifera* abundance and flower visitation frequency

Apis mellifera abundance was significantly related to distance from the apiary (-0.194 ± 0.0806, *p* = 0.016) where abundance of *A. mellifera* was significantly higher within a 100m range from the apiary than the control (figure 6.4). Similarly, frequency of *A. mellifera* visitation frequency was also related to distance (-0.23 ± 0.067, *p* = 0.00036) where trees located at 100 and 500m from the apiary had significantly higher visitation frequencies of 0.72 visits and 0.67 visits than the 1000m and control that recorded 0.41 and 0.37 visits respectively.

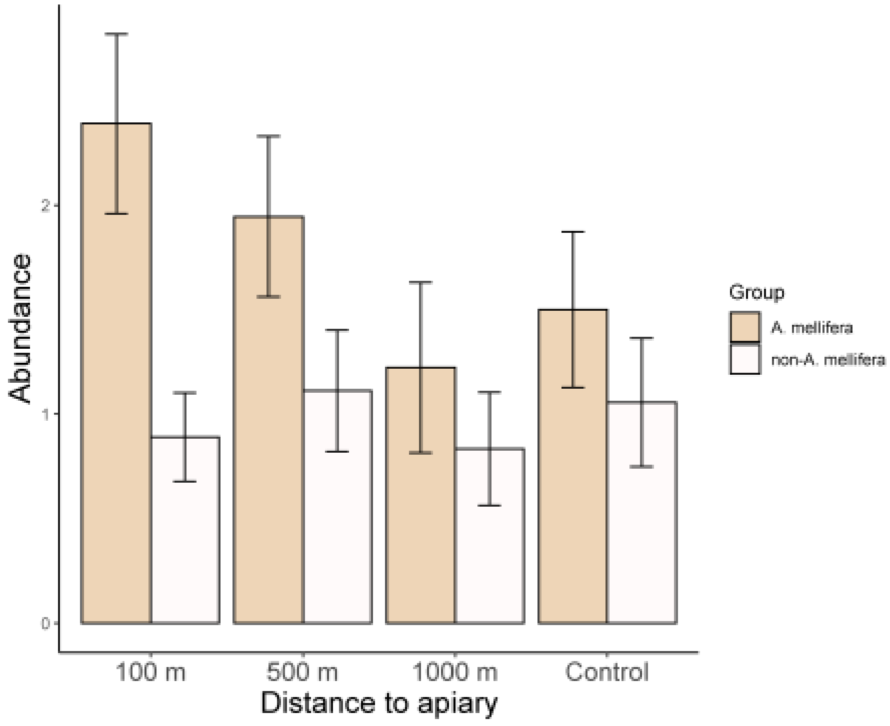

Figure 6. 4: Mean abundance of shea flower visitors per sampling day

6.5 Discussions

The dominance of Apidae among shea flower visitors corroborates with earlier studies conducted in Kenya (King et al., 2018; Mwangi et al., 2012). The findings of this study suggest the introduction of managed bees (*Apis mellifera*) into shea parklands does not have any significant impact on native flower visitor community. The ordination revealed other bee visitor community structure did not change with proximity to the apiary. This implies managed bees can be incorporated into shea parklands without distorting the native bee community. Non-significant effect of managed bees on native pollinators have been reported in other parts of Africa including Kenya (King et al., 2018), South Africa (Brand, 2009) and Sudan(El Shafie, Mogga, & Basedow, 2002). This relationship has also been reported in both agroecosystems et (Layek et al., 2021)) and natural landscapes(Reverté et al., 2019).

Notwithstanding the non-significant effect of managed bees on wild pollinators reported in this study, many studies have shown negative effects of managed bees on native pollinators in protected areas (Lázaro et al., 2021), agroecosystems (Lindström, Herbertsson, Rundlöf, Bommarco, & Henrik, 2016) and even urban landscapes (Ropars, Dajoz, Fontaine, Muratet, & Geslin, 2019). Many of these studies reported exploitative competition between honey bees and native bees for pollen and nectar resources. According Mallinger et al. (2017), the effect depends on whether the managed bees are native or introduced.

Landscape context also influences the interaction between managed bees and other native bees, which could have contributed to the non-detectable effect recorded in this study. This argument is supported by Herbertsson et al. (2016) observation of differential impact of managed honeybees on bumblebee density in homogenous and heterogeneous landscapes. Heterogeneous landscapes mitigates the impact of honey bee densities on native pollinators due to high diversity of floral resources (Herbertsson et al., 2016) . In the present study, diversity of other tree species on shea parklands might have mitigated the impact of managed *A. mellifera* on other bees, accounting for the insignificant effect. This is also buttressed by the positive effect of woody species diversity on pollinators and pollination of shea in agroforestry parklands (Delaney et al., 2020).

Moreso, shea is the most abundant economic tree in the Guinea Savanna zone of Ghana (Chimsah et al., 2013; Tom-Dery et al., 2013). The tree exhibits a mass flowering with relatively short flowering period (Okullo, 2004). This mass flowering perhaps provided sufficient pollen and nectar resources for all flower visitors which eliminated any chances of competition.

Another plausible reason for this non-detectable effect of managed bees on native flower visitors of shea might be low hive stocking densities in the present study. In South Africa, stocking density below 8 ha $^{-1}$ did not yield any unnatural honey bee densities above the natural bee population (Brand, 2009). This did not show any effect on native pollinator communities. The stocking density in this study ranged from 6 to 8 hives per parkland. These densities might be within the natural bee density of the shea landscape and perhaps did not trigger any competitive interactions. Future studies should consider an assessment of bee densities before and after installation of beehives to establish thresholds of carrying capacities. According to Lazaro (2021) insufficient gradient of variation in beekeeping intensity/bee diversity may not yield any significant effect of managed bees on native pollinators. Larger areas are required to create sufficient variability gradients for detectable effect, perhaps, the 3 - 4 km radius used in this study was not large enough to create a variability gradient.

The non-significant effect of managed bees on native pollinator abundance and richness recorded in this study have a limited interpretation as the fitness of small bees (stingless bees) can be affected without changes in their abundance (Elbgami et al., 2014). There is a direct relationship between adult bee size and the amount of pollen consumed by the larva (Bosch & Vicens, 2002). In some instances other native bees resort to the production of smaller worker in response to limited pollen/nectar resources in landscapes in response to higher *A. mellifera* densities (Elbgami et al., 2014; Goulson &

Sparrow, 2009). Similarly, Elbgami et al. (2014) revealed a negative relationship between bumble bee colony fitness and proximity to apiaries. These aspects were not considered in this study and therefore might have been overlooked. Further studies are therefore required to unravel the link between managed bees and native flower visitors of shea.

For *A. mellifera*, increasing proximity to the apiary was associated with increased visitation and abundance. Honeybees would forage on floral resources at closer proximity to hives to maximise energy use efficiency (Esch & Burns, 1996). This trend points to a potential for increasing pollen dissemination without jeopardizing native pollinator biodiversity in shea parklands. This finding however, contradicts that of Ropars et al. (2019) who reported higher visits in flowers further away from the hives than flowers closer to the hives. Honeybees have long flight distance and are known to forage further away from the hive to avoid competition

The study sought to test the effect of managed bees on shea flower visitors by observing flower visitors at different distant ranges to the apiary. The findings of this study show there is no effect of managed bees on richness and abundance of other bees. This could be good news for beekeepers and farmers for enhancing pollination services for shea without any effect on biodiversity. However, further studies, spanning longer period with larger spatial coverage would help unveil the effect of managed bees from a landscape perspective. Moreso a landscape wide assessment of the link between managed bees and native pollinators in shea parklands is required as this study was limited to flower visitors

6.7 Conclusion

The data of this study suggest there are no statistically significant effects of beekeeping on the composition, diversity and visitation frequency of other shea flower visitors. It is most likely the honey bee densities are still within the natural range. Perhaps the abundance of forage during the flowering period of shea eliminated competition. Further investigations are therefore required to ascertain the effect of beekeeping on florivorous insects from a landscape perspective over a longer term.

CHAPTER SEVEN

INFLUENCE OF CLIMATIC FACTORS ON VISITATION AND DIVERSITY OF SHEA (*VITELLARIA PARADOXA*) FLOWER VISITORS

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7.1 Abstract

Ectothermic animals are known to be sensitive to climatic changes but less is still known about the response of shea flower visitors to climate. The present study examined the effect of climatic conditions on the composition, diversity and foraging activities of shea flower visitors in six sites across three regions. Shea flower visitors were sampled with sweep nets together with the observation of visitation frequencies to tagged flowers. Temperature, relative humidity and wind speed were recorded in situ with a hand held-anemometer during field surveys. Climatic factors did not explain the composition and richness of shea flower visitors but flower visitor abundance was significantly related to temperature ($\beta = -0.43 \pm 0.13$, $p = 0.001$). Wind speed was significantly related to visit frequency of *Apis mellifera* (-1,490.37, p=0.001), but not other bees. Climatic factors significantly influence abundance and visitation, but the effect of climatic factors on shea flower-visitor composition and richness is minimal.

7.2 Introduction

Global climate change is predicted to have devastating effects on biodiversity and natural ecosystems around the world (Chapungu & Nhamo, 2016; IPCC, 2022; Weiskopf et al., 2020; Zaragoza-Trello, Vilà, Botías, & Bartomeus, 2021) but the impacts might be more severe on insect pollinators as ectothermic animals respond to small scale changes in climatic events (Willmer & Stone, 2004; Willmer & Unwin, 1981). In the last century, extreme weather events (floods, droughts, heat waves, winds) have become more frequent (IPCC, 2022). Global temperature has had an average rise of 0.7 °C over the last century and is expected to increase by an average of 1.1 to 6.4 °C by the end of the 21st century (IPCC, 2013, 2014b). Rise in temperature occurs along with increased precipitation at higher altitudes and decreased precipitation at lower altitudes (IPCC, 2014a).

