

UNIVERSITY FOR DEVELOPMENT STUDIES

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EFFECT OF INSECT POLLINATION ON FRUIT SET AND YIELD OF SHEA (*Vitellaria paradoxa*) IN THE GUINEA SAVANNAH ZONE OF GHANA

LATIF IDDRISU NASARE



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paradoxa*) IN THE GUINEA SAVANNAH ZONE OF GHANA

BY

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A THESIS SUBMITTED TO THE DEPARTMENT OF ENVIRONMENT AND RESOURCE
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MAY, 2017

DECLARATION

Student

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

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Supervisors'

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

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ABSTRACT

Shea (*Vitellaria paradoxa*) is an important economic tree in West Africa with multipurpose uses. It is the most abundant economic tree species in the three regions of northern Ghana. Understanding the contribution of insect pollination to fruit production is fundamental to effective management and conservation, yet such information on *Vitellaria paradoxa* is rare in Ghana. The study was carried out from January to August, 2016 to determine the effect of insect pollination on the reproductive success of *Vitellaria paradoxa* in cultivated parklands. The study also estimated the monetary value of the contribution of insect pollination to the yield of *Vitellaria paradoxa*. Open pollination and insect exclusion treatments were applied to the flowers of 18 randomly selected matured shea trees. Insect visitors of the flowers were identified and insect to flower visitation rates were also monitored. Six insect species comprising of three species from the stingless bees and one species from the honeybees were identified as insect pollinators of *Vitellaria paradoxa* out of the 187 insect visitors collected from the flowers. The experiment shows 73% of *Vitellaria paradoxa* yield is dependent on insect pollination. Flowers that had access to insect pollination produced a significantly higher mean number of matured fruits per inflorescence as compared to insect excluded flowers. Insect to flower visitation rate had a positive relationship with the number of matured fruits produced. The monetary value of the contribution of insect pollinators to yield was GHC 73.21 per bag of kernel (per market price in August, 2016). The study revealed that declines in insect pollination services can significantly affect fruit production. It is therefore recommended that farmers should incorporate pollinator-friendly practices into landuse to help conserve pollinators in shea parklands.



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DEDICATION

I dedicate this work in memory of my late dad, Mr. Iddrisu Naawia Nasare. May his soul rest in perfect peace.



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LIST OF ABBREVIATIONS

CRIG	-	Cocoa Research Institute of Ghana
EVI	-	Economic Value of Insect Pollination
FAO	-	Food and Agricultural Organisation
FSIE	-	Fruits Produced from Insect Exclusion
SOP	-	Fruits produced from Open Pollination
SS	-	Ghana Statistical Service
IE	-	Insect Exclusion
IPD	-	Insect Pollinator Dependence
KWIE	-	Kernel Weight from Insect Exclusion
KWOP	-	Kernel Weight from Open Pollination
MDG	-	Millennium Development Goals
MEA	-	Millennium Ecosystem Assessment
OP	-	Open Pollination
QAI	-	Quantity (kg) of kernel Attributable to Insect pollination
WDA	-	Sissala West District Assembly
UN	-	United Nations
UP	-	Unit Price of a kg of shea kernel



CHAPTER ONE

INTRODUCTION

1.1 Background

Vitellaria paradoxa (shea) is indigenous to semi-arid Sub-Saharan Africa that extends from Senegal in the West to Sudan in the East and onto the foothills of Ethiopia (Okullo et al., 2003a; Naughton et al., 2015). It is found in 21 countries of Africa and stretches across 600 to 750 km wide land area in Sub-Saharan Africa (Glew & Lovett, 2014).

Shea is a small to medium-sized tree with a dense, spreading, round to hemispherical crown (Sanou et al., 2004). It usually grows to an average height of about 15 m with profuse branches and a thick corky bark that makes it fire resistant (Orwa et al., 2009). In terms of environmental requirements, the tree thrives in a wide variety of climatic conditions, growing well in areas with annual rainfall ranging from 400 – 1500 mm per annum (Hall et al., 1996) and in diverse soil conditions such as highly degraded, arid, semi-arid and rocky soils (Dogbevi, 2007).

In Ghana, the tree occurs predominantly in the three northern regions (Lovett & Haq, 2000; Chimsah et al., 2013) with few individual species scattered across some parts of Brong Ahafo, Ashanti, Eastern and Volta regions (Yidana, 2004). It's reported as the most frequently found economic tree species in the Guinea savannah zone of Ghana (Chimsah et al., 2013) due to indigenous protection of the shea tree in traditional agroforestry systems of northern Ghana (Tom-Dery et al., 2015).

Shea is often retained on farmlands for multipurpose including economic, medicinal, cultural, nutritional and ecological benefits (Yaro, 2008; Bayala et al., 2013). It is



estimated that shea contributes to the livelihoods of 16.2 million shea collectors in Africa (Glew & Lovett, 2014). Moreover, income from sheanut constitute about 12% of rural household income during the “hungry season” thus between the end of grain stores and the new harvest season (Pouliot & Treue, 2012). According to Elias et al. (2006) sheanut processing and commercialisation is believed to be one of the few plant products primarily controlled by women and contributes directly to poverty alleviation among women.

At the international level, shea presents an additional economic opportunity for women in Sub-Saharan Africa as the global demand for shea butter is increasing (Alander, 2004; Teklehaimanot, 2004). For instance, the American shea butter market recorded a 25% growth between 1994 and 2004 (Rousseau et al., 2015). Hence, the conservation of the shea tree is critical to people living in shea growing areas due the multipurpose uses and its contribution to rural livelihoods.

1.2 Problem statement

An estimated 94% of tropical plants are known to depend on some level of animal pollination for fruit/ seed set (Ollerton et al., 2011). The transfer of pollen from the anther to the stigma of a flower was described as the first step in sexual reproduction of some plant species (Foutaine et al., 2006). Al-Obeed and Saliman (2011) posit that plant-pollinator interaction is the most important and perhaps the bedrock of ecosystem services without which many interconnected species and processes functioning within an ecosystem would collapse. This interaction provides a direct link between productivity (fruit set, yield and quality) and sustainability in terrestrial ecosystems (Klein et al., 2007).



Although other agents are involved in the process of pollination, entomophilous pollination is ranked as the single fundamental natural interaction between plants and animals that produce about one-third of the world's human food (Klein et al., 2007). Flowering plants require insect pollinators such as flies, butterflies, moths, beetles and bees for fruit and seed formation (Ingram et al., 1996a; Ricketts et al., 2008). Experimental studies in some plants have revealed that when insect associated pollination is not achieved, fruit/ seed set is often reduced and the yield output may only reflect the proportion that is mediated by self or wind pollination (Albano et al., 2009; Stanley et al., 2013; Bartomeus et al., 2014). This implies that, although self-compatible plants do not require outcross pollen for fertilization, they often produce more seeds or larger fruits (Roldan et al., 2006; Andersson et al., 2012; Garratt et al., 2013) when cross pollinated.

Aside the immense contribution of insect pollinators to the quantity of fruit set and yield, insect pollination can equally influence the quality of fruit set. Inadequate pollination can result in delayed yield and the production of low commercial grade fruits and seeds. For instance in strawberry, flowers that were adequately pollinated by honeybees produced heavier and firmer fruits with less sugar-acid-ratio and much longer commercial life than those that were pollinated by wind (Klatt et al., 2014). Thus, the quantity and quality of pollination have multiple implications on food security, species diversity, ecosystem stability and resilience to climate change (FAO, 2008).





Owing to the role of pollination in the quantity and quality of fruit set, DFPT (2005) posit that insect pollination should be considered as an input for agricultural production and not just an ecosystem service. For instance the farmer may till the soil, fertilize, control pest and diseases and adopt all the recent agricultural innovations, yet in the absence of an insect pollinator to transfer pollen from the anther to the stigma of the flower, the farmer may still record low yields (Belize, 2010).

Shea is known to be an insect pollinated plant (Hall et al., 1996) and substantial evidence suggests shea produce more fruits when pollinated by insects (Okullo, 2004). Also, experimental studies conducted by Yidana (2004) indicated that shea is generally outcrossing, an indication that the species relies more on cross pollination for fruit set. However, there is little information on the exact quantity of shea yield that is attributable to insect pollination and the monetary value of insect pollinator contribution to the yield of shea.

Several authors (FAO, 2008; Sachs, 2008; Bartomeus et al., 2013; Melin et al., 2014) have reported declining insect pollinator populations, mainly due to landuse change and pesticide use. Therefore, if it is evident that pollinators are declining, there is the need to examine the extent to which their decline or absence will affect the yield of economic tree species (Breeze et al., 2011) like shea. This study therefore sought to examine the contribution of insect pollination as an ecosystem service to the fruit set and yield of shea in the Guinea savanna zone of Ghana.

1.3 Research Questions

The following research questions were addressed:

1. Which insect species are the pollinators of shea?

2. What is the quantity of shea fruit set and yield dependent on insect pollinators?
3. Does the frequency of insect-to-flower visits determine the quantity of fruit set and yields of shea?
4. What is the monetary value of insect pollination per bag (85 kg) of shea kernel?

1.4 Research Objectives

The main objective of the study is to examine the effect of insect pollination on the reproductive performance (fruit set and yield) of shea in cultivated fields of the Guinea savannah zone of Ghana.

1.4.1 Specific Objectives

1. To identify the insect pollinators of shea.
2. To examine the insect pollinator dependence of shea.
3. To determine the relationship between insect visitation rate and fruit set/yield of shea.
4. To estimate the monetary value of insect pollination per bag (85 kg) of shea kernel.

1.5 Operational Terms

- Insect pollinator dependence: this is a measure of the proportion of total fruit or nut output that can be attributed to insect interaction with shea flowers.
- 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.
- Shea parkland: this is a discontinuous cover of dispersed shea trees under which food crops are cultivated yearly.



- Fruit set: this is a count of the number of shea fruits produced.
- Yield: this is the weight (g) of shea fruits/nuts produced.

1.6 Study Area

1.6.1 Location

The study was conducted in cultivated fields of the Zini community in the Sissala West District of the Upper West Region of Ghana. The Sissala West District lies approximately between longitude 213 W to 2:36 W and latitude 10:00 N 11:00 N. The District shares boundaries with the Jirapa and Lambusia-Kaani Districts to the west, Sissala East District to the east, Daffiama-Bussie-Issah to south-west, Burkina Faso to the north and Wa East District to the south (Sissala West District Assembly, 2010). Zini is located about 95 km north of the Upper West regional capital (Wa) and approximately 30 km west of the Sissala West district capital (Gwollu). The two experimental sites were approximately 5 km apart. Experimental site 1 was located at 10⁰ 50' 00.0" N and 002⁰ 22' 57.2" W whilst site 2 was located at 10⁰ 52' 14.1" N and 002⁰ 24' 48.8"W. Figure 1 depicts the location of the experimental sites in Zini within the district map.

1.6.2 Climate

The climatic condition of the study area is one that is common to the three regions of northern Ghana (GSS, 2014). The rainfall is unimodal with an average annual rainfall of 1000 mm (SARI, 2004). The wet season commences in April and ends in October, whilst the dry season starts in November and ends in April.



Maximum temperatures are experienced during the months of March and April, whilst the lowest temperatures are experienced in December when the north east-trade winds push the Inter Tropical Convergence Zone further south. Mean monthly minimum and maximum temperatures are 22 °C and 35 °C respectively whilst the mean annual temperature is 28 °C. Lower temperatures are recorded during the cold season (December to February) and also characterised by hazy harmattan weather conditions (GSS, 2014).

Relative humidity fluctuates between 70% and 90% in the rainy season, but can however drop to as low as 20% in the dry season (SWDA, 2010). Low humidity together with windy conditions in the dry season makes savannah woodlands susceptible to wildfires. During this period, anthropogenic activities such as charcoal burning easily trigger bushfires (Lurimuah, 2011).