These changes have heightened the concerns on pollinator population declines (Goulson et al., 2015). Long or short-term changes in climate events will influence pollinator activity, community composition, and diversity (Halsch et al., 2021). Increasing precipitation patterns will disrupt flight and increase flight energy cost as higher efforts are needed for flight during precipitation (Lawson & Rands, 2019). Change in climatic events can change pollinator behaviour as well, honey bees tend to forage for shorter periods during high winds (Brittain, Kremen, & Klein, 2013). In Tanzania, mean annual temperature has been found to have a significant impact on the specialisation of pollinator communities (Classen et al., 2020). Pollinator activity is known to be affected indirectly by change in ambient temperature (Arroyo, Primack, & Armesto, 1982). Aside the main effect of climate on pollinators, climate interactions with existing stressors (land use, pesticides, and invasive species) tend to exacerbate the impacts (Dicks et al., 2021; Ganuza et al., 2022). For example, the interaction between climate and land use altered the composition and diversity of pollinator communities

Although impact of climate on pollinators are often focused on direct impacts, there are also indirect impacts arising from plant-pollinator interactions. Timing of plant flowering is synchronised with pollinator activity to facilitate mutual interactions (Miller-Rushing et al., 2010), but extreme climatic events such as temperature, will shift flowering times and disrupt the synchrony (Chauhan et al., 2019; Jarrod et al., 2021; Kubov et al., 2022). Phenological shifts are known to affect pollinator activity and abundance (Gerard, Vanderplanck, Wood, & Michez, 2020; Tsiftsis & Djordjevic, 2020). Phenological shifts towards rainy season flowering will equally impact negatively on pollinator visitation due to nectar dilution for some plants (Villarreal & Freeman, 1990; Whitney et al., 2011). Under high temperatures, flower development tends to be rapid which reduces flower longevity affecting flower resource availability for pollinators (Arroyo et al., 2020).

Floral rewards are critical to pollinator attraction but drought-induced water stress in plants result in the production of smaller flowers with poor nectar quality and quantity (Fenster, Cheely, Dudash, & Reynolds, 2006; Gallagher & Campbell, 2017). On the contrary, severe drought seasons were found to be associated with high nectar concentration in the Mediteranean (Arroyo et al., 2020). Change in nectar quality will reduce insect attraction to flowers.

Although climate change impacts are projected to intensify around the world, vulnerabilities will be regionally unique. According to IPCC (2022), Western and Southern Africa are projected to have erratic rainfall patterns with frequent droughts whilst East Africa will have frequent floods. Temperature rise will affect biodiversity and contribute significantly to desertification in semi-arid areas and sea level rise in coastal areas. Although Africa contributed the least global emissions (IPCC, 2022), it is the most vulnerable to global change impacts (IPCC, 2014a). Aside high vulnerability of Africa's rainfed agriculture to climate change (Beillouin, Schauberger, Bastos, Ciais, & Makowski, 2018; Tacoli, 2011), major export products of the continent including cocoa, coffee, cashew, oil palm, and shea are insect pollinated (IPBES, 2017; Kwapong, 2014; Rodger, Balkwill, & Gemmill, 2004). Climate change associated impacts on pollinators will therefore affect African exports as well (Banda, Madamba, & Gumbo, 2021)

Although the long-term effects of climate change on pollinators have been projected (Arroyo et al., 2020; Lawson & Rands, 2019), pollinators respond to interannual and seasonal climate variability as well (Memmott, Craze, Waser, & Price, 2007). Therefore, pollinator response to intra-seasonal variability in climate may be overlooked in long-term studies. Savanna biomes are particularly known to be sensitive to climatic stresses (Bond et al., 2003; Sala et al., 2000). Intra-seasonal climate variability effect on pollinators of economic fruit trees like shea will be essential for climate mitigation and pollinator habitat enhancement. Shea is an insect pollinated plant that occurs naturally in arid and semi-arid areas of SSA.

Shea fruit set is highly dependent on insect pollination (Nasare et al. 2019). Although there are diverse flower visitors, honey bees and stingless bees are the primary pollinators (Kwapong, 2014; Lassen et al., 2016; Stout et al., 2018). Shea is recently reported to be pollen limited (Delaney et al., 2020) and factors accounting for pollination deficit are often attributed to pollinator habitat degradation and agriculture activities. Despite the evidence of climate effect on pollinator activities and abundance elsewhere (Arroyo et al., 2020; Banda et al., 2021; Classen et al., 2020) to the best of our knowledge, no study has examined the impact of climatic factors on shea flower visitors. To address this knowledge gap, we adopted the alternative hypothesis that, climatic factors have some effect on shea flower visitor activity, abundance and richness. We specifically tested 1) the effect of climatic factors on the abundance of shea flower visitors, 2) the effect of climatic factors on flower visitor species richness and diversity and 3) the effect of climatic factors on the visitation rates of shea flower visitors.

7.3.0 Materials and Methods

7.3.1 Study Area

The study was conducted in shea parklands of six villages in the Guinea savanna zone of Ghana. Field surveys were conducted for the 2020/2021 shea flowering season from November 2020 to April 2021. The Guinea savanna is the dominant agro-ecological zone predominantly found in Northern Ghana. The area is characterised by a monomodal rainfall pattern where rains are recorded from April to October each year with a mean annual rainfall of about 1034 mm. Monthly mean temperature of the area ranges between 27 and 35°C but highest temperatures are recorded in the dry season (Darko et al. 2019; Ghansah et al. 2018). Maximum relative humidity of the area occurs in August/September whilst the least is recorded in March-April in the dry season. The low humidity coupled with the harmattan winds predisposes the savanna to frequent bushfires in the dry season.

Grassland interspersed with discontinuous layers of tree canopy is the dominant vegetation in the area. The landuse is characterised by alternating periods of cultivation and bush fallows. Farmers in this area retain and manage indigenous economic tree species on farmlands under which annual crops are cultivated in a form of traditional agroforestry system. Agriculture is the largest landuse, but there are also patches of wild bushes and protected forest areas dotted across the savanna. Among the common woody species in the area are *Vitellaria paradoxa, Vitex doniana, Ptericarpus erinaeceus, Diospyros mespilliformis, Adansonia digitata.* However, there are also exotic species such as *Azadiracta indica*, *Mangifera indica*, *Senna siamea*, *Tectona grandis* plantations and avenue planting in the landscape

7.3.2 Site selection

The experiment was conducted in shea parklands that had apiaries in three regions of Northern Ghana (Upper West, Upper East and North East). For each region, shea parkands of two villages were selected for the experiment, thus a total of six sites. For each region sites that had a predetermined number (6 - 8) of colonised hives. We stratified each apiary parkland into three distant ranges of proximity to the hive (100 m, 500 m, 1000 m) and control site (3 – 4 km) away from the apiary. These distances were established to control for proximity of tree to apiary effect on foraging activities and abundance. In each radius, five shea trees were randomly selected for flower visitor surveys.

7.3.3 Flower visitor survey

To understand how flower visitors of shea respond to climatic factors in the shea parkland, we observed and sampled flower visitors from focal trees during peak flowering in all sites. The frequency of insect visits to five tagged inflorescences were recorded for 10 minutes on each tree in the early morning hours (6 to 8:00 am GMT) during each observation. Flower visitors of shea are most active during the early morning hours (Stout et al. 2018; Delaney et al. 2020). Flower visitors were categorised into two functional groups thus *Apis melifera* and other bees. Visitation episodes were therefore recorded separately for each functional group.

We sampled flower visitors from focal trees with an extended handle sweep net for 10-minute periods from 6:00 to 8: 30 GMT. Observations of visitation and insect sampling were done on different days to avoid interference of visitation episodes. Insect surveys were conducted once every fortnight with a total of six surveys per tree per site. All sampled insect specimen were temporally stored in vials containing 70% ethanol and labelled appropriately (site name, date, time, collector name and trapping method). The specimens were sent to the Insect Museum of the Department of Conservation Biology and Entomology, University of Cape Coast for identification by a bee taxonomist. Specimens were identified to genus or species based on the available taxonomic keys.

7.3.4 Data analysis

To predict flower visitor community response to climatic factors, a model was ran using the Constrained Correspondence Analysis (CCA). This enables an assessment of data with several dimensions in one model. The model was then plotted to visualize the linear relationship between flower visitor community and climatic factors. To examine the relationship between climatic factors and flower visitor abundance/richness, a Generalized Linear mixed effect model was fitted where insect abundance/richness was a response variable predicted by the fixed effects of climatic factors (Temperature, Relative Humidity and Wind Speed) and region as a random factor using a gaussian distribution. Model fitness was checked based on the residual plots using the the DHARMa package in R programming (Hartig, 2022). Similarly, GLMM were fitted for the relationship between climatic factors and frequency of flower visits. Visitation of *Apis mellifera* and other bees were fitted in separate models (Brooks et al., 2017). All analysis were run in R Core Team (2021).

7.4 Results

7.4.1 Effect of climatic factors on *V. paradoxa* flower visitor community

The CCA suggests that all climatic variables assessed in this study were not related to shea flower community composition ($F_{3,\ 59} = 1.32$, $p = 0.16$). The visualization of the CCA did not show any linear associations between wind speed (WS), temperature (Temp.) nor relative humidity (RH) and the occurrence of flower visitors (Figure 7.1).

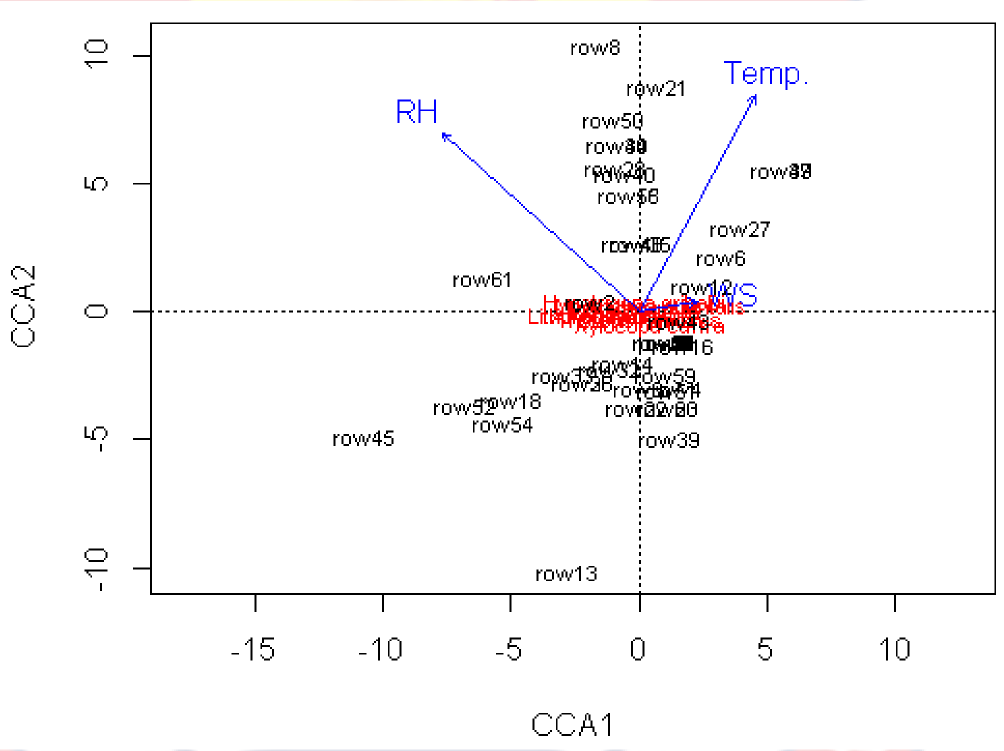

Figure 7. 1: Constrained correspondence analysis (CCA) of the climatic factors (blue) and all bee flower visitors found (red).