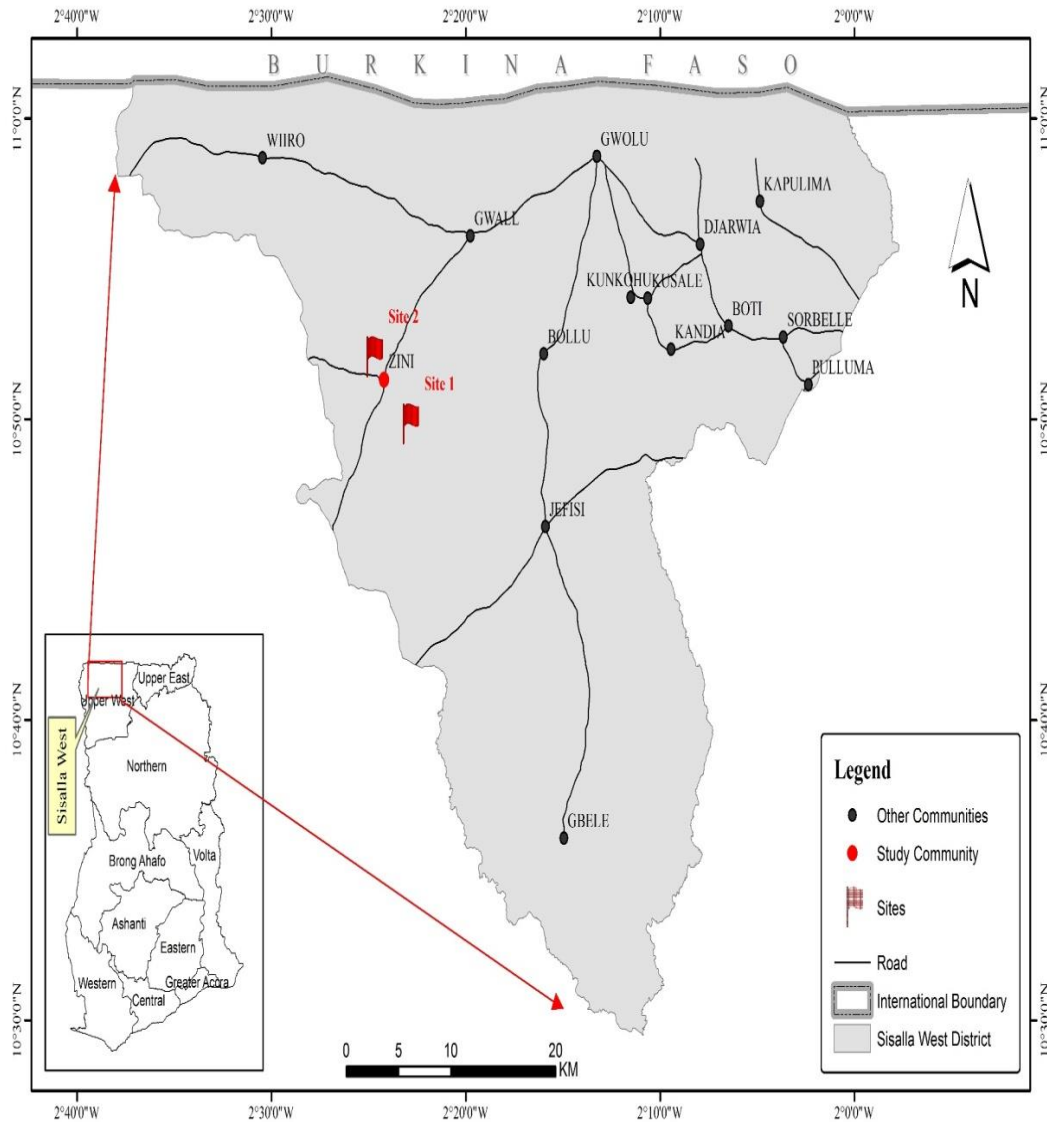


Figure 1: Map of Sissala West district showing the location of the experimental sites
(Source: modified from GSS, 2014)

1.6.3 Vegetation and Landuse

The study site is located in the Guinea savannah zone of Ghana. The vegetative cover is generally grassland with few interspersed drought resistant perennial woody species.

The major woody species include *Vitellaria paradoxa*, *Parkia biglobosa*, *Adansonia*

digitata, *Azardirachta indica*, *Faidherbia albida* and others. The high diversity of woody perennials supports domestic uses such as fuelwood, construction of houses, cattle kraals and fencing of gardens (GSS, 2014). There also exist shrubs and grasses that serve as fodder for livestock. Some common herbaceous plant species in the area include *Tridax procumbens*, *Andropogon pseudapricus*, *Panicum maximu*, *Pennisetum purpureu* and *Boerhavi diffusa* (Ziblim et al., 2015).

According to UNDP (2009) over 30% of the natural vegetation has been destroyed due to perennial bushfires, inappropriate farming practices, indiscriminate felling of trees and animal grazing. Although these anthropogenic disturbances are common to other districts in the region, the location of the Sissala West District makes it prone to overgrazing by Fulani cattle herds from neighbouring Burkina Faso (GSS, 2014).

The dominant landuse practices in the District are crop production and livestock rearing. Lands located about 3 km or more away from settlements are often used for crop production whilst lands close to settlements are reserved for pastures. There also exist a natural game reserve in the district (Gbelle Resource Reserve) and some few patches of degraded forest reserves. Infrastructural development such a settlements and schools also constitutes some of the common landuse in the District (SWDA, 2010).

1.6.4 Soil

The major kinds of soil in the district include the savannah ochrosols, tropical brown earth and the terrace soils. As a characteristic of most Guinea savannah soils, the savannah ochrosols are poor in organic matter and nutrients due to the absence of



dense vegetative cover. However, the tropical brown earth can support the cultivation of maize, beans, millet and other staple crops in the area. The terrace soils are found along rivers and are good for grain crops (SWDA, 2010).

1.6.5 Economic Activities

The people are dependent on three main industries for livelihood thus agriculture, manufacturing and services. Agriculture is however the major economic activity which employs about 82.3% of the population in the District (GSS, 2014). The major staple food crops produced include maize, groundnut, cowpea, yam, sorghum and vegetables such tomatoes and pepper. Farmers depend on traditional methods of farming using simple tools such as hoe and cutlass. However, some farmers employ mechanized methods especially tractor ploughing and animal traction in land tillage. For this reason, food crop production is generally on subsistence level with output per yield being low (GSS, 2014)

The predominant cash crops in the district include cashew, cotton, shea and dawadawa. Although shea and dawadawa are not cultivated, they are known to contribute significant to livelihoods in the district. Aside cotton, cashew is not also cultivated on commercial quantities in the district due to market uncertainties. Livestock production is also carried out in small scale within the district. Through this, individual households across the district earn some income to supplement their socio-economic needs. Most farmers practice the free range system of animal rearing. The common animals kept by households include goat, sheep, cattle and poultry birds.



In the manufacturing sector, the people are engaged in cottage industries such as shea butter and other oil and fat extraction industries, brewing of local drinks (pito), blacksmithing, metal/wood works, weaving, and pottery. They depend on indigenous resources and often use labour intensive technologies in production (GSS, 2014). National and cross border marketing of goods and services go on between Ghana and Burkina Faso. The location of the district provides an economic opportunity that empowers natives and other investors to create and expand businesses.

1.7 Justification of the Study

According to Tietenberg and Lewis (2012) human inability to place economic values on some environmental services imply those services has been valued at zero and this value does not inform the right trade-offs between the conservational and alternative uses of a natural resource. Monetary estimates of ecosystem goods and services are useful for justifying resource allocation for conservation purposes, because most human decisions are largely driven by financial implications (Gill, 1991; Curtis, 2004). The findings of the study could inform tradeoffs between the conservational value of insect habitats and the other alternative landuses with reference to the monetary value of insect pollination per bag of shea kernel.

Although Ollerton et al. (2011) posit 94% of tropical plants depend on some level of insect pollination for fruit set, only rough estimates of the proportion of plants that require insect pollination may be deceptive without information on the degree to which each species depend on insect pollinators (Klien et al., 2007). The present study provides an estimate of the extent to which the yield of shea will be affected by the absence of insect pollination services. Owing to the role of shea in livelihood



empowerment, it is expected that such information could be used by the District Assembly in predicting the consequences of yield declines on livelihoods of shea nut collectors in the District.

According to API (2007) farmers have limited knowledge on the importance of insect pollination in Ghana, and they often lump pollinators with pest. This limited knowledge does not prompt farmers to adopt eco-friendly land management practices to conserve insect pollinators. The mainstreaming of ecosystem friendly landuse practices into contemporary landuse will remain a mirage until farming communities understand the extent to which their livelihoods will be affected by the loss of these services. The outcome of this study provides a link between pollination and the yield of the most abundant economic tree species (shea) in northern Ghana. The study findings may serve as reference point for linking biological diversity to the sustainability of shea. The general hope is that local authorities, the District Assembly in the study area and the Environmental Protection Agency will intensify environmental education to conserve insect pollinators.

Pollination has been described as an understudied ecosystem service in Africa with several inadequacies in knowledge and understanding of pollination (Rodger et al., 2004; Gemmill-Herren et al., 2014). Although often overlooked, pollination deficit in wild and agricultural ecosystems can significantly affect crop productivity (Adjaloo, 2012). The findings of this study will provide relevant knowledge on the pollination of shea that could be useful to foresters, agronomist and farmers working towards the domestication of the plant. That has not only promoted academic successes through



the contribution to body of knowledge but will alert rural communities to work towards biodiversity conservation to sustain shea.

1.8 Research Challenges

Although the effect of insect pollination on fruit set and yield of shea was the main focus of this study, other variables such as edaphic and climatic conditions of the area can influence yield. These factors constitute extraneous variables that were difficult to control in the study. Notwithstanding, the selection of experimental sites across different farm lands offered an opportunity for mitigating the effect of an individual farmer' soil management practices on fruit set and yield of shea.

Again the selection of two experimental sites has been recognised by the researcher as a limitation to the findings of the study since the entire shea parkland of the community could not be studied due to time and resource limitations. Access to experimental sites was also difficult owing to the bad nature of the road network in the community.

1.9 Organisation of Thesis

The study was organised into five chapters. Chapter one contains a general introduction of the study. It elucidates the extent of the problem, the significance of the study as well as the profile of the study area. Chapter two contains a review of relevant literature on the mechanism of pollination with specific emphasis on the pollination ecology of shea. It also contains a synthesis of existing literature on the contribution of insect pollinators to fruit yield of some major crops from which relevant lessons were drawn.



Chapter three is a description of the methodology that was employed in gathering data from the field. This includes the research design, sampling procedures and the techniques used in data collection and presentation. Chapter four contains a presentation of results and discussion of findings with reference to relevant literature. This chapter enabled the transformation of data in to information. Chapter five is a summary of the key findings of the study, conclusion and recommendations.



CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

This chapter explored pollination as an ecosystem service and its contribution to fruit set and yield of some major food crops. The chapter looks at the mechanism of pollination as well as the agents of pollination. Other issues addressed in the chapter include the role bees in pollination, pollinator dependence of fruit trees, effect of insect visitation on fruit set, economic value of insect pollination, geographical distribution of shea, flowering and fruiting in shea, pollination ecology of shea, the economic importance of shea, contribution to livelihood and anthropogenic threats to shea. The chapter ends with an overview of shea in Ghana

2.2 Pollination as an Ecosystem Service

Ecosystem services can be defined as the outputs from nature which are of benefits to human (MEA, 2003). These services include conditions and processes through which the constituent species contribute to life (Daily, 1997). The term “ecosystem service” unlike ecosystem itself is a relatively new concept that was coined in the 1960s to present the environment as an economic resource capable of providing goods and services (Martín-López et al., 2009).

The significance of ecosystem services attracted United Nation (UN) attention in 2000 following the increasing burden degraded ecosystems were placing on human wellbeing and economic development as well as the potential of harnessing resilient ecosystems for the achievement of Millennium Development Goals (MDGs) on



poverty eradication (MEA, 2003). This necessitated a multi-disciplinary global assessment of the health of the world's ecosystems in 2000 known as the Millennium Ecosystem Assessment. Ecosystem services can be classified base on function, description or organisation (Moberg & Folke, 1999; De Groot et al., 2002). The Millennium Ecosystem Assessment classified ecosystems services on functional bases into provisioning, supporting, regulating and cultural services (MEA, 2003).

The contribution of ecosystem services to human wellbeing provides a direct link between sustainability and ecological integrity (Martín-López et al., 2009). The sustainability of these services is however under threat despite their importance to human wellbeing (Daily, 1997; Palmer et al., 2004). For instance, pollination which is a key ecosystem service is often cited as an endangered service by many authors (Kevan and Phillips, 2001; Ghazoul, 2005; Steffan-Dewenter et al., 2005). Based on the relationship between ecosystem services and human wellbeing, Carpenter and Folke (2006) posit that an effective assessment of ecosystem services requires an interdisciplinary approach that includes ecologists and social scientists.

MEA (2003) categorised pollination as a regulatory ecosystem service along with climate regulation, disease regulation, water purification and regulation. Although considered a regulatory service, it contributes directly to provisioning services. According to Aluri (1990) biotic pollination is a broad concept that includes animal behaviour, ecology, plant physiology, genetics, physiology and reproduction. Biotic pollination is produced on a local scale via wind, water or mobile animals foraging within or between habitats and can be influenced by individual behaviour, population biology and community dynamics (Lundberg & Moberg, 2003). Pollination has the



potential of changing the dynamics of plant communities and ecosystem properties (Lundberg & Moberg, 2003).

The value of insect pollination to the world's economy in terms of human food production was estimated at €153 billion per year (Gallai et al., 2009). The availability of this service can influence the quantity of world food production as well as the nutritional and cultural value of plant products to human societies (Steffan-Dewenter et al., 2005). Aside the provision of pollination services, the diversity and behaviour of insect pollinators serve as an important bio-indicator for assessing ecosystem health (Kevan, 1999).