7.4.2 Effect of climatic factors on richness and abundance of flower visitors

The analysis was aimed at predicting the richness and abundance of flowers visitors based on climatic conditions. The model did not show any significant association between climatic factors and flower visitor richness. However, flower visitor abundance was significantly related to Temperature (β

= - 0.43± 0.13, p = 0.001) (Table 1). The aggregation of data from all three regions showed an inverse relationship between temperature and Abundance but flower visitor abundance association with climatic variables tended to be unique to each region (Figure 7.2).

Table 7. 1: GLMM for shea flower visitor abundance and climate

	Climatic factors	β	*SEβ*	Wald Chi-square	95% C. I Lower	 Upper	*P* value
Richness							
	(Intercept)	5.29	2.28	2.31	0.81	9.77	0.0201*
	Temp.	-0.08	0.07	-1.17	-0.21	0.053	0.24
	RH	-0.01	0.007	-1.47	-0.02	0.0032	0.14
	WS	-0.82	0.42	-1.93	-1.66	0.011	0.05
Abundance							
	(Intercept)	18.84	4.57	4.12	9.89	27.79	0.001**
	Temp.	-0.43	0.13	-3.38	-0.68	-0.18	0.001**
	RH	-0.03	0.02	-1.82	-0.07	0.001	0.069
	WS	-1.14	0.73	-1.56	-2.56	0.29	0.12

*β = Beta, SEβ =standard error of Beta, ** = significance at 1%, significant at 5%*

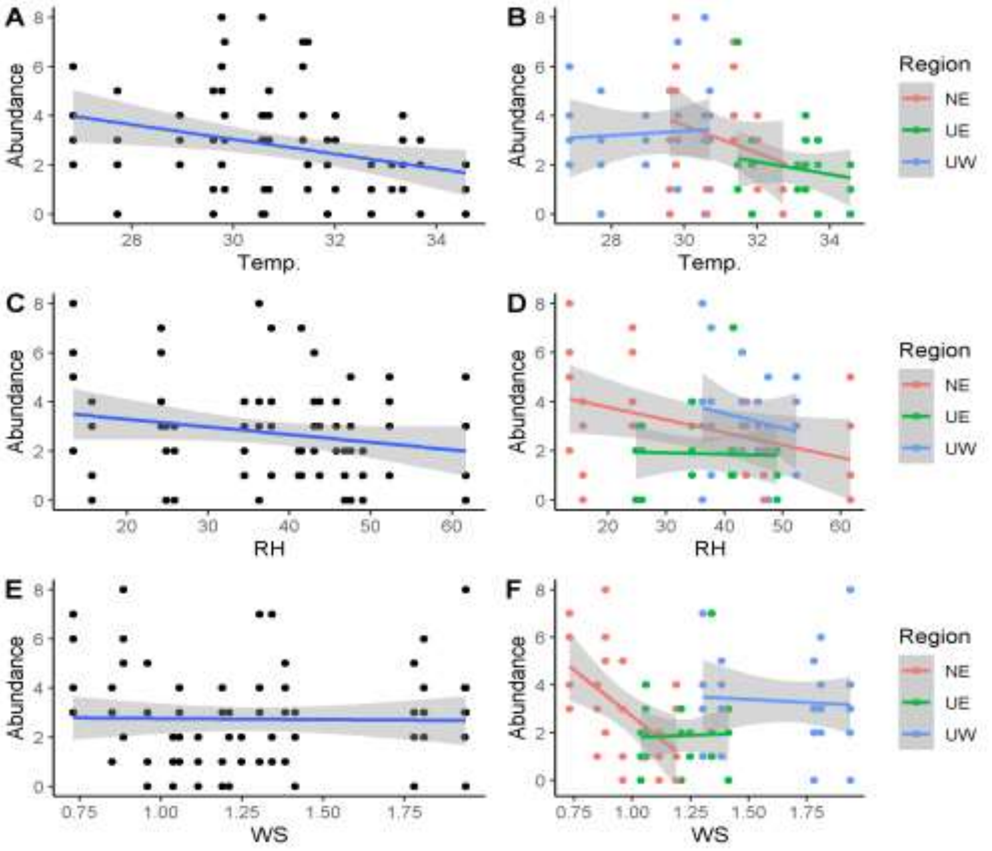

Figure 7. 2: Relationship between climatic factors and insect abundance. A = aggregated temperature and abundance, B= temperature and abundance by regions, C= aggregated Relative humidity and abundance, D = RH and abundance by region, E = aggregated WS and abundance, F= WS and abundance by region.

7.4.3 Effect of proximity to apiary on flower visitation frequency

The frequency of other bee visits was not significantly explained by any climatic factor. On the contrary, A. *mellifera* visitation was significantly related to wind speed (-1.49±0.37, *p* = 0.001) but not Relative humidity nor Temperature (Table 7.2; Figure 7.3).

Table 7. 2: GLMM for the relationship between climatic factors and visitation frequency

	Climatic factors	**Estimate**	**SE**	**Wald Chi-square**	**p value**
Non- Apis					
	(Intercept)	1.91	1.83	1.045	0.29
	Temp.	-0.07	0.05	-1.26	0.21
	RH	0.004	0.01	0.65	0.52
	WS	-0.5	0.29	-1.72	0.086
Apis mellifera					
	(Intercept)	2.15	2.22	0.97	0.33
	Temp.	-0.05	0.07	-0.81	0.42
	RH	0.011	0.006	1.79	0.074
	WS	-1.49	0.37	-3.98	0.001

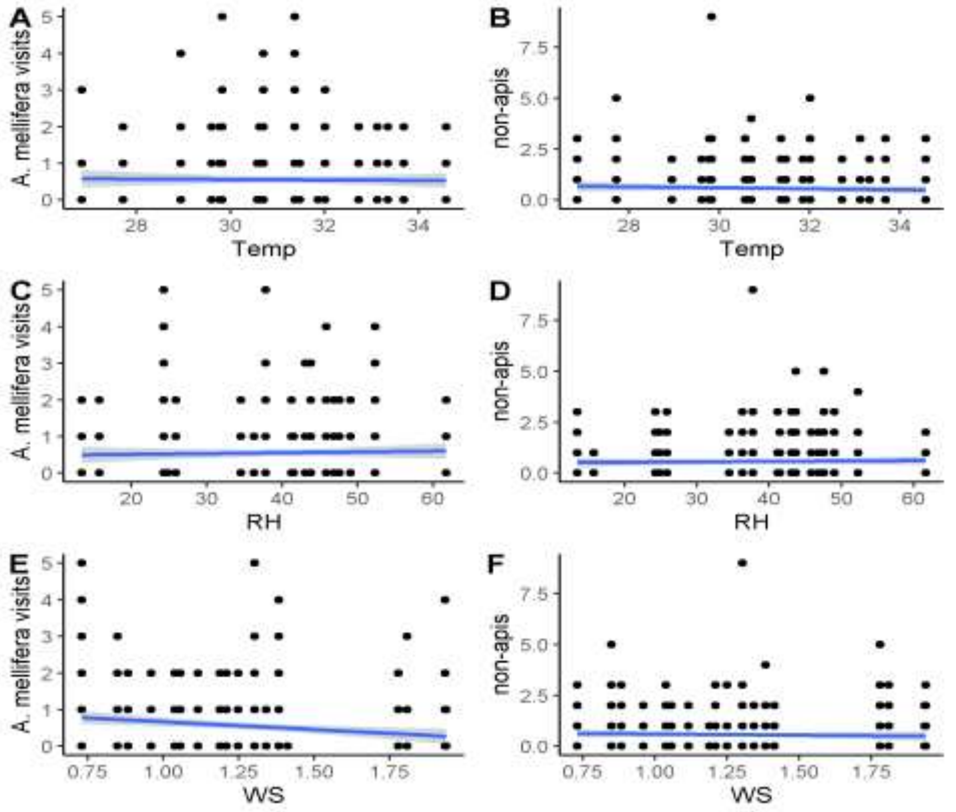

Figure 7. 3: Scatterplots of climatic factors and visitation frequency of *A. mellifera* and other bees (non-apis). A = temperature and *A. mellifera* visits, B= temperature and non-apis visits, A = relative humidity and *A. mellifera* visits, B= relative humidity and non-apis visits, A = wind speed and *A. mellifera* visits, B= wind speed and non-apis visits

7.5 Discussion

The insignificant association between climatic factors and flower visitor community composition implies shea flower visitor community is not determined by climatic conditions but some other factors in the shea parkland. A possible explanation for this relationship is the confounding effect of floral resource diversity and nesting sites. Floral resources and availability of nesting sites are key determinants of wild bee populations (Smith, Warren, Thompson, & Gaston, 2006). In the Forest Savanna Transition zone of Ghana, bee diversity was found to be associated with flowering plant diversity in cultivated landscapes (Boadu, 2016). In Burkina Faso, tree diversity in shea landscape was significantly correlated with pollinator diversity and visitation. Therefore, the confounding effect of floral resources and availability of nesting sites might have influenced flower visitor composition recorded in this study (Delaney et al., 2020).

Landuse and land management practices is another factor known to influence pollinator communities (Ganuza et al., 2022). Agricutural extensification and intensification has reduced fallow lands coupled with increased use of pesticides, creating homogenous agricultural landscapes. This exposes beneficial insects to hazardous chemicals used in annual crop cultivation. However, the effect of agricultural landuse on flower visitor communities is still largely unknown. Studies elsewhere have revealed negative effects of landuse and land management practices on pollinators (Ganuza et al., 2022; Ropars et al., 2019). Although the experiment was conducted in the dry season, the residual effect of these agrochemicals on pollinators could have influenced flower visitor communities.

The insignificant relationship between climatic conditions and flower visitor composition can possibly be explained by the dominance of *A. mellifera* in the landscape. *Apis mellifera* is recorded as the most dominant flower visitor in shea parklands (Lassen et al., 2016). Aside shea parklands, *A. mellifera* has been reported as the dominant bee species in the Forest Savanna Transition zone of Ghana (Boadu, 2016). *Apis mellifera* exhibits a polylectic foraging behavior and known to be well adapted to a wide range of climatic conditions. *A. mellifera* dominance in the bee fauna of Ghana could have eclipsed any detectable effect of climate on flower visitor composition.

Moreso, all study sites were located in the same agro-ecological zone with similar trends in monthly weather conditions. There was perhaps no sharp difference in geographic gradient to account for any detectable effect of climate on flower visitor composition. Another possible explanation is the short sampling duration (three months), which might be too short to reveal any trend in climate variability for a detectable effect on flower visitor community.

Notwithstanding the insignificant effects on flower visitor community, flower visitor abundance was significantly related to temperature. This relationship was not surprising in ectothermic animals as temperature determines the costs of foraging flight (Willmer & Stone, 2004; Willmer & Unwin, 1981). In Tanzania, temperature was found to be significantly related to specialisation in pollinator communities (Classen et al., 2020). According to Inouye (2008), optimal foraging activity occurs on sunny days with low wind speed and intermediate temperatures. The findings of Inouye(2008) are in concordance with this study since an inverse relationship between abundance and temperature was detected. One possible explanation for the negative effect of temperature on abundance is reduced flower attractiveness under warmer conditions (Descamps, Jambrek, Quinet, & Jacquemart, 2021).

Flower visitation by *A. mellifera* was found to be significantly related to wind speed which is in concordance with earlier studies (Combes & Dudley, 2009; Hennessy et al., 2020, 2021). Wind poses a challenge to insects in flight due to turbulence associated with strong winds (Combes & Dudley, 2009). Bees lower their hindlegs to attain stability during strong winds which increases energy expenditure during flight (Combes & Dudley, 2009). Increasing wind speed increases take-off hesitation in bees as well (Hennessy et al., 2020). Aside the direct effect, strong winds make flowers sway thereby making landing and take-off difficult for bees (de Langre, 2008). These effects on insect flight and foraging accounted for the inverse relationship between *A. meliferra* visitation and wind speed. Notwithstanding the inverse relationship between wind and visitation of *A. mellifera* recorded in this study, Crall et al. (2020) found a direct association between wind speed and visitation to orchids. Their findings were attributed to the role of wind turbulence in dispersing attractive odours through diffusion.

Conclusion

The climatic factors did not structure flower visitor community composition between regions but abundance is significantly influenced by temperature. Visitation rate of *Apis mellifera* was significantly related to wind speed. Notwithstanding flower visitor richness was not significantly related to climatic factors.

CHAPTER EIGHT

ALTERNATIVE FORAGE FOR SHEA (*VITELLARIA PARADOXA*) FLOWER VISITORS IN NORTHERN GHANA

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8.1 Abstract

Shea is known to rely heavily on insect pollinators for fruit set but the pollinators depend on many other plants for nectar and pollen especially when shea is not in bloom. These plants are essential to providing forage for shea pollinators all year round. The present study examined the floral calendar of plants foraged by florivorous insects in shea parklands through a monthly survey of plants and their flower visitors from January 2021 to December 2021. A total of 32 plant species belonging to 13 plant families were identified to be visited by florivorous insects. Leguminosae family had the highest abundance of flowering plants. Plants flowering were most abundant in the dry season, and the largest number of plants flowering was recorded in May. Over two thirds of plants flowering in shea parklands were visited by the primary pollinators of shea (bees). Considering the high diversity of melliferous plants, pollinator habitat restoration strategies should incorporate the planting and conservation of melliferous plants in to shea parklands.

8.2 Introduction

Insect pollination is an essential ecosystem service required for fruit/seed set in about 94% of tropical plants(Ollerton et al., 2011). The global economic value of insect pollination services was estimated at €153 billion representing 9.5% of global human food production in 2005(Losey & Vaughan, 2006). Insect pollinated plants are also economically valuable than non-insect pollinated crops, as a ton of insect pollinated crop is worth €761 whilst a non-pollinator dependent crops is averagely €151 (Gallai et al., 2009). Economic fruit and nut crops including apple, watermelon, cocoa, coffee, and shea are insect pollinator dependent (Burns & Stanley, 2022; Delaney et al., 2020; Khalifa et al., 2021).

Notwithstanding the value of pollination, there are increasing reports of pollinator population decline (Brown et al., 2016; Dibble et al., 2020; Dicks et al., 2021; IPBES, 2016). On the contrary, Aizen et al. (2008) postulate there is no shortfall in pollination but an increased cultivation of insect-pollinated plants. In both cases, however, there is limited pollination services which is evident in plants such as macadamia, apple, cocoa, and shea (Delaney et al., 2020; Grass et al., 2018; Osterman et al., 2021; Pritchard & Edwards, 2006). To mitigate pollinator decline, Gemmill-Herren et al. (2014) emphasized documentation of insect-pollinated plants and their pollinator dependencies as a first step but such studies have generally been anthropocentric and focused mainly on economic plants. Economic plants of every landscape bloom for a few months, but pollinators forage on many other plants for the rest of the year. A systems thinking approach encompassing all year-round floral forage of pollinators would be relevant for sustainable pollinator conservation.

About one third of described insects are known to depend directly or indirectly on floral resources for food (Wardhaugh, 2015). The density and distributions of plants flowering in a landscape is associated with colony size in the case of honeybees (Baden-Böhm, Thiele, & Dauber, 2022; Essenberg, 2012). For honeybees, lack of floral resources affects foraging behaviour (Decourtye, Mader, & Desneux, 2010; Naug, 2009) which exacerbates the impact of other stressors such as pathogens, pests, predators and climate (P. Neumann & Carreck, 2010; Potts et al., 2010b). Limited forage resources in agricultural landscape have been the main driver of bee colony declines in cultivated lands (Decourtye et al., 2010). Natural and semi natural lands are alternative sites for conserving floral diversity across space and time but there are increasing concerns about the impact of landuse change on floral resource availability for pollinators (Brown & Paxton, 2009; Kremen et al., 2007; Potts et al., 2010b; Williams, Regetz, & Kremen, 2012).

Despite the positive relationships between forage resources and pollinator population, landscape wide studies on forage resources in Africa are often limited to melliferous plants relevant to the honey industry (Abdullahi, Sule, & Chimoya, 2011; Arega, Gemechu, & Debela, 2020; Khabbach, Libiad, & Ennabili, 2013; Oluwaseyi, Munkaila, & Mustapha, 2021). Aside the honey bee (*Apis melifera* adansonii), there are many other bee species in Sub-Saharan Africa (Eardley, Gikungu, & Schwarz, 2009; Gikungu, Wittmann, Irungu, & Kraemer, 2011; Mayer et al., 2011). Most African bees work throughout the year (Abdullahi et al., 2011) and identifying the forage resources of bees would guide pollinator habitat enhancement practices. This requires an observation of plant phenology in relation to monthly flowering to reveal the floral calendar of bees.

Shea is an economic plant endemic to the Sudano-Sahelian zone of Africa, occurring in an area that stretches from Senegal in the West through Central African Republic to Uganda in the East (Hall et al., 1996). The kernel contains edible fat that is extracted and processed into shea butter, used industrially to make ointments, cosmetics, and confectionery (Allal et al., 2013; P. N. Lovett, 2005; Maranz et al., 2003). Shea butter has become a major export commodity in countries such as Burkina Faso, Mali, Ghana, and Benin (Lovett, 2013; Munialo et al., 2019). Locally, it is used in domestic cooking across its native growing areas (Naughton et al., 2015). Aside shea butter, the edible fruit is eaten as a dessert in SSA (Karambiri et al., 2017; Maranz et al., 2004).

Despite the economic importance, inadequate pollination services in shea parklands poses a threat to fruit yield sustainability (Delaney et al. 2020). Shea is primarily pollinated by honey bees and stingless bee species (Delaney et al., 2020; Basga, 2018; Stout et al. 2018; Lassen et al., 2016; Nguemo et al., 2014; Kwapong, 2014; Okullo, 2004)but other flower visitors including parasitic wasps, beetles, flies, butterflies and birds forage on shea flowers (Delaney et al., 2020; Basga, 2018; Stout et al. 2018; Lassen et al., 2016; Nguemo et al., 2014; Kwapong, 2014; Okullo, 2004). According to Stout et al. (2018), an estimated 88.2% of insects foraging on shea flowers are bees belonging to six species.

Notwithstanding the relatively high flower visitor diversity, shea is reported to be pollen limited (Delaney et al., 2020). Pollination deficit in shea is attributed to pollinator population declines in shea parklands. In shea parklands of Burkina Faso, a positive relationship was established between native tree diversity and shea pollinator population as well as visitation (Delaney et al. 2020). This relationship pre-empts a potential contribution of other tree species to the forage resources of shea flower visitors but the identity of these species is still unknown. Moreso, shea blooms for three to four months in Ghana, spanning a period from November/December to April/May with some geographic variation in flowering onset (Nasare et al., 2022). Meanwhile, little is known on the alternative forage plants for shea flower visitors in the other months (June to November). Pollinator enhancement strategies in shea parklands, might yield little success until these alternative forage resources are identified and prioritised for conservation. Based on this knowledge gap, the present study observed the flowering phenology of woody species and floral calendar of bees in shea parklands of Northern Ghana.

8.3 Materials and Methods

8.3.1 Study Area

The survey was conducted in the Guinea savanna zone of Ghana from January to December 2021. The area records a monomodal precipitation pattern, with the amount and onset of rainfall varying significantly between years (Incoom et al., 2020). The wet season commences in April and ends in October having a mean annual rainfall of 1,034 mm (SARI, 2015). Maximum mean monthly temperatures are recorded in March/April whilst the lowest temperatures are recorded in December. Mean monthly temperatures range between 27 and 36 °C (Darko et al. 2019; Ghansah et al. 2018).

The vegetation of the area is composed of grasses dotted with indigenous woody species (Darko et al., 2019). The most frequently occurring woody plants of the zone are (*Vitellaria paradoxa),* baobab (*Adansonia digitata),* dawadawa (*Parkia biglobosa),* African mahogany (*Afzelia Africana),* ebony *(Diospyros mespiliformis),* Linnea *(Lannea acida*), acacia (*Faidherbia albida*) among others. Herbaceous plants and grasses such as *Tridax procumbens, Andropogon pseudapricus, Panicum maximu, Pennisetum purpureu, Boerhavi diffusa* are the most common in the area (Ziblim et al., 2015).