2.3 Mechanism of Pollination

Matured pollen grains go through structured dehydration prior to their release from anthers; this occurs concurrently with dehydration of anther cells as well as sugar-starch conversions (Pressman et al., 2002). The anther then dehisces to release pollen grains (Bots & Mariani, 2005) into a compatible stigma with the help of a pollen vector. When the dehydrated and metabolically inactive pollen grain lands on a compatible stigma, it draws water from the stigma and forms a pollen tube. This process may take minutes to hours depending on the species. The pollen tube then extends through the tissues of the pistil towards the ovary where sperm cells are delivered for the accomplishment of fertilisation (Edlund et al., 2004). Pollen-stigma interface may vary from one flower to another depending on flower morphology, stigma exudate content, exine layers and pollen coat structure (Edlund et al., 2004).

In angiosperms, reproduction is very selective, female tissues have the ability to discriminate between pollen grains by detecting pollen from the appropriate species



as well as rejecting pollen from unfamiliar species including the same plant in self-incompatible species (Edlund et al., 2004). Molecular mechanisms in the stigma and pistil can prevent fertilisation from genetically distant or closely related pollen (McCubbin & Kao, 2000). In self-incompatible flowers, stigmas reject self-pollen by preventing pollen hydration, germination and tube invasion (Nasrallah, 2000; Silva & Goring, 2001; Kao & Tsukamoto, 2004). The tendency of heterospecific pollen transfer increases when several plant species share pollinators (Arceo-Gómez et al., 2016).

The success of pollination does not only depend on insects but also the flowering plants “pollen performance” thus the traits in the male gametophyte that enhances its ability to attain a highly specialised function such as reaching to the stigma, germinating, developing a pollen tube that acquires adequate resources, being able to reach the base of the style and enter the ovary as well as locating the ovule to deliver sperm cells to a receptive egg (Williams & Mazer, 2016). The study of Mazer et al. (2016) revealed a positive correlation between style length and pollen receipt after observing pollen germination rates and pollen tube growth. The intrinsic features of an individual flowering plant or taxa can equally influence the quantity and quality of pollen received by the stigma (Arceo-Gómez et al., 2016; Mazer et al., 2016).

Pollination represents an essential stage in a plant’s life cycle, the viability of pollen is therefore critical for efficient sexual reproduction of flowering plants (Bots & Mariani, 2005). A viable pollen grain should be able to live, grow, germinate or develop (Beyhan & Serdar, 2008). Pollen viability can be affected by drought, heat stress and ultra violet beta (UV-B) radiation. Endothecia thickenings remain closed



in wet conditions. Hence, pollen grains are often released from anther during dry and warm weather conditions through which pollen grains appear dormant and dehydrated with low metabolic rates (Okullo, 2004). Plants ability to keep pollen viable in this dry state over relatively long periods is considered an important adaptation to adverse environmental conditions (Hills, 1997).

2.4 Pollen Morphology

According to Taylor and Helper (1997) the pollen grain is structurally made of a multi-layered pollen wall produced from saprophytic cells of the anther and pollen itself. The outmost layer of the pollen wall is referred to as the pollen coat or pollen kit. The coat is primarily responsible for the protection of pollen cells from excess desiccation, UV radiation and pathogens (Edlund et al., 2004). The pollen coat is structured according to its delivery mechanism, insect pollinated flowers have thicker pollen coats whilst wind pollinated plants have limited coating (Edlund et al., 2004).

The pollen coat constitutes about 15% of the entire pollen grain mass in entomophilous plants (Pacini & Franchi, 1996). The pollen coat does not only protect the pollen but also aid in pollination (Dickinson et al., 2004). It contains pollinator attractants such as polyunsaturated C18 free fatty acids which are potent honeybee attractants. A chemical analysis of plant pollen from 15 different plant species revealed that each species produces its own mixture of volatiles with varying degrees of the three major floral scents (isoprenoids, fatty acids and benzoids) (Dobson & Bergstrom, 2000).



Pollen grains occur in spherical, elongated, oval, triangular and tetrahedral shapes with an average diameter of 3 to 300 μm (Wunnachit et al., 1992). The water content of a pollen grain at the point of release ranges from 15-35% after dehydration (Buitink et al., 2000). They are uniquely structured according to the mechanism (biotic or abiotic) of transport (Ackerman, 2000; Dobson & Bergstrom, 2000; Lunau, 2000). In insect pollinated plants, the pollen grains tend to be copious, coloured and sticky whilst wind pollinated plant pollen are usually less sticky (Richards, 1997). There also exist variations in germination and stigma penetration abilities of pollen (Wunnachit et al., 1992). The quantity of pollen grains produced often varies between plant species.

2.5 Agents of Pollination

The transport of pollen grains from the anther of a flower to the stigma of flower is a fundamental event in the process of fertilisation (Bots & Mariani, 2005). Edlund et al. (2004) posit that the agents involved in pollen transfer could be biotic or abiotic (animal or wind). Although some plant species can rely on both biotic and abiotic agents for pollination services, others depend on one for pollen transfer (Klein et al., 2007). The type of pollination agent can determine pollination success in plants due to its influence on the viability of pollen deposited in the stigma (Luna et al., 2001; Aylor, 2003)

Allen-Wardell et al. (1998) further classified biotic (animal) pollinators into vertebrate and invertebrates. Some vertebrates are involved in pollen transport services mostly in tropical, desert and oceanic Islands (Fleming, 1993). Bats serve as



the major pollinators for many economic plants that include neem, eucalyptus and palm species (Fujita, 1991). In the Samoa Island, bats have been identified as the major pollinators of dominant rainforest canopy tree species (Cox et al., 1991). This makes bat species extinction, in regions where they are major pollinators, a threat to biodiversity and food security (Cox et al., 1991; Nabhan, 1996).

The interaction between non-flying arboreal mammals and flowering plants also provide pollination services that are generally left unnoticed in many pollination studies (Mittermeier et al., 1994). In many natural habitats, non-flying mammalian species of monkeys, squirrels and lemurs serve as agents of cross-pollination services (Mittermeier et al., 1994). For instance, in Madagascar, the black and white ruffed subspecies of lemur is known for its ability to open the floral bracts of travelers' tree (*Ravenula madagascarensis*) to effect pollination (Kress et al., 1994).

Nabhan (1996) stated that although the value of pollination services provided by these vertebrates is yet to be estimated in most regions of the world, habitat fragmentation, changes in forest canopy and hunting may lead to their extinction and eventual loss of this service. Substantial knowledge gaps still exist in understanding flower nectar-feeding and the pollination efficiency of most non-flying mammals (Allen-Wardell et al., 1998). There seems to be a wide gap of knowledge in verifying successful pollination of tree species that are not in isolation. Despite, the paucity of information on the importance of non-flying mammals in pollination, some studies have recorded reduced seed set in areas where their populations are limited (LeMont et al., 1993).



The invertebrate pollinators are predominantly bees, including *Apis* spp (honeybees) and other invertebrates such as flies, moths, butterflies, wasps and beetles that important roles as primary or secondary pollinators of both cultivated and wild plants (Buchmann, 1996; Rader et al., 2016). Many of the world's most important economic fruit and seed crops such as coffee, cocoa, strawberry and shea benefit from animal pollination (Free, 1993; Klein et al., 2007).

2.5.1 Role of Honeybee in Pollination

The honeybee, *Apis mellifera* L. (Hymenoptera: Apidae) is regarded as the most ubiquitous, versatile and well managed insect pollinator (Bots & Mariani, 2005; Klein et al., 2007). The term wild honeybee is used to describe indigenous unmanaged honeybees living in natural vegetation like woodlots, windbreaks, wastelands and parks (Chang & Hoopingarner, 1991). The honeybee is ranked as the most economically valuable animal pollinator of crop monocultures in many parts of the world (Watanabe, 1994). The absence of honeybee could result in 90% decline in the yield of some fruit, seed and nut crops (Southwick & Southwick, 1992).

In the United State (US) alone, the honeybee is known for pollinating about 100-150 plant species (Watanabe, 1994). It is reported that honeybee visitation can increase the number of fruit set in about 14% of crop systems worldwide (Garibaldi et al., 2013). In North America and other regions of the world farmers depend on managed honeybees for pollination services in agricultural fields (Kearn et al., 1998; Potts et al., 2010).

However, flower pollination occurs as a side effect of pollen collection by bees (Bots & Mariani, 2005). Pollen is a source of protein, fatty substances, vitamins and



minerals for bees and considered inseparable from the survival of bees. Among the apidae, Pollen is collected in the mouth parts and later moistened and kept on the posterior pair of legs in pollen baskets. Aside the mouth parts and the legs, pollen grains get stuck to body hair. The hairiness of bees makes them great pollen carriers as compared to non-bee insect pollinators. Another reason accounting for the spectacular success of honeybee in pollination is the habit of foraging on flowers of the same species repeatedly until it becomes unattractive (flower constancy) (Graham, 1992). This behaviour can promote within-species pollen transfer, and reduce heterospecific pollen transfer, making it a favourable strategy from the plants point of view.

A flower becomes unattractive when there is less pollen, cessation of nectar and aroma production, change in flower colour, wilting, permanent flower closure and the shedding of flower petals (Delaplane & Mayer, 2000). Bees can forage on fields located at relatively longer distances of more than 4 km away from their hive (Eastham & Sweet, 2002), which makes them important long-distance pollen transporters.

Studies on the determinants of circadian-species specific activity patterns indicate that certain species of hymenoptera have specific daily durations of foraging activity (Stone, 1994). This is influenced by insect species morphology (body size and colour) (Pereboom & Biesmeijer, 2003), physiology and the time of pollen release from main food sources (Stone, 1994). The study of Hoehn et al. (2008) revealed that larger body sized bees visit flowers earlier (during cooler morning hours) as compared to smaller body sized bees. The early large sized bees tend to transport



more pollen than the small sized bees. However, the foraging behaviour of late small sized bees were found to enhance within flower pollen transfer to the stigma than the large sized bees (Chagnon et al., 1993).

2.5.2 Role of Stingless Bees in Pollination

Aside the honeybee, stingless bee species play an important role as pollinators of some cultivated and wild plant species (Mathiasson et al., 2015). Stingless bees (Hymenoptera: Apidae) comprise of a diverse group of eusocial bees in tropical and subtropical regions that belong to the tribe Melipolinini. An estimated four hundred stingless bee species have been identified worldwide of which eleven species have been found in Ghana (Kwapong et al., 2010). These species predominantly exhibit a generalist flower foraging habit which is an essential quality for pollination and biodiversity conservation as a whole (Danaraddi et al., 2007; Karikari & Kwapong, 2007). Indigenous knowledge from the study of Karikari and Kwapong (2007) revealed that pollination services provided by stingless bee species was known to contribute to the yield of some crops.

Following the declining honey bee populations in most regions, Karikari and Kwapong (2007) posit stingless bees could supplement honeybee pollination services. More importantly, the non-functional sting of these species makes them ideal for the provisioning of pollination services in enclosed areas such as greenhouses (Slaa et al., 1999). Moreover, honeybee is not the most efficient pollinator of some plants due to miss-match between body size and flower size, low nectar production and specialized pollen release mechanisms in some plants (Kearn



& Inouye, 1997a). The inefficiencies of honeybee pollination create gaps in pollination service delivery that stresses the need for pollinator diversification. Stingless bee species are relatively more resilient to floral resource scarcity as compared to honeybees because honeybees often migrate in situations of limited floral resources (Hepburn & Radloff, 1998; Roubik, 2006).

Aside the biological significance of non-honeybee pollination, the commercial value of non-honeybee pollinator contribution to crop yield in US alone was estimated at \$6.7 billion per year (Kearns et al., 1998). Stingless bee pollination is reported to increase fruit set in both quantity and quality, for instance the fresh weight of strawberry fruits produced from stingless bee (*Trigona angustula*) pollinated plants was 41% higher than those that received open pollination (Malagodi-Braga & Kleinert, 2004). Similarly, green house experiments conducted by Malagodi-Braga (2002) revealed that one *T. angustula* colony allowed to forage freely on 1350 strawberry plants resulted in nearly 100% of the primary flowers developing in to commercial grade fruits as compared to 88% in open pollinated plants in the field. In the study of Lassen et al. (2016) shea trees with stingless bee colonies nesting on trunks had a significantly higher fruit set than trees without colonies.

Stingless bees are often described as true generalists because a single species can collect floral rewards from up to 100 plant species annually (Biesmeijer et al., 2005). However, some individual species tend to specialize on single floral species for certain amount of time (Slaa et al., 2003). In the past, stingless bees were known as effective pollinators of nine (9) major crops, however recent studies confirmed nine (9) more crops putting the total at eighteen (18) crops (Slaa et al., 2006).



Further studies could therefore reveal more potentials of the stingless bee with regards to pollination efforts. Some of the common crops pollinated by stingless bee species include Mango, strawberry, sweet pepper, cucumber, shea, coffee, avocado and others (Heard, 1999; Klein et al., 2003a; Lassen et al., 2016). According to Mathiasson et al. (2015) the peak daily forage activity of *Hypotrigona* spp. occurs in the morning session (between 9:00 and 10:00 am) but weather conditions (temperature and humidity) can significantly influence the foraging activity.