8.3.2 Survey of woody plants flowering in shea parkland

A 1000 m transect was established, and woody plants located at 50 m radius to the transect were identified and observed monthly for the occurrence of flowering. The month of flower initiation was recorded for each plant species. Plants were identified in-situ with the help of plant identification guides by (Arbonnier, 2004). Plants that could not be identified in the field had samples of twig with leaves and flowers collected with the help of a sharp penknife and placed in-between two pages of newspapers. The plant specimens were then transported to the herbarium of the University for Development Studies for identification by a plant taxonomist. The botanical nomenclature of plants flowering followed the International Plant Names Index (http://www.ipni.org).

8.3.3 Sampling of flower visitors

Flower visitors of each plant were sampled for 10 minutes using an extended handle sweep net on two sampling days (every fortnight) following the methodology of Abdullahi et al. (2011). All sampled insect specimen were temporally stored in vials containing 70% ethanol and labelled appropriately (site name, date, time, collector name and trapping method). The specimens were brought to the Insect Museum of the Department of Conservation Biology and Entomology, University of Cape Coast for identification. Specimens were identified to genus or species based on the available taxonomic keys.

8.4.0 Results

8.4.1 Floral resources in the Guinea savanna zone of Ghana

A total of 32 flowering plant species belonging to 15 plant families were recorded from the survey. The number of plants flowering in the family Leguminosae was more the than two folds that of Anacardiaceae, Malvaceae and Rubiaceae. Families Bombacaceae, Combretaceae, and Euphorbiaceae had doubletons whilst nine other plant families had singletons (Table 1). The highest number of plants flowering (24.3%) was recorded in May (24.3%) whilst the least was recorded in April, September, November, and December

(Figure 8.1). The first quarter of the calendar year has the highest number of plants flowering.

Table 8. 1: Woody plants and month of flowering

Family	Plant species	Month of flowering
Leguminosae	*Erytrina senegalensis*	January
	Parkia biglobosa	February
	Daniella oliveri	March
	Acacia nilotica	March
	Albezia lebbeck	March
	Acacia sp.	May
	Acacia dudgeoni	May
	Acacia sieberiana	October
Anacardiaceae	*Lannea acida*	January
	Annacardium occidentale	February
	Mangifera indica	March/May
Malvaceae	*Sterculia setigera*	April
	Adansonia digitata	July
	Ceiba pentandra	November
Rubiaceae	*Gardenia erubscens*	February
	Gardenia aqualla	May
	Mitragyna inermis	May
Bombacaceae	*Bombax costatum*	January
	Bombax buonopozanse	March
Combretaceae	*Combretum sp*	March
	Combretum ghalensis	March
Euphorbiaceae	*Jatropha curcas*	June
	Securinega virosa	July
Ebenaceae	*Diospyros mespiliformis*	May
Bignoniaceae	*Stereospermum kunthianum*	December
Rutaceae	Citrus	May
Zygophyllaceae	*Balinites egypticaa*	January
Sapindaceae	*Blighia sapida*	May
Meliaceae	*Azadirachta indica*	June
Moringaceae	*Moringa oleifera*	October
Icacinaceae	*Icacina oliviformis*	August
Lamiaceae	*Tectonia grandis*	September

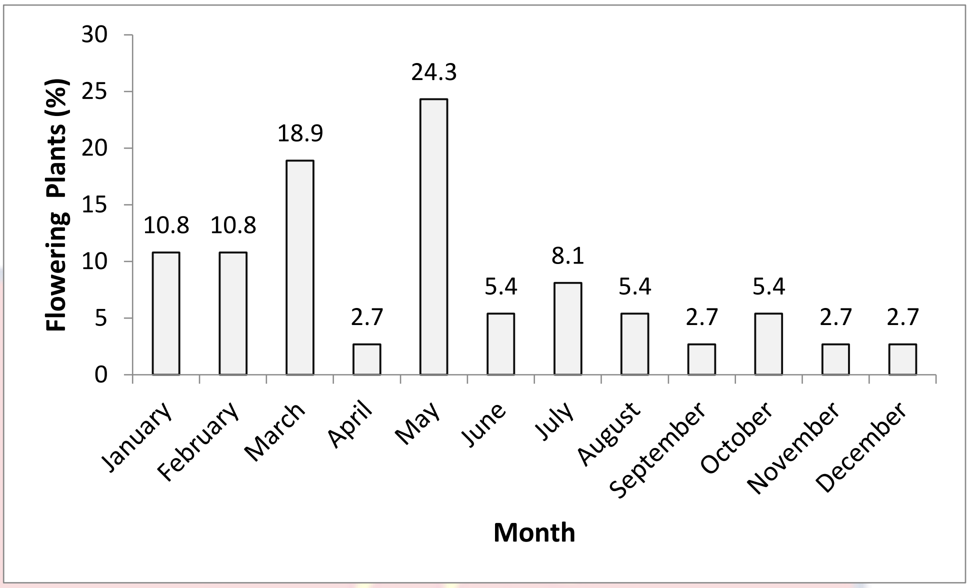

Figure 8. 1: Monthly distribution of plants flowering in shea parkland

8.4.2 Florivorous insects of woody plants in the Guinea savanna

A total of eighteen (18) species belonging to the orders, Hymenoptera, Coleoptera, Hemiptera and Lepidoptera were recorded. These consist of *Apis mellifera*, nine species of other bees and nine non-bee species (beetles, wasps, moths, bugs and butterflies) (Table 8. 2).

Table 8. 2: Insect visitors of flowers

Visitor group	Order	species
Apis mellifera	Hymenoptera	*Apis mellifera*
non-*A. mellifera*		*Xylocopa caffra*
		Hypotrigona gribodoi
		Thyreus ramosus
		Lipotriches orientalis
		Amegilla calens
		Lithurgus pullatus
		Pseudapis squamata
		Enicophilus sp. (Ichneumonidae)
		Colonite sp. (Vespidae)
Non-bee	Coleoptera	*Plinthocoelium suaveolens*
		Clytus arietis
		Mylabris sp (meloidae)
		Anoplodera spp 2
	Hemiptera	*Palomena* sp. (Pentatomidae)
		Anoplocnemis coreidae
		Dysdercus sp.
	Lepidoptera	Glyphodes (crambidae)
		Cirina sp.(saturnidae)

8.4.3 Alternative floral resources foraged by primary pollinators of shea (bees) and others

Apis mellifera adansonii was recorded in over two thirds (78.1%) of all plants flowering whilst other bees (non-*Apis mellifera*) visited 31.3% of plants surveyed. Over half (59.3%) of the plants flowering were also visited by non-bee species (wasps, butterflies, beetles, moths and bugs) (Figure 8.2).

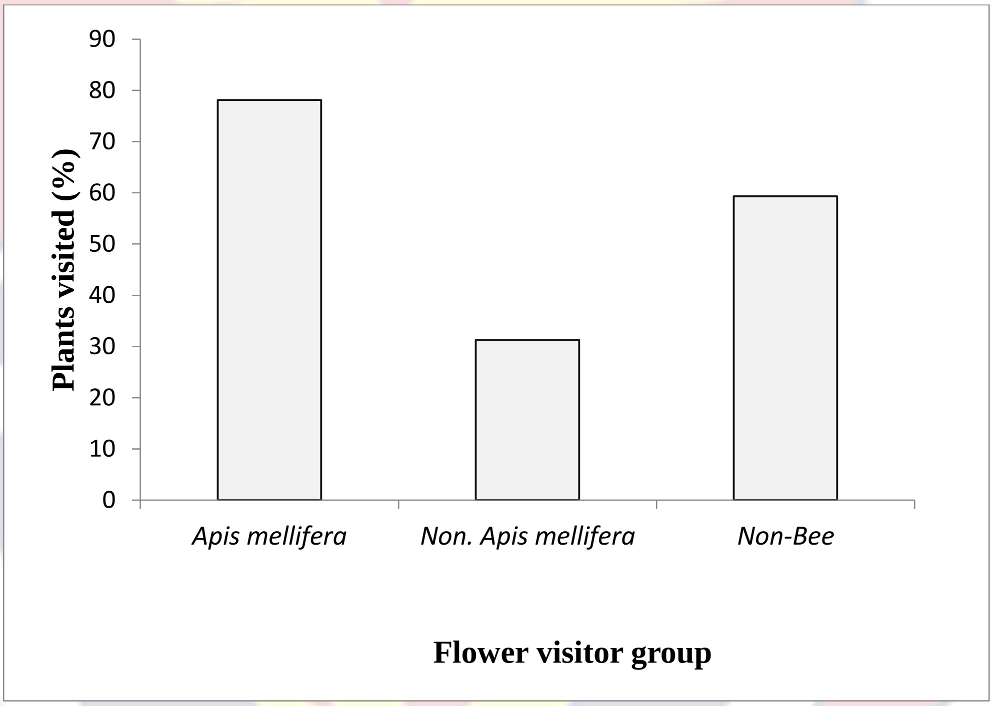

Figure 8. 2: Distribution of plants foraged by shea pollinators and other florivorous insects

Table 8. 3: Plants visited by shea pollinators (bees) and other florivorous insects

	Bees		
Plant species	***Apis mellifera***	**Other bees**	**non-bee**
Erytrina senegalensis	-	-	x
Parkia biglobosa	x	-	-
Daniellia oliveri	x	-	-
Acacia nilotica	x	-	-
Albezia lebbeck	-	-	x
Acacia sp.	x	x	x
Acacia dudgeon	-	-	x
Acacia sieberiana	x	x	x
Lannea acida	x	-	-
Annacardium occidentale	x	-	x
Mangifera indica	x	-	-
Sterculia setigera	x	-	x
Adansonia digitata	x	-	x
Ceiba pentandra	x	x	x
Gardenia erubscens	x	-	-
Gardenia aqualla	x	-	x
Mitragyna inermis	x	-	x
Bombax costatum	x	x	-
Bombax buonopozanse	-	-	x
Combretum sp	x	-	-
Combretum ghalensis	x	x	-
Jatropha curcas	-	-	x
Securinega virosa	x	x	x
Diospyros mespiliformis	x	-	x
Stereospermum kunthianum	x	-	x
Citrus	x	x	-
Balinites egyptica	x	-	-
Blighia sapida	x	x	-
Azadirachta indica	-	x	x
Moringa oleifera	x	-	x
Icacina oliviformis	x	-	-
Tectonia grandis	-	x	x

X = Group recorded on flowers, - = Group not recorded on flowers

8.5 Discussions

The highest number of plants recorded in the family Leguminosae is due to the dominance Leguminosae in the woody flora of the savanna. Leguminosae has been widely reported as the most abundant plant family in the Guinea savanna zone of Ghana (Asase, Patrick, & John, 2009; Tom-Dery et al., 2013; Yeboah et al., 2022). On the contrary Asteraceae was reported as the dominant nectivorous plant family in Nigeria (Akunne, Akpan, & Ononye, 2016). This disparity could be explained by the fact that the present study was limited to woody plants unlike Akunne et al. (2016) who surveyed all plant forms including trees, herbs, crops and grasses.