2.6 Pollinator Dependence of Major Fruit/ Seed Crops

A pollinator dependence ratio is a theoretical metric that depicts the proportion of total crop output lost in the absence of pollination services (Breeze et al., 2016). These ratios are relevant in estimating the degree to which each crop species rely on insect pollinators for fruit/seed yield (Klein et al., 2007). In a similar opinion, Kevan and Phillips (2001) posit that an adequate assessment of the economic value of animal pollination to global food supply will require an extensive review of breeding systems, flower animal visitors as well as the level of crop yield increases from insect pollination under controlled experiments.

The exclusion of pollinators from accessing flowers is a better control method for estimating the actual contribution of insect pollinators to crop yield (Bartomeus et al., 2014). However, most conventional studies employed the observational approach with very few studies manipulating insect flower visitations in studying the pollinator dependency of major crops (Steffan-Dewenter & Tschardt, 1999; Heohn et al., 2008; Bartomeus et al., 2014).





Garibaldi et al. (2013) opined number of fruit set as a good proxy for measuring the effect of pollination on crop yield although some plants tend to record a low correlation between yield and fruit set. Notwithstanding, the total number of fruit set per plant is positively correlated with yield (weight) for most plant species (Zebrowska, 1998). However, plants with equal fruit set may differ in yield due to differences in fruit size (Bos et al., 2007). The quantity of fruit yield cannot represent productivity completely since economic standpoint focuses on the quality of fruit set as well. Fruit quality can be negatively correlated with quantity in some crops especially in situations where there is high fruit load on a tree (Ferguson & Watkins, 1992). Inconsistent relationships between fruit quantity and quality are common in plants with indeterminate flowering such as oilseed rape (Bommarco et al., 2012).

A global review of animal pollinator dependence of 115 leading food, fruit, seed and vegetable producing crops indicate that 87 of the world's economically important crops rely on some level of animal pollination (Klein et al., 2007). After assessing pollinator needs of 264 crop species in Europe, Williams (1994) revealed that 84% of crop species depend on some level of animal pollination for reproduction. Animal pollination is required for the sexual reproduction of many cultivated and wild plants that provide calories and micronutrients for humans (Larson & Barrett, 2000; Westerkamp & Gottsberger, 2000; Ashman et al., 2004; Sundriyal & Sundriyal, 2004). About 50% of the plant-derived sources of Vitamin A come from animal pollinated plants in many parts of Southeastern Asia (Chaplin-Kramer et al., 2014).

Klein et al. (2007) classified crop species into five categories base on the degree of dependence on animal pollination for reproduction; (i) essential (crops with which

production can be reduced by 90% or more in the absence of animal pollination), (ii) high (crop species that will record 40 to less than 90% reduction in yield without animal pollination, (iii) modest (10 to less than 40% reduction in yield without animal pollination), (iv) little (greater than 0 to less than 10%), and (v) crops with no yield decline in the absence of animal pollination services.

Similarly, Bartomeus et al. (2014) kept the average animal pollinator dependency at 18 to 71% for most species. Base on Klein et al. (2007) categorisation of pollinator dependence of crop species, animal pollination is essential for thirteen (13) of the major crops traded in the world market, thirty (30) are highly dependent on animal pollination with twenty seven (27) crops considered moderately dependent on animal pollination. It is estimated that insect pollination contributes to about 35% increase in both yield and quality of world crop production (Kremen et al., 2004). A percentage increase in yield does not only reflect plant productivity but also translates into significant amount of income for crop farmers (Zebrowska, 1998).

Controlled experiments conducted by Bartomeus et al. (2014) indicated that insect pollination contributed to about 20% increase in yield of oilseed rape and strawberry, 40% increase in yield of field bean and as high as 71% increase in the yield of buckwheat when the yield of insect pollinated flowers were compared with bagged flowers of the same species. Strawberry fruits produced from flowers that received sufficient pollination had better fruit quality as compared to fruits produced from flowers with insufficient pollination (Albano et al., 2009). Stanley et al. (2013) recorded a 27% decline in seed set and 30% decrease in seed weight per pod of oilseed rape when insect pollinators were excluded from pollinating flowers.



The animal pollinator dependence of a crop species can vary from one region to another. It can also differ between varieties of the same crop species (Breeze et al., 2016). This was evident in studies that assessed the pollinator dependence of oilseed rape, Stanley et al. (2013) recorded a pollinator dependence of 30% whilst Bartomeus et al. (2014) recorded 20% for different varieties of the same crop. However, Klein et al. (2007) posit that the positive effect of pollination on crop yield can be confined when other variables that influence crop yield such as soil nutrients, macroclimate, water and pest and disease status are suboptimal. Again, estimates of pollinator dependence of world food production are criticised because some authors depend on unreliable data sources for making estimates (Cook et al., 2007; Klein et al., 2007).

2.7 Effect of Insect Visitation on Fruit/ Seed Set

Higher insect visitation rate is consistently associated with enhanced crop yield (Bartomeus et al., 2014). Moreover, substantial evidence suggest that adequate pollination results in improved fruit or seed quality in entomophilous plants, major fruit crops such as citrus, strawberry, tomato and pepper all recorded better yields under adequate pollination in both temperate and tropical environments (Roldan et al., 2006; Garratt et al., 2013).

Not only does the intensity of pollination influence yield quantitatively, the study of Bartomeus et al. (2014) discovered a higher oil content with less chlorophyll when oil rape seed was adequately pollinated as compared those with insufficient pollination. Similarly, strawberry produced more homogenously shaped fruits with high commercial grade when it received sufficient pollination (Zebrowska, 1998). In



the study of Klatt et al. (2014) strawberry plants that were adequately pollinated by honeybees produced high commercial grade fruits with a longer shelf life. The level of pollination received and resource allocation were identified as the major determinants of fruit size variability in *Actinidia deliciosa* (Gonzalez et al., 1998).

According to Bartomeus et al. (2014) dynamics of insect visits to a crop species can be influenced by the foraging behaviour of a single insect pollinator species. For instance, honeybees influenced the insect visitation patterns of three out of four crops that were studied in Europe. The study of Garibaldi et al. (2013) recorded a positive association between fruit set and wild insect visits to the flowers of 41 crops worldwide. High insect pollinator richness resulted in an increase in the mean number of pumpkin seeds per fruit (Hoehn et al., 2008).

In contrary to the general high insect pollinator richness in the natural environment than cultivated lands, Norfolk and Gilbert (2014) recorded higher insect visits to wild trees in agricultural gardens than those in surrounding natural environment. According to Klinkhamer et al. (1994) an increase in insect pollinator visitation rate to a flower does not always result in an increased seed set. In some plants, it may rather result in lower seed set due to higher levels of selfing, clogging of stigmatic surfaces with self-pollen and may end in reduced pollen export (Klinkhamer et al., 1994). For instance, Norfolk and Gilbert (2014) observed no significant difference in seed set of wild plants in agricultural gardens and those in the surrounding natural environment though insect visitation rate was significantly higher in the gardens than the natural environment. The flower visitors of a species can also vary tremendously from one region to another, In Ecuador, Veddeler et al. (2006) reported flower



visitors of coffee to be made of 95% social and less than 5% solitary bees but Klein et al. (2003b) recorded 70% social and 30% solitary bees for coffee in Indonesia.

2.8 Economic Value of Insect Pollination

Insects are known to contribute to an estimated 10% of the economic value of the world's food production (Chaplin-Kramer et al., 2014). The positive effect of insect pollination on fruit quality indirectly contributes to economic value by enhancing the commercial grade of food produce. Estimates of economic value of pollination can however vary from one region to another due to differences in produce prices, production cost, labour and other factors of production (Breeze et al., 2016). Although several factors influence these variations, Chaplin-Kramer et al. (2008) posit that most of the variations in estimates are significantly influenced by the methodological approach.

Existing methodological approaches used in estimating the value of insect pollination services include total production value approach, proportion of total production value attributable to insect pollinator approach (Morse & Calderone, 2000; Losey & Vaughan, 2006), cost of replacement approach (Allsopp et al., 2008) and direct managed pollination value approach (Burgett et al., 2004). However, each approach has been criticised on its flaws. For instance total production value approach has been flawed by the fact that equating pollination value to total production output is an overestimation of pollination service value because many other factors contribute to plant production success (Losey & Vaughan, 2006). This could therefore be an assumption that all other cost of production such as irrigation



and labour cost are discounted. Hence this method overestimates the value of insect pollination especially among cultivated crops.

The proportion of production value attributable to insect pollination approach has also been criticized because authors depend on unreliable data sources for estimating pollinator dependence ratios (Cook et al., 2007; Klein et al., 2007). This approach requires series of experimental based studies on insect pollinator dependence of major food crops across different regions of the world to make meaningful estimates. However, there currently exist little reliable data on pollinator dependences of food crops especially in the developing world (Rodger et al., 2004; Klein et al., 2007).

The weaknesses of these methodological approaches were exhibited in managed bee pollination service value estimates. In the USA, the annual value of managed honeybee pollination was estimated between US\$1.6 billion and US\$14.6 billion but in Australia, annual value of the honey bee pollination was estimated at US\$12.6 to 30.7 million (Cook et al., 2007). Although ecosystem service valuation is essential for valuing natural resources, inconclusive estimates present a risk to unsustainable resource allocation for conservation (Allsopp et al., 2008).

Substantial variation in the estimates of economic value of insect pollination to the world's economy does not only reflect variation in methods but also reflects the paucity of accurate information on pollination. This therefore supports calls for more studies on pollination in to help provide better estimates of the value of pollination (Klein et al., 2007). Assigning economic values to insect pollination is important because managed honey bee pollination is now considered as an agricultural input for production and not just an ecosystem service (DFPT, 2005). Therefore, since



economic values are attached to all other factors of production, pollination should be recognised as an input for production in insect pollinated plants.

2.9 Insect Pollinator Decline and World Food Production

Natural habitats provide support for diverse species of wild pollinators and serve as resilient and complementary sources of pollination services for agricultural landscapes (Kremen et al., 2002; Carvalheiro et al., 2011). Wild insect pollinators require undisturbed habitats for nesting, roosting and foraging (Aluri, 1990). Moreover, some pollinators require plants that flower sequentially to provide a sustainable source of food all year round (Öckinger & Smith, 2007). Unfortunately, the constant human interference in intensive resource exploitation and grazing of livestock tend to fragment natural habitats that are required for the survival of insect pollinators (Aluri, 1990; Bartomeus et al., 2013). Recent studies reported shifts in community composition of insect flower visitors of many crops (Bartomeus et al., 2013).

On the contrary, agricultural land use tend to favour pollinators in arid environment where insects exploit resources from weed floral verges and field boundaries (Hopwood, 2008; Norfolk et al., 2012). For instance, Norfolk and Gilbert (2014) reported higher pollinator species richness in agricultural gardens of Egypt than the surrounding natural environment. Similarly, irrigated gardens in Israel recorded more bee species abundance than the external habitat of the same locality (Gotlieb et al., 2011).

The advent of inorganic farming practices with an increased application of agrichemicals also pose a threat to insect pollinators (Ingram et al., 1996b; Öckinger



and Smith, 2007; Goulson et al., 2015). At the global level, organophosphates and neonicotinoids are known to pose the highest risk to honeybees (Sanchez-Bayo & Goka, 2014). Neonicotinoids for instance contain neurotoxins that are often targeted at the central nervous system of insects causing overstimulation, paralysis and mortality (Tomizawa & Casida, 2005). In the northern region of Ghana, about 62% of the chemicals used in legume production are reported to be highly toxic to the biological environment (Sowley & Aforo, 2014). The gradual adoption of inorganic farming practices by farmers in shea growing areas presents a threat to insect pollinators.

There are also reported declines in managed honeybee colonies as well (Delaplane & Mayer, 2000). The spread of parasitic pests and low market prices for bee services have been identified as the major causes (Graystock et al., 2013). Johnson (2008) also reported Colony Collapse Disorder (CDD) as a serious threat to the pollination industry in recent times.

Despite the declining insect pollinator populations in some regions, attempts to introduce foreign pollinator species has resulted in complications in nearly all countries, foreign pollinators introduce pathogens that affect wild pollinators of the same species or other species in the local habitat (Plischuk et al., 2009; Graystock et al., 2013). The introduction of these species poses several other threats including hybridisation, competition with native bees and changes in plant pollinator interactions (Goulson and Huges, 2015). A classic example of the consequences of honey bee introduction into new environment is the mite *Varoa destructor*, which was originally associated with Asian honey bee *Apis cerena*, it has since infested the



European honey bee *Apis mellifera* which unfortunately have little resistance to the pest (Goulson et al., 2015). Native bees are often recommended because they can survive the local environmental conditions and also adapt well to extreme weather events (De Oliveira et al., 1991).

Paradoxically, global food crop demand is increasing with decreasing number of pollinating insects. According to Gallai et al. (2009) pollination service declines could lead to shortages in some food crops. Pollinator decline will equally have consequences on human health (Vanbergen, 2013) since insect pollinated crops provide 70% of the micronutrients needed for human health (Eilers et al., 2011). Coincidentally, most pollinator dependent crop species are among the richest crops in micronutrients needed for human health (Chaplin-Kramer et al., 2014). Steffan-Dewenter et al. (2005) indicated that further decline in pollination services could as well impoverish human diet in terms of cultural attachment. Insect pollinator decline will equally lead to a corresponding loss in plant species richness and abundance (Beismeyer, 2006). On the contrary, Ghazoul (2005) and Richards (2001) posit world caloric intake will not be affected by the decline in animal pollinators because reproduction of major world staple crops is independent of insect pollination services. Although caloric intake might not be affected by pollinator decline, some important micronutrients may be lost from human diet.

Classical examples of the consequences of insect pollinator decline was evident in Alfalfa and pumpkin seed losses in New York in the 1950's due to limited pollination services (Watanabe, 1994). Aside the ecological consequences, the effect of honey bee population decline on crop production together with the economic



burden of reduced crop yield was estimated at \$1.5 million yearly (South-wick & Southwick, 1992). However, there is a difficulty in completely disentangling the effect of pollination on crop yield from the other factors that influence yield, for instance almond yield decline in California was attributed to a combined effect of weather and insufficient pollination services (Allen-Wardel et al., 1998). Again in 1977, Cherry prices rose in Ontario due to the combined effect of bad weather and decline of honeybee population after mites' parasitisation.

2.10 Flower Morphology and Fruiting in Tropical Fruit Trees

All flowers generally have common basic structures but there are huge variations in structural morphology (Okullo, 2004). According to Dafni (1992) flowers are predominantly composed of male and female organs protected by petals in the form of a tube or crown like corolla. Flower petals occur in various colours as an adaptive response (Richards, 1997). The petals are often supported and protected by green coloured structures called sepals (calyx) (Okullo, 2004). Flowers have different aroma, ranging from odourless to highly aromatic odours which is used as a fundamental attractant of flower visitors from long range (Richards, 1997).

The gynoecium (female part) of the flower is often referred to as the pistil, made up of an ovary with one or more ovules. A fully developed pistil consists of one or more carpals with specialized tissues developed for pollen reception and the transport of the male gametes to the ovules (Okullo, 2004). The flower stigma is structurally composed of a stigma coat defining the stigma as uniquely water-permeate. The primary functions of the stigma include pollen capture, provision of support for



hydration and germination. Stigmas also promote outcrossing or self-fertilisation by coordinated timing of their development with pollen release (Edlund et al., 2004).

The androecium (male part) of a flower is the stamen which is made of a hair like filament, vascular tissue and a two-lobbed anther. The anther is primarily responsible for pollen production (Bots & Mariani, 2005). The anthers dehisce or split open to discharge pollen at the most appropriate time (Edlund et al., 2004). Pollen grains in the anther develop into two nuclei (vegetative nucleus and generative nucleus) through mitosis (Hills, 1997). Figure 2 is a diagrammatic representation of the most common parts of a flower.

Phenological events in most tropical plant species fluctuate with varying climatic conditions though some are independent of the climatic factors (Grouzis, 1991). Substantial evidence suggests patterns of phenological events in most fruit trees in warm climates are highly correlated with air hygrometry, soil moisture and topography (De Bie et al., 1998; Law et al., 2000; Okullo et al., 2004). Another vital climatic factor triggering flowering in plants is atmospheric temperature (Lyndon, 1992). Temperature was found to be correlated with many phenological cycles including flowering in tropical environments (Marques et al., 2004; Stevenson, 2004). In seasonal climates, flowering can be induced tremendously by heavy rains after long periods of drought (Sakai et al., 2006).

The level of resource accumulation in a plant can also trigger the initiation of flowering (Sakai et al., 2006). Tropical plants may undergo interspecific or intraspecific synchronisation in response to internal physiological processes (Marques et al., 2004). Intraspecific synchronised flowering is considered more



advantageous for the creation of high opportunities for cross pollination. However, interspecific synchronisation can result in more fitness when predator satiation and shared attraction of floral visitors occur (Sakai, 2002; Pellegrino et al., 2005).

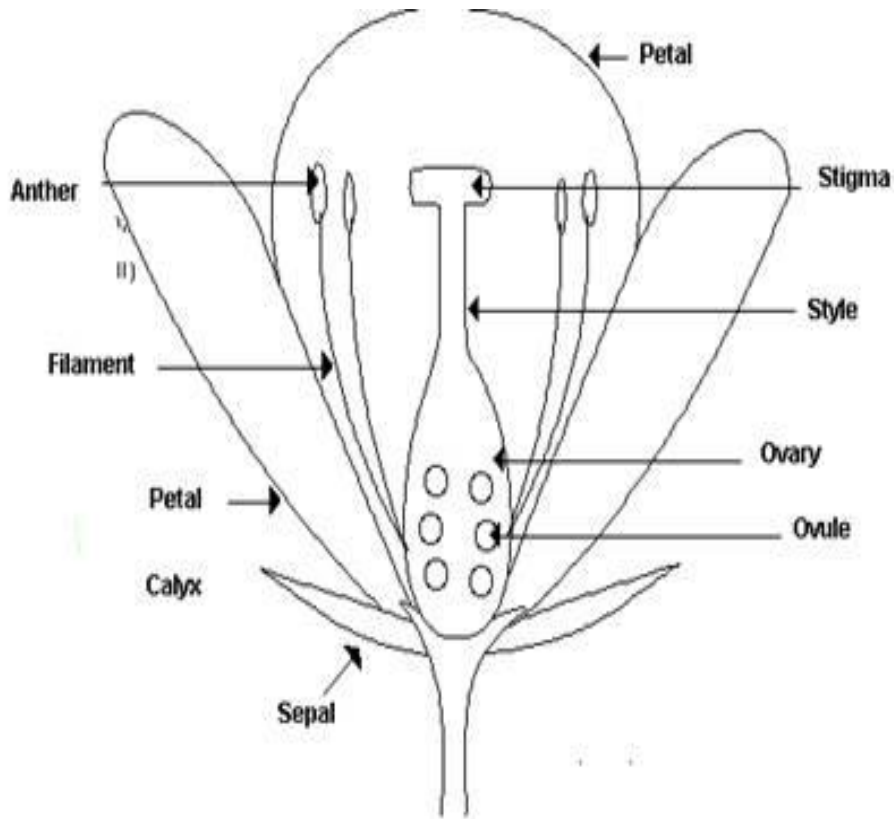


Figure 2: Structural parts of a typical flower (source: www.meritnation.com)

Pollination also plays a significant role in the evolution of flowering patterns of tropical plants owing to the fact that phenological events take into account actors such as bees (Sigrist & Sazima, 2004; Ramirez, 2006). Some plant species produce excessive flowers on inflorescences as an advertisement for the attraction of pollinators (McFarland, 1996). The avoidance of seed predation and herbivory in tropical landscape are important processes that influence phenological synchronization as well (Curran & Leighton, 2000; Curran & Webb, 2000; Sakai,



2002). Similarly, resource allocation has been speculated to have contributed to the flowering abortion in some tropical plants. Other factors influencing flower abortion include sterility, poor floral visits by insect pollinators and high rate of self-pollination (Diallo et al., 2008).

According to Sakai et al. (2006) fluctuation in fruit production in the tropics is often an outcome of flower production. The length of the fruiting phase can vary significant from one ecological zone to another, this was evident in Fandohan's (2015) study that revealed that *Tamarindus indica* has a longer fructification period in the Sudan-Guinea zone (wetter zone) than the Sudan zone (drier zone). The size of fruit/ seed can also fluctuate in response to environmental conditions with fluctuation in yield often occurring much more than anticipated (Sakai et al., 2006).

Some tree species also exhibit an alternate fruiting pattern where successful fruiting in a given year occurs at the expense of vegetative growth and the vice versa (Kelly & Sork, 2002). According to van Schaik et al. (1993) plants timing of their seed dispersal and early seedling developmental stages to coincide with seasons of favourable climatic conditions also influences the timing of flowering and fruiting of tropical plants.

2.11 *Vitellaria paradoxa*

2.11.1 Geographical Distribution of *V. paradoxa*

V. paradoxa is indigenous to twenty one (21) countries in Sub-Saharan Africa (Hall et al., 1996). Land suitability mapping by Naughton et al. (2015) predicted an area of 3.41 million km² across twenty three (23) countries as potentially suitable for the



growth of *V. paradoxa*. This predicted area is larger than the twenty one (21) countries reported with botanical records of *V. paradoxa* in most studies.

There are two reported subspecies of the genus *Vitellaria*, the *paradoxa* subspecies and *nilotica* subspecies (Allal et al., 2013). The natural ranges of the two subsp. are mutually exclusive, although they have been found within 175km of one another (Hall et al., 1996). The *V. paradoxa* subsp. is found in West Africa, stretching from Senegal to Central African Republic whilst the *V. nilotica* is restricted to East Africa occurring in Southern Sudan, Ethiopia, Uganda and Zaire (Salle et al., 1991; Boffa, 1999; Okullo, 2004; Sanou et al., 2005; Djekota et al., 2014). Aside the differences in geographical locations, Joker (2000) reported that *V. nilotica* prefers higher altitudes (650 – 1600 m) as compared to *V. paradoxa* which is found in places with low altitudes (100 – 600 m); the *V. paradoxa* is also more resistant to drought conditions as compared to *V. nilotica*.

The land area suitable for *V. paradoxa* varies tremendously from one country to another. In Senegal, *V. paradoxa* grows in an estimated land area of 1 million km² occurring between Senegal and northern Uganda (Salle, 2001). In Ghana, *V. paradoxa* predominantly occurs in northern Ghana. In Benin, *V. paradoxa* extends from the Zou River to Malanville, geographically located between latitude 07° 06' and 12° 03' N (Gbedji, 2003; Gnangle, 2005).

It does not only vary with respect to land coverage in Sub-Saharan countries, tree density also varies considerably from one location to another (Hall et al., 1996; Djossa et al., 2008a). In Mali, an average of fifteen (15) matured trees was recorded per hectare whilst in Uganda ten (10) matured trees occur in a hectare (Masters &



Puga, 1994). Similarly, *V. paradoxa* constitutes about 70% of woody species composition in shea growing areas of Benin and as high as 80% in northern Ghana and Burkina Faso (Boffa, 1999; Lovett & Haq, 2000). The significant variations in tree density across different regions have been attributed strongly to landuse and climate (Okullo, 2004; Byakagaba et al., 2011; Elias, 2012).

2.11.2 General Physiognomy, Leaf and Flower Morphology

V. paradoxa is a perennial deciduous woody species which usually grows to a height of 7 to 13 m tall and can reach 25 m in exceptional cases (Okullo, 2004). The average bole length is 3 - 4 m with stem girth usually less than 1 m (Joker, 2000). However, some trees can attain a girth of over 1.75 m at maturity (Yidana, 2004; Sanou et al., 2006). Bark colour could be black, dark gray or light gray but dark barks are predominantly found in forest reserves while light and dark gray barks are common on cultivated lands (Kafilatou et al., 2015). It has a thick corky bark with reddish slash which enable the matured tree resist perennial bush fires (Joker, 2000). Kafilatou et al. (2015) classified *V. paradoxa* tree crowns into broom-like, ball-like and elliptical shaped crowns with landuse identified as a major determinant of crown shape. Leaves are borne in terminal whorls with 20-30 simple leaves developing together (Joker, 2000). Kafilatou et al. (2015) described the leaves as oblong shaped with pointed apex having average length of 18.33 cm and a width of 6.92 cm. However, elliptical and oboval shaped leaves have also been reported (Okullo, 2004). Petiole length ranges from 5.7 to 11.9 cm.

There exist morphological variations in the leaves of *V. paradoxa* across different agro-ecological zones (Nyarko et al., 2012). The study of Kafilatou et al. (2015)



recorded a leaf length of 3.21 to 18.33 cm and a width of 1.28 to 6.92 cm. However, in Chad, Djekota et al. (2014) reported longer leaves of 15.5 - 26.3 cm as compared to that of Kafilatou et al. (2015). In Ghana, Nyarko et al. (2012) reported longer leaves among *V. paradoxa* growing in the transitional forest zone as compared to the Guinea and Sudan savannah zones. Leaf flushing occurs concurrently with leaf shedding or immediately after leaf shed (Okullo, 2004). Phenological events such as leaf fall, flushing, flowering and fruiting can vary greatly within and between shea populations (Hall et al., 1996). An observation of shea leafing pattern in Uganda by Okullo (2004) reported leaf flush between March and April with peak leaf shed occurring between December and February. Schreckenber (1996) posit *V. paradoxa* has a relatively long leaf fall period (October to March) as compared to other woody species. Most woody species shed their leaves within a relatively short period and sometimes occur along with leaf sprouting (De Bie et al., 1998). Despite the shedding, *V. paradoxa* tree is hardly found without leaves (Okullo, 2004).