The occurrence of larger number of plants flowering in the month of May is contrary to Kebede & Gebrechirstos (2016) who recorded highest abundance from August-November in Ethiopia. In Nigeria, peak flowering of melliferous plants was observed from September to November (Akunne et al. 2016). In the present study, largest number of woody plants flowering was recorded in the driest period of the year (March to May) which tends to contradict Kebede & Gebrechirstos (2016) who recorded least number of plants flowering in the driest period of the year. The findings of this study equally deviates from that of Tesfa et al. (2013), who recorded peak scarcity of flowering of plants in the between February and April in the Western Amhara ranges. The variation in this can be attributed to differences in climatic conditions and the plant pollinator interaction networks between regions.

In this study, plants flowering were more abundant in the dry season compared to the rainy season (June –October) which is consistent with the assertion of Oni et al. (2014), that most tropical plants flower in the dry season prior to onset of rains. Flowering during dry season is known to be an adaptation for plants that are largely dependent on insect pollination as rains results in nectar dilution and loss of olfactory cues that affect pollinator attraction (Cnaani et al., 2006). Plants that flower in the dry season also have higher advantage for pollen dissemination as high relative humidity, moisture and windstorms associated with rains are known to disrupt foraging activities of pollinators(Combes & Dudley, 2009; Hennessy et al., 2020, 2021). The large number of plants flowering in the late dry season might perhaps be an adaptation to optimise pollination in the dry season whilst synchronising fruiting with periods of soil moisture availability in the early rainy season.

Another possible explanation for the abundance of plants flowering in the dry season might be an adaptation to ovoid an overlap between flowering period of woody perennials and annuals (grasses and herbs). Several grasses are reported to be visited by nectivorous insects especially bees (Akunne et al., 2016; Kebede & Gebrechirstos, 2016; Tesfa et al., 2013). Grasses are predominantly annuals that only thrive in the rainy season, most woody perennials might be flowering in the dry season to reduce competition for pollinators. This could perhaps also be an outcome of a co-evolution process between plants and pollinators to ensure all year-round supply of floral resources.

In either way the dominance of flowering woody plants in the dry season is good news for shea pollinator conservation as grasses and herbs flower in the rainy season ensuring an all-year round pollen supply for shea pollinators. Future studies should identify these non-woody plants foraged by shea pollinators. The flowering period of shea (January to April) seems to coincide with the flowering of many other woody species and herbs in the savanna and this requires further investigations to examine any possible competition for pollinators between these plants.

The florivorous insect orders identified in the present study are all holometabolous insects except Hemiptera. This finding is consistent with Wardhaugh (2015) observation that holometaboly is a conspicuous commonality of most florivorous insects. The occurrence of bees as the dominant flower visitors of most woody plants agrees with the assertion that bees and lepidopterans have developed proboscides and suctorial mouthparts as morphological adaptations for specialised obligate flower feeding (Krenn, 2010; Labandeira, 2010). Some morphological modifications are required for efficient collection and handling of floral resources (nectar and pollen) among obligate flower feeders (Wardhaugh, Stork, & Edwards, 2013). This special morphological adaptation of *Apis mellifera* explains its occurrence on most (78%) of the plants flowering.

Notwithstanding the morphological adaptations required for efficient foraging, many other insects with limited modifications for pollen and nectar collection such as wasps and beetles were recorded among florivorous insects. Nectar is rich in carbohydrates and easily digested by all insects that can access it without a specialized digestive system (Wardhaugh, 2015). Many opportunistic feeders therefore feed on nectar to get energy for relocation, mate finding and reproduction. According to Krenn et al. (2005), there are many facultative flower feeders that have little morphological modification for nectar collection. Another reason accounting for the presence of many non-specialised florivorous insects is the fact that flowers seem to be the closest free lunch in nature as they are often undefended or minimally protected and advertised to attract insects unlike other plant parts (Wardhaugh, 2015).

Majority of plants flowering being visited by bees implies that most woody plants of shea parkland are essential to pollinator forage conservation. Therefore, restoration of shea landscapes should be expanded to include melliferous woody plants for a comprehensive pollinator conservation.

8.6 Conclusion

The study identified diverse alternative floral resources foraged by the primary pollinators of shea, but floral resources are not evenly distributed throughout the year. Flowering of most woody plants is skewed to the dry season. Grasses and herbs are major melliferous plants that might be supplementing forage supply in the rainy season, further investigations are therefore required to identify these species. Among all florivorous insects, *Apis mellifera* visits about two thirds of the plants flowering in shea parklands. This implies that holistic pollinator conservation would require the conservation of many other woody plants species in shea parklands. Although shea pollinators were recorded in many plants, an observation of foraging behaviour would be essential to identify the specific floral reward(s) collected from each plant to help characterise forage resources of shea pollinators.

CHAPTER NINE

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

9.1 Summary

This study was focused on the pollination ecology of shea in northern Ghana and specifically assessed the effect of beekeeping on pollination, fruit yield, and other native pollinators of shea. The thesis also examined the geographic variation in shea floral phenology and morphology, the response of shea flower visitors to climatic factors and identified alternative forage resources of shea flower visitors in the Guinea savanna. All field works and data collection were conducted from August 2020 to December, 2021.

Study on floral morphology and phenology of shea concentrated on climatic factors influencing the onset and rate of shea flowering and the variation in floral traits in different geographic locations of northern Ghana. The study revealed soil moisture and temperature significantly determined the onset and rate of shea flowering. Shea flowering commenced during the driest months of the year when soil moisture and relative humidity were low. There was a geographic variation in the onset of flowering in northern Ghana where flowering in the UW region commenced in November whilst that of NE and UE commenced in January and February respectively. The study revealed significant variation in floral density and morphometric traits (pedicel length, pedicel diameter, petal length, style length, filament length) between the three regions. However, there were no significant differences in flower density, stem diameter, and petal length between NE and UE. Despite variability in floral phenology, the interpretation of the findings is limited by the one-year phenological data which could not account for year-to-year climate variability.

The experiment on effect of beekeeping on pollination and fruit yield of shea sought to assess the effect of proximity to the apiary on pollination and reproductive success. The results showed an increased number of fertilised inflorescences near the apiary. A significantly larger number of fertilised inflorescences were recorded among trees within 100 m of the apiary compared to the control. The presence of a mature fruit on the open pollinated inflorescence was significantly related to the distance away from the apiary. On the other hand, the number of mature fruits produced per inflorescence was not related to distance away from the tree. Moreso the study found no significant effect of tree proximity to the apiary on fruit traits. The implication of this findings is that the positive effect of pollination on number of fruits is detected with a 500m radius of the apiary but pollination does not influence fruit and seed traits.

The investigation on response of other flower visitors to the presence of managed honey bee hives detected no significant effect of apiaries on composition, abundance, richness and visitation of other bee visitors. However, honey bee visitation was significantly related to distance as visitation frequencies were highest on trees located at 100 m. This finding implies a complementary relationship between honeybees and other native bees. However, landscape level assessment is required for a comprehensive understanding of the presence of unnatural bee colonies on other native pollinators in shea parklands. This study was limited to flower visitors of shea which could have overlooked landscape level effects.

Observation of the relationship between climatic factors and flower visitors revealed visitor composition and richness is not explained by climatic conditions but flower visitor abundance is significantly influenced by temperature. Flower visitation by *Apis mellifera* was also significantly influenced by wind speed. This implies pollinators forage less under high winds due to the higher energy cost of flight. Therefore, if future climate change results in increased wind speed, foraging activities and pollination of shea would be affected.

The survey of alternative forage resources for shea flower visitors revealed a total of 32 woody plants, 78% of which were foraged by bees (primary pollinators of shea). This implies that sustainable conservation of forage resources for pollinators would require protection of many other multipurpose plants in shea parklands. Most woody plants were found to flower in the dry season, future studies should identify herbaceous plants foraged by shea flower visitors for comprehensive pollinator conservation.

9.2 Conclusion

Observing the floral phenology and morphology in the 2020/2021 flowering season, this study established that soil temperature and moisture predicted shea flowering. Timing of shea flowering onset and floral traits onset varies between different geographical locations. Testing the effect of tree proximity to apiary on pollination shows the presence of apiary in the parkland has a positive effect on pollination and fruit set within a 500m radius of the apiary. Notwithstanding, proximity to the apiary does not influence fruit/seed weight and size. Despite the competitive interactions between managed bees and native pollinators elsewhere, this study did not find any effect of proximity to apiary on foraging activities, abundance and diversity of other shea flower visitors. This finding shows a possible complementary effect of managed honey bees and other pollinators for improved fruit set of shea as *Apis mellifera* visits to flowers increased with proximity to apiary. There are diverse floral resources used by shea pollinators in the Guinea savanna zone. Over two thirds of flow woody plants of the savanna are visited by bees.

9.3 Recommendations

- Based on the geographic variation in floral phenology and morphometric traits, the study recommends plant breeders, foresters, and farmers working on genetic improvement and domestication to select ideotypes specific to geographic location ensure compatibility with environmental conditions.
- To boost pollination services for shea, farmers and beekeepers should place hives within a distance range of 500 m from the shea parkland.
- The Global Shea Alliance, local government, the Forestry Services Division, civil society organizations and environmentally-focused NGOs should integrate melliferous plants into parkland restoration and conservation projects.
- Future studies should observe floral phenology over multiple years to account for year-to-year climate variability on flowering.
- The effect of meliponiculture on fruit set and yield of shea should be studied, since several stingless bee species are known to pollinate shea.

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Zida, I., Nacro, S., Dabiré, R., Ouédraogo, S. N., & Somda, I. (2020). Shea fruit-infesting fruit flies (Diptera : Tephritidae) and evaluation of infestation level according to the ethno-varieties in Western Burkina Faso. *Int J Trop Insect Sci*.