The flowers of *V. paradoxa* have a creamy white to yellow colour and appear in dense fascicles on short twigs (Maranz & Wiseman, 2003). According to Maranz & Wiseman (2003) the flowers develop from the axils of scale leaves at the extremes of dormant twigs and inflorescences dense follicles of 5 - 7.5 cm in diameter (Plate 1c). Yidana (2004) stated that an average of 48 flowers occurs per an inflorescence but Maranz and Wiseman (2003) reported 30 - 40 flowers with Lassen et al. (2016) reporting up to 50 flowers. The tree produces hermaphrodite flowers (Joker, 2000) with each flower made of eight stamens inserted at the base of the corolla and anthers dorsally attached to filliform filaments. A flower contains one ovoid



pubescent ovary (Okullo, 2004). Although the two sub species have the same number of floral parts, significant variations occur in morphology (size). The *paradoxa* subsp. produces smaller flower sepals, filaments and styles as compared to the *nilotica* subsp. (Hall et al., 1996).

Flowering in *V. paradoxa* is triggered by changes in moisture stress in the dry season and lasts for 30 - 75 days (Hall et al., 1996). The intralocal variation in the phenology of woody species of the savannah is evident in the timing of *V. paradoxa* flowering. Hall et al. (1996) reported differences in the timing of flowering within Mali, with *V. paradoxa* in Sikasso noted for early flowering than Bamako. In Uganda, Okullo (2004) observed flowering from January to February with some few trees extending flowering in to May. In Benin, flowering starts in December and ends in February (Schreckenber, 1996).

Okullo (2004) opined the late dry season flowering of shea as a natural adaptation strategy for escaping fire damage to reproductive structures. However, shea flowering in Ghana is reported to coincide with the peak season of bushfires (November – December) (Yidana, 2004). Shea tree leafing is independent of flowering although the two phenomena occur concurrently in most trees (Hall et al., 1996).



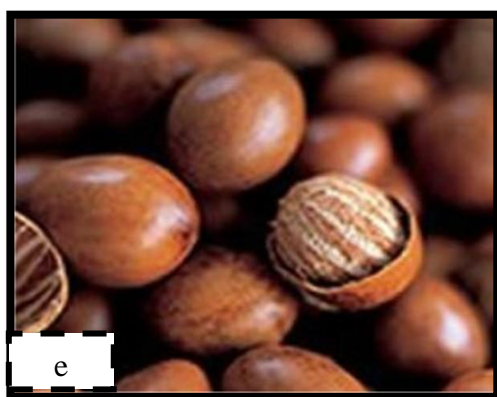


Plate 1: Parts of *V. paradoxa*

a= shea tree (www.icuskintherapy.com)

b = tree bark (www.alamy.com)

c = flowers (field survey, 2016)

d= fruits and leaves (www.usaid.gov/sites)

e = nuts (www.thebftonline.com/)

f= shea kernels (www.21food.com)



2.11.3 Fruit Morphology and Fructification of *V. paradoxa*

Vitellaria paradoxa fruit is often made of a single seed enclosed in a thin epicarp and a soft mesocarp. The oval to slightly round, reddish/brown seed in the fruit is referred to as shea nut (Maranz & Wiseman, 2003). A fruit can however contain two to four seeds in exceptional cases (Elias et al., 2006). Abbiw (1990) reported a maximum of 3 solitary seeds per fruit. The epicarp and mesocarp together make up 33 - 75% of the fresh fruit weight with an average weight of 55% (Elias et al., 2006). The edible mesocarp is highly nutritious with a sweet pear-like taste (Maranz & Wiseman, 2003).

According to Kafilatou et al. (2015) the shea fruit has an average length of 4.49 cm and a diameter of 3.56 cm. In Ghana, the average fruit length range from 2.33 to 3.15 cm with a width of 2.06 to 2.54 cm. Fresh fruit weight ranges between 10.00 to 39.58 g (Maranz & Wiseman, 2003). The shiny smooth surface seed measures about 1- 3.9 cm long and 1.4 - 2.8 cm wide (Kafilatou et al., 2015). Similarly, Maranz and Wiseman (2003) reported a seed length of 2 - 4 cm and a width of 1.4 - 2.8 cm. Nyarko et al. (2012) revealed variations in fruit size across the three main ecological zones with botanical records of *V. paradoxa* in Ghana.

V. paradoxa fruit yield varies considerably from one location to another, Yidana (2004) recorded 1 to over 60 kg of fresh fruit weight per tree. Joker (2000) reported a higher fruit yield of 10-200 kg per tree. A fresh shea fruit weigh between 11.65 g and 20.20 g whilst fresh pulp weight ranges from 6.06 to 12.04 g (Nyarko et al., 2012). According to Maranz and Wiseman (2003) the seed constitute about 50% of the fresh weight of shea fruit.





However, Lassen et al. (2016) revealed a significant difference between the mean weight of seeds produced from insect pollinated inflorescences and that of bagged inflorescences. Though a tree consistently produces fruits of the same size and shape, variations in fruit morphology and yield have been reported among trees (Yidana, 2004). There also exist variations in fruit morphology and yield across different landuse; Kafilatou et al. (2015) recorded longer and larger fruits on shea growing in cultivated/fallow lands than those in reserve forest lands. Similarly, Masters (2002) reported early fruiting and higher yields in cultivated fields than uncultivated lands.

Kafilatou et al. (2015) categorised fruits into oblong and spherical shaped shea fruits with most fruits (68.33%) having the oblong shape. However, Yidana (2004) categorised shea fruits into four based on morphological variation in size and shape. Type 1 fruits being large rounded fruits with length approximately equal to the breadth, type 2 fruits have length twice that of the breadth, type 3 fruits have rounded proximal ends and pointed distal ends and type 4 fruits have tapered or elongated proximal ends with rounded distal ends.

Fructification in *V. paradoxa* takes 4 - 6 months but can last for nine months in some trees (Hall et al., 1996; Okullo, 2004). It takes 100 to 150 days for a fruit to mature after flowering (Schreckenber, 1996). The initial phases of fruiting occur in the dry season whilst fruit ripening and dissemination occurs in the raining season (Okullo, 2004). Yidana (2004) observed fruit dissemination between April and August during which shea collectors pick fruits under trees. Okullo (2004) opined the ripening of fruits in the rainy season as an adaptation strategy for seeds to germinate prior to harsh savannah conditions of persistent fires.

According to Hall et al. (1996) the tree takes over 12 years to bear first fruits. On the contrary, Yidana (2004) kept the minimum natural gestation period at 10 years but often reaches 16 - 20 years in most cases. However, fruits produced by juvenile (10-15 years) trees are reported to be smaller in both size and quantity as compared to adult trees (Sanou et al., 2004). Although, the tree is slow growing with a long natural gestation period, it can continue to produce fruits for over 300 years after the gestation period (Joker, 2000).

V. paradoxa exhibits a natural cyclical fruit yield pattern (Joker, 2000; Yidana, 2004; Elias, 2015). An observation of fruit set pattern by Okullo (2004) revealed low fruit yield on trees that had higher yields in the previous year and the vice versa. Elias (2015) also reported this yearly fluctuation in yield patterns in Burkina Faso after examining indigenous knowledge systems in the management of shea parklands. Yearly alternation in fruit and seed production has been reported as a common trait in fruit trees (Pias & Guitian, 2006). However, there is higher consistency in yearly fruit yield patterns of *V. paradoxa* in cultivated lands than those in wild bushes (Yidana, 2004). Climatic factors can also influence fruit set as Okullo (2003b) reported a positive correlation between fruit set and maximum temperatures.

According to Djossa et al. (2008b) shea fruits constitute major food resource for flying foxes (Chiroptera: Pteropodidae). Seed dispersal in shea requires regular visits from frugivorous animals (Tellería et al., 2005) because disseminated seeds under mother trees are often collected by rural women for commercial purposes (Yidana, 2004). This ecological service is essential for natural regeneration of uncultivated plants species (Balcomb & Chapman, 2003)



About eight species of flying foxes are known to feed on shea fruits (Djossa et al., 2008b). Flying foxes have the ability to carry large fruits away from mother trees for processing at feeding roosts, an important quality in seed dispersal (Eigbo, 2004). Although the seeds of shea are too large to be ingested (Naranjo et al., 2003), the handling of shea seeds by flying foxes was reported to have contributed to germination success (Djossa et al., 2008b). Hall et al. (1996) posit the mechanical removal of the pulp facilitates germination of shea seeds.

Moreover, fruit bats predominantly occur in shea parklands in the wet season, coinciding with the peak fruiting period of shea trees just like seed dispersers of other plants (Richter & Cumming, 2006). The conservation of flying foxes is therefore crucial for the sustainability of shea because other small mammals such as rodents and primates that feed on shea fruits mostly exhibit seed predating habits of harvesting and manipulation of immature fruits (Tang et al., 2007).

2.11.4 Pollination Ecology of *V. paradoxa*

Shea pollen matures just before anthesis, this stage is often characterised by a partial appearance of white strips of corolla as the calyx begins to open (Yidana, 1989). The pollen is copious and sticky in nature and therefore adheres to insects, an important quality for pollen dispersal (Yidana, 1994; Hall et al., 1996). The mass flowering of *Vitellaria* within a relatively short period has been noted as a mechanism for enhancing the availability of pollination services (Okullo, 2004). According to van Schaik et al. (1993) the abundance of floral resources during this period attracts diverse insect pollinators with different foraging behaviour. This therefore enhances pollen exchange among the mass flowering individuals (Okullo, 2004).



The pollination of *V. paradoxa* is also enhanced by the extruding flower style through the unopened bud, during this extrusion there is strong nectar production for attracting flower visitors even before complete bud opening (Yidana, 1991). Although *V. paradoxa* produces hermaphroditic flowers, it relies heavily on cross pollination services for fruit set (Yidana, 1991; Hall et al., 1996). This was evident in the study of Yidana (2004), where inflorescences that were self-pollinated could not bear fruits except one exceptional case attributed strongly to pollen contamination. *V. paradoxa* preference of cross pollen suggest the species is highly insect pollinator dependent (Kwapong, 2014) and fruit yield can be influenced by the availability of pollination services (Okullo, 2003). Buttressing shea yield dependence on insect pollination, Lassen et al. (2016) detected a positive correlation between fertilisation percentage and the number honeybee colonies within 900 and 1000 m radii in Burkina Faso. Hence, the proximity and abundance of flower visitors could enhance shea yield.

Moreover, *V. paradoxa* fruit set was found to respond positively to hand pollination by pollen crossing (Okullo, 2004; Yidana, 2004). In the study of Okullo (2004) fruit production in inflorescences that were hand pollinated by pollen out-crossing recorded 32% as compared to 26% on inflorescences pollinated by natural agents in the environment. Yidana (2004) recorded a percentage fruit production of 39.4% in hand pollinated twigs as compared to 8.9% in twigs pollinated by the natural agents. The outcome of these studies point out inadequacies in pollination services provided by the natural agents and yield could decline further in the absence of insect pollination services. For instance, Number of matured fruits produced from



inflorescences that were opened to insect pollinators was significantly higher than that of bagged inflorescences with the opened inflorescences producing 4-6 times more fruits per inflorescence than the bagged (Lassen et al., 2016). According to Okullo (2004) floral structures of *V. paradoxa* as well as sequence of events in anthesis all tend to favor pollen out-crossing.

The *Apis* spp. has been identified as the major insect pollinators of *V. paradoxa* (Okullo, 2004; Yidana, 2004; Kwapong, 2014; Lassen et al., 2016). Kwapong (2014) identified three bee species; *Apis mellifera*, *Meliponula* spp. and *Hypotrigona* spp. as the dominant insect pollinators of *V. paradoxa* in Ghana with the minor pollinators being *Xylocopa* spp. and some Lepidoptera. Aside these, Lassen et al. (2016) reported solitary bee (*Compsomellissa borneri*) as an equally important pollinator that could supplement honey bee pollination in shea. In Uganda, Okullo (2004) identified the bees as the main pollinators with wasps, butterflies, sunbirds and bats regarded as possible pollinators of shea.

An observation of pollinator foraging behaviour also revealed that aside bees that sought for both nectar and pollen all other flower visitors sought for nectar only (Okullo, 2004). Lassen et al. (2016) observed that honeybees often crawl across the fascicle from one flower to another and touches the protruding stigma of buds in the process. However, some honeybees take off after visiting one flower and then lands again in other flower of the same branch. The honey bees were noted for visiting



flowers earlier than the stingless bee but stingless bees forage for much longer periods than the honeybees (Okullo, 2004; Lassen et al., 2016).

2.11.5 Economic Importance of *V. paradoxa*

Shea tree provides valuable non-timber forest products ranging from fruits to edible oil (Djossa et al., 2008a). The edible oil extracted from the kernel is used for cooking in many parts of Sub-Saharan Africa (Kafilatou et al., 2015). In the Sudanian region, sheabutter is the most affordable plant oil widely used by peasant farmers (Boffa et al., 2000). Shea butter is highly recognised in social and traditional rituals such as funerals, marriages, coronations and rainmaking (Gwali et al., 2011; Djekota et al., 2014).