APPENDICES

Appendix A

List of articles included in systematic reviewe

Author(s)	Title	Year
Akpona T.J.D., Akpona H.A., Djossa B.A., Savi M.K., Daïnou K., Ayihouenou B., Glèlè Kakaï R.	Impact of land use practices on traits and production of shea butter tree (*Vitellaria paradoxa* C.F. Gaertn.) in Pendjari Biosphere Reserve in Benin	2016
Aleza K., Villamor G.B., Nyarko B.K., Wala K., Akpagana K.	Shea (*Vitellaria paradoxa* Gaertn C. F.) fruit yield assessment and management by farm households in the Atacora district of Benin	2018
Bayala J., Ouedraogo S.J., Teklehaimanot Z.	Rejuvenating indigenous trees in agroforestry parkland systems for better fruit production using crown pruning	2008
Bokary Allaye Kelly, Mahesh Poudyal, Jean-Marc Bouvet	Impact of land use and land use history on fruits production of Vitellaria paradoxa (Shea tree) according to agroclimatic zones in Mali (West Africa)	2019
Bokary Allaye Kelly, Mahesh Poudyal, Jean-Marc Bouvet	Variation of *Vitellaria paradoxa* phenophases along the north-south gradient in Mali	2018
Bondé L., Ouédraogo O., Ouédraogo I., Thiombiano A., Boussim J.I.	Variability and estimating in fruiting of shea tree (Vitellaria paradoxa C.F. Gaertn) associated to climatic conditions in West Africa: implications for sustainable management and development	2018
Bondé L., Ouédraogo O., Traoré S., Thiombiano A., Boussim J.I.	Impact of environmental conditions on fruit production patterns of shea tree (Vitellaria paradoxa C.F.Gaertn) in West Africa	2019
Byakagaba P., Eilu G., Okullo J.B.L., Mwavu E.N., Tumwebaze S.B.	Shea butter tree {vitellaria paradoxa gaertn.) fruit yield in relation to dendrometric traits and land-use in Uganda	2012
Delaney A., Dembele A., Nombré I., Gnane Lirasse F., Marshall E., Nana A., Vickery J., Tayleur C., Stout J.C.	Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands	2020
Nguemo, D.D., Mapongmetsem, P.M., FFohouo, F.T., Gounhagou, D. and Yougouda, H.	Flower biology of a beeplant Vitellaria paradoxa (Sapotaceae) in the sudano- sahalian zone of Cameroon	2014
Nafan, D., Divine, B. N., César,K., Christophe,K., and Sangare, A	phenotypic diversity of shea tree populations across four agro ecological zones in Cameroun	2009
Dwomoh E.A.	Damage by the fruit borer *Nephopterix* sp. and other factors in sheanut tree, and their distribution in northern Ghana	2004
Borketey-La, E.B., Kwapong,P., Botchey, M.A. and Vanderpuije, G.	Assessment of knowledge of Shea nut tree (*Viterallia paradoxa*) stakeholders (Shea nut collectors , processors and exporters) in pollination , Shea pollinators , their roles and the need for their conservation in the Northern region of Ghana	2019
Emmanuel Basga, Fameni Topé Sidonie and Fernand-	Foraging and pollination activity of *Xylocopa olivacea* (Hymenoptera: Apidae) on Vitellaria	2018

Nestor Tchuenguem Fohouo	paradoxa (Sapotaceae) flowers at Ouro-Gadji (Garoua, Cameroon)	
Glèlè Kakaï R., Akpona T.J.D., Assogbadjo A.E., Gaoué O.G., Chakeredza S., Gnanglè P.C., Mensah G.A., Sinsin B.	Ecological adaptation of the shea butter tree (Vitellaria paradoxa C.F. Gaertn.) along climatic gradient in Bénin, West Africa	2011
Gwali S., Nakabonge G., Okullo J.B.L., Eilu G., Nyeko P., Vuzi P.	Morphological variation among shea tree (*Vitellaria paradoxa* subsp. nilotica) 'ethnovarieties' in Uganda	2012
Gwali S., Okullo J.B.L., Eilu G., Nakabonge G., Nyeko P., Vuzi P.	Folk classification of shea butter tree (*Vitellaria paradoxa* subsp. nilotica) ethno-varieties in Uganda	2011
Houehanou T.D., Kindomihou V., Stevart T., Tente B., Houinato M., Sinsin B.	Variation of Loranthaceae impact on Vitellariaparadoxa C. F. Gaertn. fruit yield in contrasting habitats andimplications for its conservation	2013
Karambiri M., Elias M., Vinceti B., Grosse A.	Exploring local knowledge and preferences for shea (Vitellaria paradoxa) ethnovarieties in Southwest Burkina Faso through a gender and ethnic lens	2017
Kelly B.A., Gourlet-Fleury S., Bouvet J.-M.	Impact of agroforestry practices on the flowering phenology of Vitellaria paradoxa in parklands in southern Mali	2007
Lamien N., Boussim J.I., Nygard R., Ouédraogo J.S., Odén P.C., Guinko S.	Mistletoe impact on Shea tree (Vitellaria paradoxa C.F. Gaertn.) flowering and fruiting behaviour in savanna area from Burkina Faso	2006
Lamien N., Tigabu M., Dabiré R., Guinko S., Oden P.C.	Insect (Salebria sp.) infestation and impact on Vitellaria paradoxa C.F. Gaertn. fruit production in agroforestry parklands	2008
Lamien N., Tigabu M., Guinko S., Oden P.C.	Variations in dendrometric and fruiting characters of Vitellaria paradoxa populations and multivariate models for estimation of fruit yield	2007
Lassen K.M., Nielsen L.R., Lompo D., Dupont Y.L., Kjær E.D.	Honey bees are essential for pollination of Vitellaria paradoxa subsp. paradoxa (Sapotaceae) in Burkina Faso	2018
Lovett, P. N., & Haq, N.	Diversity of the Sheanut tree (Vitellaria paradoxa C.F. Gaertn.) in Ghana	2000
Maranz S., Kpikpi W., Wiesman Z., De Saint Sauveur A., Chapagain B.	Nutritional values and indigenous preferences for shea fruits (Vitellaria paradoxa C.V. Gaertn. F.) in African agroforestry parklands	2004
Maranz Steven, Zeev Wiesman, Johan Bisgaard and Giorgio Bianchi	Germplasm resources of Vitellaria paradoxa based on variations in fat composition across the species distribution range	2004
Maranz S., Wiesman Z.	composition across the species distribution range	2003
Nasare L.I., Kwapong P.K., Doke D.A.	Insect pollinator dependence of shea (Vitellaria paradoxa C.F. Gaertn.) in the Guinea Savanna zone of Ghana	2019
Nyarko, G., Mahunu, G. K., Chimsah, F. A., Yidana, J. A., Abubakari, A-H., Abagale, F., Quainoo, K., and Poudyal, M.	Leaf and fruit characteristics of Shea (Vitellaria paradoxa) in Northern Ghana	2012
Okullo J.B.L., Hall J.B., Obua J.	Leafing, flowering and fruiting of Vitellaria paradoxa subsp. nilotica in savanna parklands in Uganda	2004
Okullo, J. B. L., Obua, J., & Okello, G.	Use of indigenous knowledge in predicting fruit production of shea butter tree in agroforestry parklands of North-Eastern Uganda	2004

Payne C., Badolo A., Sagnon B., Cox S., Pearson S., Sanon A., Bationo F., Balmford A.	Effects of defoliation by the edible caterpillar “chitoumou” (*Cirina butyrospermi*) on harvests of shea (Vitellaria paradoxa) and growth of maize (Zea mays)	2020
Sandwidi A., Diallo B.O., Lamien N., Vinceti B., Sanon K., Coulibaly P., Pare S., Sawadogo M.	Participatory identification and characterisation of shea butter tree (Vitellaria paradoxa C.F. Gaertn.) ethnovarieties in Burkina Faso	2018
Sanou H., Picard N., Lovett P.N., Dembélé M., Korbo A., Diarisso D., Bouvet J.-M.	Phenotypic variation of agromorphological traits of the shea tree, Vitellaria paradoxa C.F. Gaertn., in Mali	2006
Stout, J., Nombre, I., Bruijn, B. de, Delaney, A., Doke, D. A., Gyimah, T., … Kwapong, P.	Insect pollination improves yield of Shea (*Vitellaria paradoxa* subsp. paradoxa) in the agroforestry parklands of West Africa	2018
Ugese F.D., Baiyeri P.K., Mbah B.N.	Agroecological variation in the fruits and nuts of shea butter tree (Vitellaria paradoxa C.F. Gaertn.) in Nigeria	2010
Ugese F.D., Baiyeri P.K., Mbah B.N.	Nutritional composition of shea (Vitellaria paradoxa) fruit pulp across its major distribution zones in Nigeria	2008
Yidana, J. A.	Progress in developing technologies to domesticate the cultivation of shea tree (Vitellaria paradoxa) in Ghana	2004
Zida I., Nacro S., Dabiré R., Ouédraogo S.N., Somda I.	Shea fruit-infesting fruit flies (Diptera: Tephritidae) and evaluation of infestation level according to the ethno-varieties in Western Burkina Faso	2020

Appendix B

Correlation Matrix for climatic factors and ANOVA of floral traits

Correlation matrix

	(Intr)	RH	Soil Moisture	Soil Temp	Mean Air Temp.	Max. Air Temp.	Min. Air Temp.
RH	0.183						
Soil Moisture	-0.694	-0.242					
Soil Temp.	-0.647	0.098	0.383				
Mean Air Temp.	0.266	-0.473	-0.158	-0.627			
Max. Air Temp.	-0.527	0.38	0.285	0.612	-0.917		
Min. Air Temp.	0.124	0.462	-0.099	0.22	-0.839	0.652	
Wind Speed	-0.39	-0.225	0.256	0.032	-0.144	0.304	-0.01

Pedicel length

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Region	2	7163	3581	322.856	< 2e-16	***
C	3	164	55	4.924	0.00221	**
Residuals	533	5912	11			

Pairwise comparison of pedicel means

	diff	lwr	upr	P adj
UE-NE	-6.46673	-7.29299	-5.64047	0
UW-NE	2.108333	1.283224	2.933443	0
UW-UE	8.575062	7.748801	9.401323	0

Pedicel diameter

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Region	2	0.63	0.3162	5.219	0.005695	**
C	3	1.11	0.3707	6.119	0.000427	***
Residuals	533	32.29	0.0606			

Pairwise comparisons of pedicel diameter between regions

Region	diff	lwr	upr	p adj
UE-NE	-0.052352	-0.113417	0.008714	0.109591
UW-NE	0.030667	-0.030314	0.091647	0.464471
UW-UE	0.083019	0.021953	0.144084	0.004218

Style length

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Region	2	247.5	123.77	45.71	< 2e-16	***
C	3	147.7	49.23	18.18	3.02E-11	***
Residuals	533	1443.1	2.71			