At the international scale, shea butter is used in commercial quantities in confectionary industry for the manufacture of chocolates (Glew & Lovett, 2014). Sheabutter provides an important raw material for Cocoa Butter Replacers (CBRs) in the manufacture of chocolates (Hall et al., 1996). The shea tree has gained substantial recognition in recent years as an important economic plant due to the increasing shea butter demand in local and international markets (Chimsah et al., 2013).

The fruits of the shea tree serve as an important source of diet for rural household consumption (Okullo, 2004). The edible mesocarp is highly nutritious with a sweet pear-like taste (Maranz & Wiseman, 2003). Elias (2015) reported that the food value of shea fruits during the active agricultural season is among the leading factors that influence farmer's choice of tree retention on farmlands in Burkina Faso. The fruits



quell the hunger of children and farmers in the early part of the farming season. Similarly, Yidana (2004) reported that shea fruits are eaten as a dessert or a main meal during farming in Ghana. According to Elias (2015) farmers intentionally retain and protect trees producing fruits with good taste on farmlands. Ecologically, the fruits provide food for bats and other animals in the raining season (Djekota et al., 2014).

In Ghana, all parts of the shea tree are used for medicinal purposes; the butter is used as an eye lotion and also for the treatment of muscular aches and rheumatism (Bennet-Lartey & Asare, 2000). Shea butter contains an important healing element called “allantion” which is used for the stimulation of ulcerous wounds (Wallace-Bruce, 1995). The healing properties of sheabutter are explored in both local and conventional medicine for healing wounds, dislocations, swelling and bruises. Aside from the butter, the decoction of young leaves is used as a vapour bath for treating headaches and migraines in Ghana. The leaves in warm water form a frothy opalescent liquid, with which the patient’s head is bathed (CRIG, 2002). The bark of *V. paradoxa* is also used for the treatment of stomach ache (Tita & Foundjem, 2015). The wood of *V. paradoxa* can be utilised in many ways.

According to Lovett and Haq (2000) the wood is used for furniture, local construction and carving of mortars and pestles. The wood is also an important source of fuelwood for domestic cooking in many shea growing areas (Boffa et al., 2000). The latex tapped from the bark of *V. paradoxa* can be explored in glue making (Lovett & Haq, 2000).



Rural women benefit most from *V. paradoxa* as they usually gain income and employment opportunities from shea. The sheanut industry is noted as one of the few plant industries that contribute directly to the economic empowerment of women with sheanut collection, processing and commercialisation mainly controlled by women (Yidana, 2004; Elias et al., 2006). The retailing of shea butter provides business opportunities for rural women for instance local retailers in Cameroon purchase an average of 50 kg of butter per transaction (Tita & Kwidja, 2015).

The period of sheanut availability coincides with periods of food insecurity (April to July) in most rural households, hence income accrued from sheanut is used in purchasing food stuffs and other household needs (Yidana, 2004). According to Pouliot and Treue (2012) income from shea constitutes 12% of rural household income between during this period.

2.11.6 Overview of *V. paradoxa* in Ghana

V. paradoxa is predominantly found in the interior savannah (8 – 1 N) of Ghana with few trees scattered across some parts of Brong Ahafo, Ashanti, Eastern and Volta regions (Yidana, 2004) as shown in figure 3. In 1980, the shea tree population in Ghana was estimated at 9.4 million with the potential of producing 100, 000 tonnes of nuts per annum (Abbiw, 1990). However, Adomako (1985) posit Ghana has the potential of producing 135,000 tonnes of dried sheanut per annum. Despite, the high potential for sheanut production in Ghana, the highest export quantity ever reported was 40,000 tonnes in 1985 (Yidana, 2004). This quantity is still far below the estimated potential quantity of sheanut in Ghana.



It is worth noting that the yield of *V. paradoxa* naturally fluctuates from year to year and hence does not have a steady yield pattern (Yidana, 2004; Elias, 2015). This is reflected in the yearly quantity of sheanuts purchased locally and exported from 1976 to 1996 as shown in Table 1. Yidana (2004) posit this phenomenon as a limitation to the development of the shea industry due to unstable supply base of nuts.

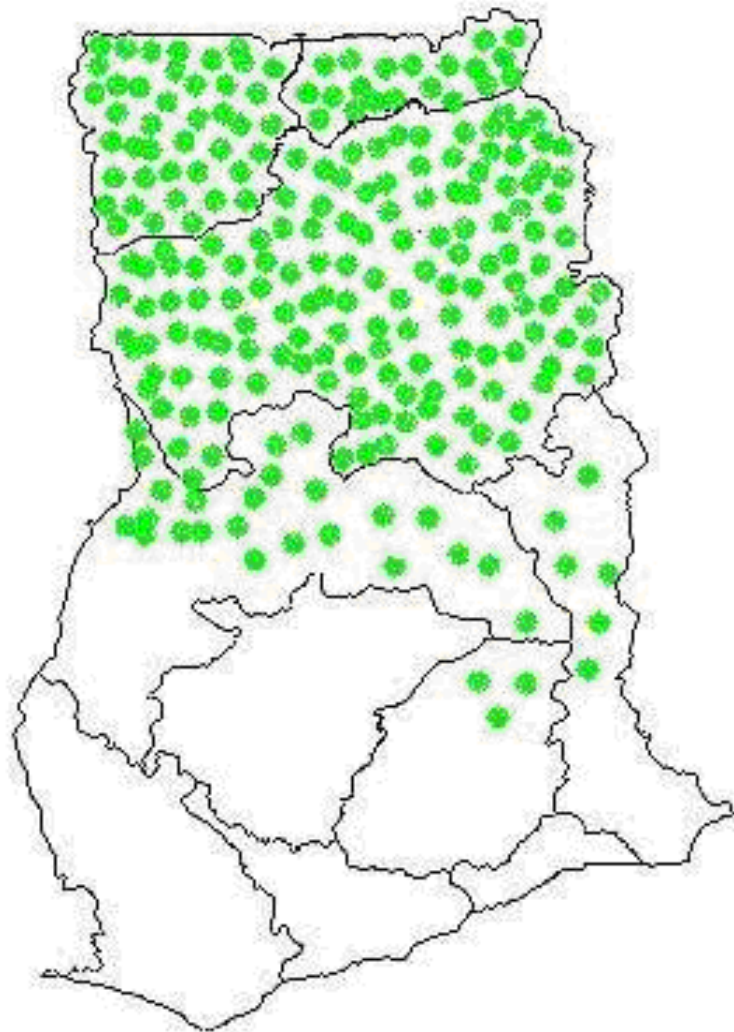


Figure 3: A map of Ghana showing shea growing areas (Source: Chimsah et al. 2013)



Table 1: Local purchase and export quantities of sheanut in Ghana from 1976 to 1996 (metric tonnes)

Year	Local Purchases	Export
1976	19076	5334
1977	1823	1826
1978	506	497
1979	Na	Na
1980	765	764
1981	2205	2275
1982	2300	2392
1983	115	2000
1984	1385	Na
1985	4	Na
1986	40267	Na
1987	10093	Na
1988	Na	Na
1989	Na	Na
1990	3959	2856
1991	5040	3200
1992	1852	2015
1993	9479	Na
1994	7808	Na
1995	22680	Na
1996	32018	Na

na = Not available

Source: Adopted from Yidana (2004)



2.11.7 Anthropogenic Disturbances and the Sustainability of *V. paradoxa*

The retention of multipurpose trees and shrubs on farmlands is an integral part of farming systems in West Africa (Tom-Dery et al., 2015). In northern Benin and Mali the concept of agroforestry is built around the retention of indigenous tree species with desired traits on cultivated lands (Djossa et al., 2008a). *V. paradoxa* is deliberately left and managed on farmlands for multipurpose uses (Sanou et al., 2004; Teklehaimanot, 2004) leading to the formation of vast shea parklands (Boffa, 1999).

Shea parkland is a discontinuous cover of dispersed shea trees under which food crops are cultivated yearly. This indigenous conservation facilitated the dominance of *V. paradoxa* in some parts of semi-arid West Africa (Boffa, 2000; Breman and Kessler, 2011; Chimsah et al., 2013). Aside *Vitellaria paradoxa*, other useful economic tree species such as *Diospyros mespiliformis*, *Annona senegalensis*, *Azadirachta indica*, *Diospyros mespiliformis*, *Terminalia albida* and *Senna siamea* are retained on parklands (Djossa et al., 2008a; Chimsah et al., 2013).

Chimsah et al. (2013) posit that the density of a specific tree species on the parkland is a measure of the relationship between conservation and productive value of the species. The trees are preserved for multipurpose functions such as food, fuelwood, medicine, microclimate amelioration, demarcation of farm boundaries and others (Lamien et al., 1996). The state of the shea parkland reflects the natural and anthropogenic processes involve in species selection, tree density management and growth (Young & Young, 1992).



However, tree density on shea parklands is gradually declining due to growing land demand and short fallows (Lovett & Haq, 2000; Kafilatou et al., 2015). Traditionally, farming systems in West Africa consist of alternating cycles of cultivation and fallow periods on the same piece of land to aid soil rejuvenation along with natural regeneration of desired tree species (Boffa 1999; Lovett & Haq, 2000). Recent studies suggest fallow periods are progressively being shortened with severe degradation of parklands due to land pressure (Boffa, 1999; Lovett & Haq, 2000).

Long cultivation periods without fallows impacts negatively on the regeneration of *V. paradoxa*, for instance Byakagaba et al. (2011) detected more stable sapling densities and better regeneration in young fallows than cultivated fields. Similarly in Ghana, fallow lands are reported to have higher sapling density with better regeneration as compared to other land uses (Tom-Dery et al., 2014). Masters and Puga (1994) reported a mature tree density of 10 ha⁻¹ in cultivated fields and as high as 20-25 ha⁻¹ in uncultivated fields of Uganda. Effect of anthropogenic disturbances on *V. paradoxa* was also evident in the study of Djossa et al. (2008a) which reported reduced regeneration and poor sapling growth on cultivated lands as compared to the Biosphere Reserve of Pendjari.

Anthropogenic threats to *V. paradoxa* are not only limited to cultivated lands, tree population is progressively declining in wild bushes as well (Boffa, 1999; Lovett and Haq, 2000; Nikiema et al., 2001; Djossa et al., 2008a). Tree density has reduced drastically to a minimum of 11 tree ha⁻¹ by the early 2000s due to anthropogenic disturbances (Nikiema et al., 2001). The common disturbances include bushfires,



felling of trees for fuelwood and carvings, debarking for medicinal purposes and decline of seed dispersal agents (Lovett & Haq, 2000; Fa et al., 2002; Thibault & Blaney, 2003; Tita & Foundjem, 2015).

Although there are natural causes of fires, most savannah fires are lit by human with burning regimes regarded as outcomes of anthropogenic phenomenon (Cochrane, 2009; Kull and Laris, 2009). Annual bushfires that occurs in the savannah leads to indigenous tree species mortality and poor regeneration among saplings. Fire severity is a function of timing or seasonality, late dry season fires are more intense with more devastating effects on juvenile trees than early dry season fires. Field experiments reported that late dry season fires prevent regeneration of trees in the savannah (Menaut et al., 1995; Govender et al., 2006).

Recent models indicate that a shift to more frequent and intensive fires can significantly change the tree-to-grass ratio of the savannah landscape in general (Hoffmann et al., 2003; Furley et al., 2008). For instance the study of Okullo (2004) recorded as high as 185 natural regenerating *V. paradoxa* seedlings per hectare but only few ($> 3 \text{ ha}^{-1}$) of the young seedlings survived to the pole stage due to fires and other landuse practices. Bushfires can equally limit the availability of pollination services (Okullo, 2004; Yidana, 2004). Bush fires come with high temperatures and smoke that makes insect pollinators inactive to undertake pollination services during the flowering season of *V. paradoxa* (Millogo, 1989).

Although fire presents a threat to the regeneration of *V. paradoxa* (Hall et al., 1996), fires are reported to have a positive correlation with flowering of *V. paradoxa* and can aid in stimulating fruit production in trees that have stopped fruiting for two to



three years (Schreckenber, 1996). Early dry season burning can also stimulate regeneration from suckers and coppice shoots in the savannah (Swaine et al., 1995). However, seedlings can die out of repeated late burning (Menaut et al., 1995).

Moreover, the felling of trees for firewood and charcoal presents another anthropogenic threat to the sustainability of *V. paradoxa* (Lovett & Haq, 2000). The extensive felling of the *V. paradoxa* is a threat to the existence of the species in the savannah (Masters & Puga, 1994). Gradual extinction of alternative fuelwood species in the savannah has led to the overdependence on this important tree species for fuel. *V. paradoxa* wood is also used for carving hoe handles, mortars and pestles (Abbiw, 1990) contributing to shea population decline in many parklands.

V. paradoxa is not cultivated by rural farmers due to the long gestation period (Boffa, 1995), with regeneration in most areas largely dependent on natural agents for seed dispersal. The gradual extinction of many large vertebrates particularly the flying foxes, which are major agents for shea seed dispersal (Djossa et al. 2008b), have been identified as a contributory factor to the reduced regeneration of *V. paradoxa* (Fa et al., 2002; Thibault & Blaney, 2003).