Pairwise comparisons of style length between regions

	diff	lwr	upr	p adj
UE-NE	-0.74972	-1.15793	-0.34151	5.61E-05
UW-NE	0.908333	0.500689	1.315978	7.00E-07
UW-UE	1.658054	1.249841	2.066267	0.00E+00

Filament length

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Region	2	417.5	208.73	191.5	< 2e-16	***
C	3	65.1	21.69	19.9	3.06E-12	***
Residuals	533	580.9	1.09			

Appendix C

Summary statistics for fruit set and traits

Number of immature fruits per inflorescence

Region	Treatment	Distance (m)	Mean	Std	N	Min	Max
NE	Bagged	100	0.6	0.9	30	0	3
		500	0.7	1.1	30	0	3
		1000	0.6	1.0	30	0	3
		Control	0.5	0.9	30	0	4
	Hand	100	3.9	2.2	30	0	8
		500	3.5	2.4	30	0	8
		1000	3.3	2.4	30	0	10
		control	3.2	2.2	30	0	8
	Open	100	4.0	2.5	30	0	9
		500	3.3	3.0	30	0	9
		1000	2.3	2.2	30	0	9
		control	1.8	1.7	30	0	6
UE	Bagged	100	0.8	1.1	30	0	3
		500	0.6	0.9	30	0	3
		1000	0.5	0.6	30	0	2
		Control	0.6	0.8	30	0	3
	Hand	100	2.8	1.8	30	0	7
		500	2.0	1.4	30	0	5
		1000	3.1	2.2	30	0	9
		control	2.0	1.4	30	0	6
	Open	100	2.6	1.7	30	0	5
		500	1.3	1.4	30	0	7
		1000	1.1	1.0	30	0	3
		control	1.0	1.3	30	0	5
UW	Bagged	100	0.8	1.3	30	0	4
		500	0.7	1.0	30	0	3
		1000	0.8	1.1	30	0	3
		Control	0.6	0.9	30	0	3
	Hand	100	4.1	1.9	30	1	9
		500	3.3	2.0	30	0	7
		1000	3.0	1.9	30	0	6
		control	2.2	1.6	30	0	5
	Open	100	4.0	2.2	30	0	7
		500	2.8	2.1	30	0	7
		1000	1.7	1.3	30	0	4
		Control	1.7	1.3	30	0	5

Number of mature fruits per inflorescence

Region	Treatment	Distance (m)	Mean	Std	N	Min	Max
NE	Bagged	100	0.3	0.6	30	0	2
		500	0.4	0.7	30	0	3
		1000	0.3	0.7	30	0	2
		Control	0.2	0.5	30	0	2
	Hand	100	1.6	1.1	30	0	4
		500	1.5	0.9	30	0	3
		1000	1.5	0.8	30	0	2
		control	1.5	1.1	30	0	3
	Open	100	2.3	1.6	30	0	5
		500	1.8	1.9	30	0	6
		1000	1.4	1.4	30	0	6
		control	1.3	1.4	30	0	4
UE	Bagged	100	0.3	0.4	30	0	1
		500	0.3	0.4	30	0	1
		1000	0.3	0.5	30	0	2
		Control	0.2	0.4	30	0	1
	Hand	100	1.8	1.3	30	0	5
		500	1.2	1.0	30	0	3
		1000	1.6	0.7	30	0	2
		control	1.4	1.5	30	0	5
	Open	100	1.3	1.0	30	0	3
		500	1.2	1.1	30	0	3
		1000	0.9	1.0	30	0	3
		control	1.0	1.3	30	0	4
UW	Bagged	100	0.4	0.7	30	0	2
		500	0.3	0.4	30	0	1
		1000	0.3	0.5	30	0	1
		Control	0.2	0.4	30	0	1
	Hand	100	2.1	1.1	30	0	5
		500	2.1	1.2	30	0	5
		1000	1.3	0.9	30	0	2
		control	1.6	0.9	30	0	5
	Open	100	2.3	1.5	30	0	5
		500	1.9	1.1	30	0	4
		1000	1.5	0.9	30	0	4
		Control	1.4	1.2	30	0	4

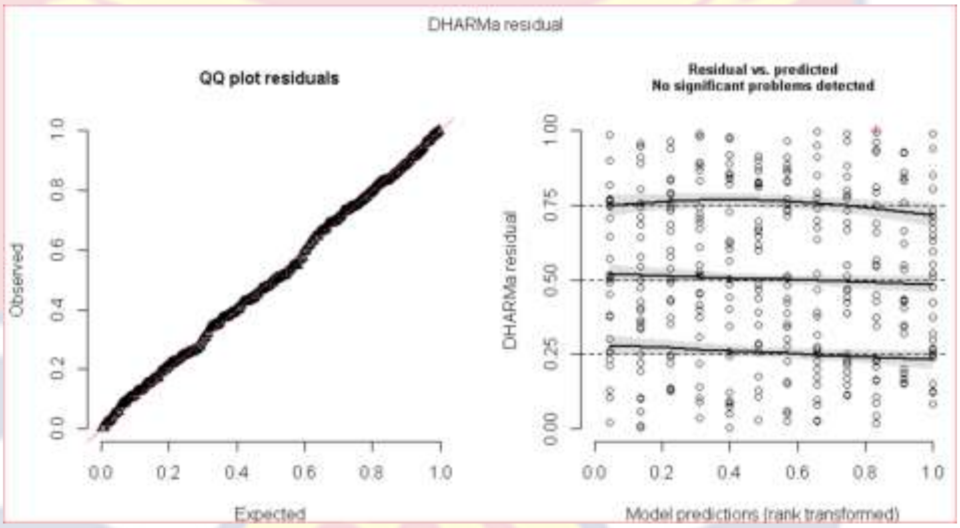
Mean weight of fruit/seed

Fruit/seed trait	Treatment	Distance (m)	Mean	Std	N	Min	Max
Fruit weight	Bagged	100	14.5	3.7	18	6.2	21.2
		500	15.4	3.2	7	11.3	20.4
		1000	14.2	4.5	6	10.5	20.6
		Control	13.9	3.3	13	6.1	19.2
	Hand	100	16.4	4.2	16	11.2	24.6
		500	17.8	2.3	10	15.22	22.89
		1000	16.1	3.4	11	12	24.1
		control	16.4	3.9	12	10.09	21
	Open	100	17.2	3.1	33	10.2	23
		500	16.8	5.0	33	10.49	28.5
		1000	17.0	6.4	47	5.7	35.4
		control	15.9	4.4	33	7.5	24
Seed weight	Bagged	100	6.6	2.2	16	4.1	12.2
		500	6.0	1.3	7	3.6	7.3
		1000	5.8	1.1	6	4.5	7.1
		Control	6.4	0.9	12	4.2	7.4
	Hand	100	7.2	3.4	16	1.2	14.8
		500	7.0	1.6	10	4.7	9.6
		1000	6.6	1.3	11	4.2	8.1
		control	7.0	0.6	12	5.8	8.1
	Open	100	7.3	1.8	32	4.6	10.5
		500	6.3	2.4	30	2.4	12.1
		1000	7.0	2.0	47	2.5	13.5
		Control	7.0	1.1	33	3.2	9.5

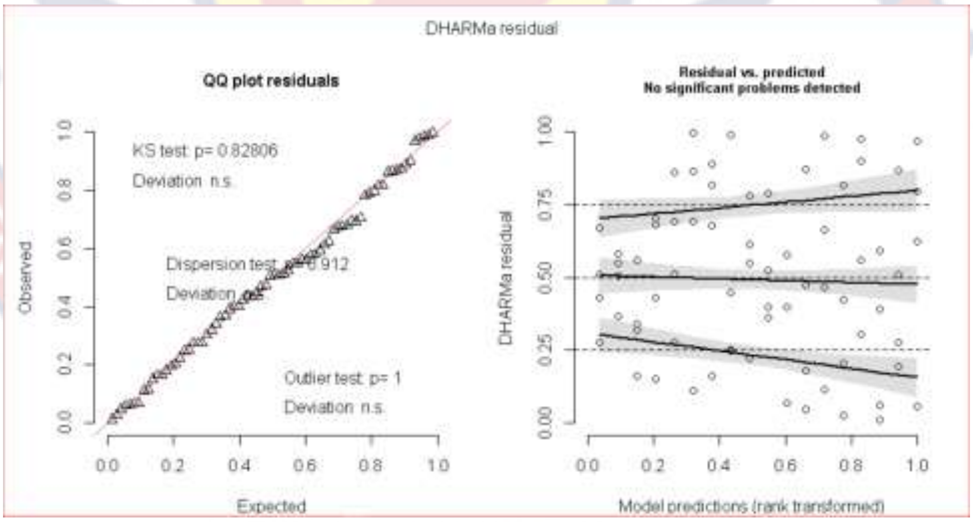
Appendix D

Residual plot of models predicting frequency of insect visits, abundance and richness

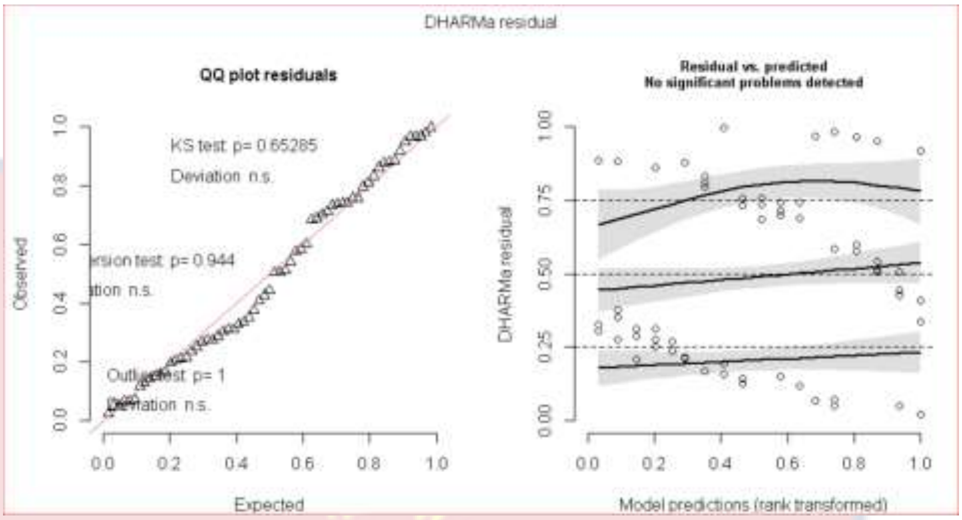
Apis mellifera flower visitation and distance to apiary model



Visitation frequency of other bees and distance to apiary model



Flower visitor abundance and climatic factors model



Flower visitor richness and climatic factors model