The severity and frequency of these anthropogenic threats can determine the state, structure and health of *V. paradoxa* stands in Africa (Djossa et al., 2008a). *V. paradoxa* is currently under IUCN list of endangered species (Tita & Foundjem, 2015). Minimising the effects of these threats especially the gradual loss of customary protection of *V. paradoxa* in indigenous agroforestry systems will require an integrated conservation strategy for the species (Okullo, 2004). According Tita and Foundjem (2015) effective conservation should anchor on genetic



characterisation of shea trees and fruits across the shea growing regions. Chimsah et al. (2013) opined the conservation of other tree species on shea parklands as alternative sources of fuelwood in order to reduce the over reliance on *V. paradoxa* for fuel. Similarly, Tita and Foundjem (2015) suggested the planting of fuelwood species on farmlands and home gardens as alternative sources of fuel. Government policies on forestry should pay attention to economic tree species on farmlands similar to the efforts on management of gazzeted forest reserves (Okullo, 2004).



CHAPTER THREE

MATERIALS AND METHODS

3.1 Introduction

This chapter presents the steps, processes, procedures and techniques employed in achieving the set objectives of this study. Some key issues discussed in the chapter include the experimental design, sampling procedures, sources of data, data gathering methods and techniques for data analysis and presentation.

3.2 Selection of Experimental Sites

The experiment was preceded by a one week (January, 2016) reconnaissance survey in farmlands of Zini to select suitable sites for the experiment. The factors considered were accessibility of the field, shea tree density, period of cultivation and the cooperation of the land owner. The experiment focused on the effect of pollination on fruit yield of *V. paradoxa* in cultivated fields. Extensive farmlands with good representation of *V. paradoxa* were therefore identified during the reconnaissance survey. To ensure uniformity of landuse on experimental sites, only medium cultivated (6–10 years) farmlands were selected for the study.

Again to avoid potential bias due to specific farmers' land management practices on pollinators and also to increase independence of sampling sites, the study considered a minimum distance of 1 km between experimental sites as prescribed by Stanley et al. (2013). Two sites were finally selected for the study and located at 5 km apart. The geographical location of each site was taken with a Global Positioning System (GPS) apparatus. Experimental site 1 was located at 10° 50' 00.0" N and 002° 22' 57.2" W whilst site 2 was located at 10° 52' 14.1" N and 002° 24' 48.8"W.





Plate 2: Experimental site 1

3.3 Experimental Design

A Randomized Complete Block Design was used with two treatments (open pollination and insect exclusion) and 54 replicates. Three plots were laid on each site within which experimental trees were sampled. A plot measured 50 x 50 m (0.25 ha) (Fig. 3), justified by the fact that previous studies used this plot size in studying *V. paradoxa* on cultivated fields (Byakabaga et al., 2011; Chimsah et al., 2013; Aleza et al., 2015). Three flowering matured trees (DBH \geq 30 cm) with accessible branches were sampled in each plot because Okullo (2004) reported higher consistency in yearly flowering and fruiting among *V. paradoxa* that had attained a DBH of 30 cm and above. This was done to eliminate the potential bias associated with inconsistent



fruiting (fruit size and quantity) of juvenile (10-15 years) shea trees (Sanou et al., 2004).

Treatments were applied to inflorescences of the selected trees following a Complete Randomised Block Design. Three accessible branches were randomly selected as experimental blocks on a tree. Each treatment was applied to one inflorescence in a block (branch) at the onset of the flowering season.

Open pollination treatment (control) (Plate 3a) - tagged inflorescences that were un-manipulated and left exposed to pollination by natural agents in the environment throughout the flowering phase

Insect exclusion treatment (Plate 3b) - inflorescences bagged with tulle netting (1.2 mm diameter mesh) to restrict insect pollinators from accessing the flowers throughout the flowering season but allowing wind pollination to occur (Jacobs et al., 2009). Inflorescences were bagged as soon as flower buds were observed on them in the last week of January (Yidana, 2004). The bags were however removed immediately after the end of the flowering phase to enable continued plant growth (Dafni et al., 2005).

Experimental trees and inflorescences were given unique labels to enable continuous data collection on data variables (Tables 2 and 3). Tree Labels were written on aluminum sheets and hung on respective tree trunks whilst inflorescences were tagged with purple and yellow ribbons to differentiate between treatments (Plate 3a). Inflorescence labels were written on plastic materials and attached to the base of the twig on which the inflorescence is located.



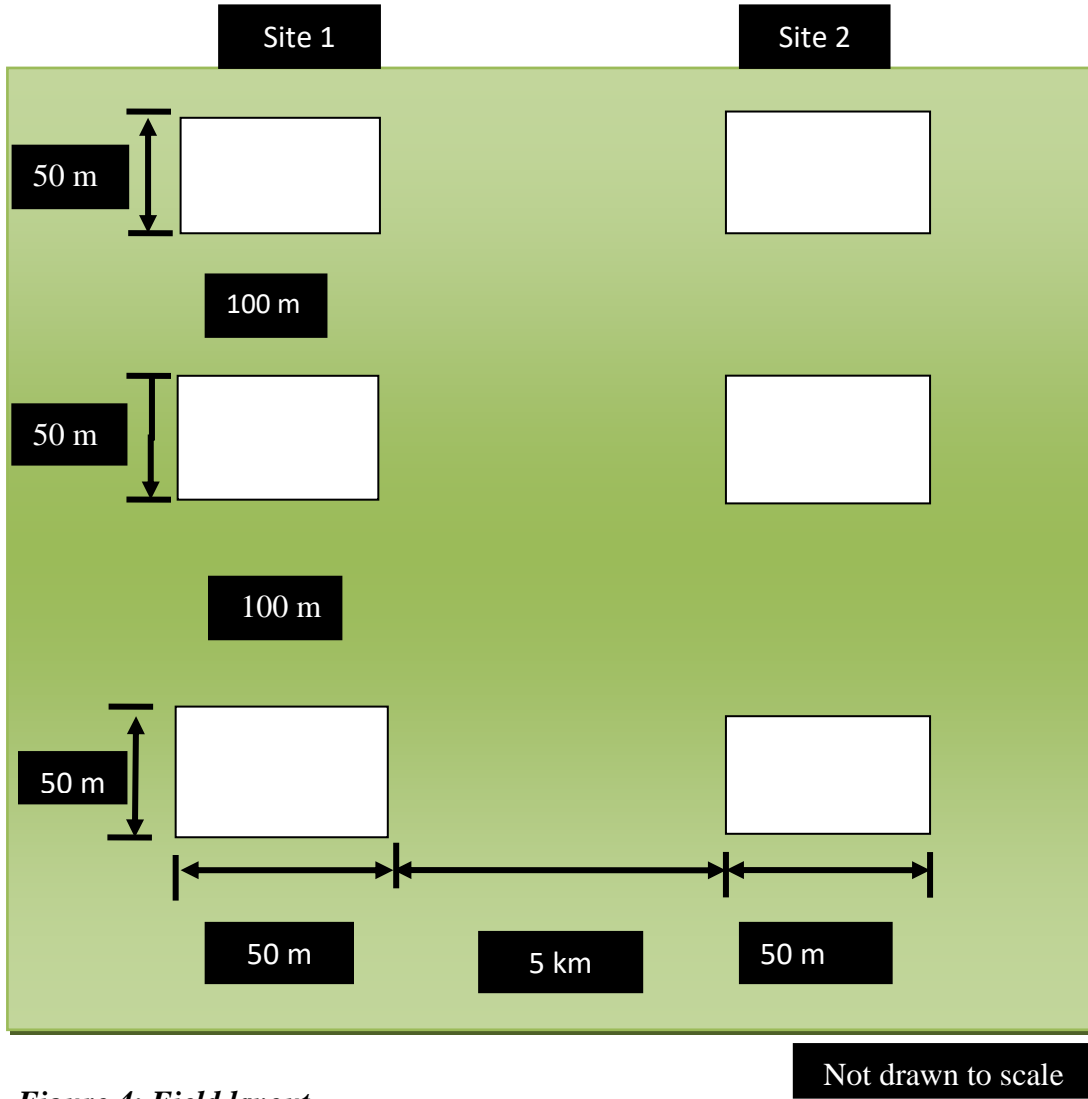


Figure 4: Field layout



Table 2: Tree and inflorescence labels for site 1

Tree	Open pollination inflorescence	Insect exclusion inflorescence
ZT1	ZT1NP1	ZT1IE1
	ZT1NP2	ZT1IE2
	ZT1NP3	ZT1IE3
ZT2	ZT2NP1	ZT2IE1
	ZT2NP2	ZT2IE2
	ZT2NP3	ZT2IE3
ZT3	ZT3NP1	ZT3IE1
	ZT3NP2	ZT3IE2
	ZT3NP3	ZT3IE3
ZT4	ZT4NP1	ZT4IE1
	ZT4NP2	ZT4IE2
	ZT4NP3	ZT4IE3
ZT5	ZT5NP1	ZT5IE1
	ZT5NP2	ZT5IE2
	ZT5NP3	ZT5IE3
ZT6	ZT6NP1	ZT6IE1
	ZT6NP2	ZT6IE2
	ZT6NP3	ZT6IE3
ZT7	ZT7NP1	ZT7IE1
	ZT7NP2	ZT7IE2
	ZT7NP3	ZT7IE3
ZT8	ZT8NP1	ZT8IE1
	ZT8NP2	ZT8IE2
	ZT8NP3	ZT8IE3
ZT9	ZT9NP1	ZT9IE1
	ZT9NP2	ZT9IE2
	ZT9NP3	ZT9IE3



Table 3: Tree and inflorescence labels for site 2

Tree	Open pollination inflorescence	Insect exclusion inflorescence
ZT10	ZT10NP1	ZT10IE1
	ZT10NP2	ZT10IE2
	ZT10NP3	ZT10IE3
ZT11	ZT11NP1	ZT11IE1
	ZT11NP2	ZT11IE2
	ZT11NP3	ZT11IE3
ZT12	ZT12NP1	ZT12IE1
	ZT12NP2	ZT12IE2
	ZT12NP3	ZT12IE3
ZT13	ZT13NP1	ZT13IE1
	ZT13NP2	ZT13IE2
	ZT13NP3	ZT13IE3
ZT14	ZT14NP1	ZT14IE1
	ZT14NP2	ZT14IE2
	ZT14NP3	ZT14IE3
ZT15	ZT15NP1	ZT15IE1
	ZT15NP2	ZT15IE2
	ZT15NP3	ZT15IE3
ZT16	ZT16NP1	ZT16IE1
	ZT16NP2	ZT16IE2
	ZT16NP3	ZT16IE3
ZT17	ZT17NP1	ZT17IE1
	ZT17NP2	ZT17IE2
	ZT17NP3	ZT17IE3
ZT18	ZT18NP1	ZT18IE1
	ZT18NP2	ZT18IE2
	ZT18NP3	ZT18IE3

Where ZT = Zini Tree 1.....18, NP = Open pollination inflorescence 1....3, IE = Insect exclusion inflorescence 1.....3.





Plate 3: Experimental treatments (a= open pollination, b = insect exclusion)



3.4 Sampling Procedures

3.4.1 Systematic Random Sampling

Systematic random sampling was used in laying experimental plots. The first plot was laid at a random location in an experimental site after which subsequent plots were located at a regular distance of 100 m apart in accordance with Chedzon et al. (2005) and Chimsah et al. (2013). Tree plots were laid at each site with a total of six plots for the entire study.

3.4.2 Simple Random Sampling

The simple random sampling was used in selecting experimental trees and branches (blocks). All accessible matured flowering trees with $DBH \geq 30$ cm constituted a sampling frame for a plot. Each candidate tree in the sampling frame was given a unique code after which a simple random sampling technique was used in selecting experimental trees with the help of Microsoft excel (random number generation). Nine trees were selected at each site with a total of 18 experimental trees for the study. Similarly, all accessible branches (ease of climbing) in a sampled tree constituted a sampling frame within which three branches were selected.

Inflorescences on which insect visitation rate was observed were selected from the lower crown layer to enable focal observation of insect visitors from the ground. A branch was chosen at random from the lower crown layer from which five inflorescences were tagged and monitored.



3.5 Sources of Data

Both primary and secondary data were collected and used in the study.

3.4.1 Primary Data

3.5.1.1 Insect Pollinators of *V. paradoxa*

Insect visitors of *V. paradoxa* flowers were collected with a long handled sweep net (Plate 4) for ten (10) minute periods on each tree at two different time periods of the day (6:00 am – 8:00 am and 4:00 pm – 6:00 pm). Weekly collections of flower visitors were carried out for five weeks of the flowering period. Collected specimen were temporally stored in vials containing 70% alcohol and labeled appropriately (site name, date, time, collector name and trapping method) (Plate 5). Labeled vials containing specimen were sent to the Department of Entomology and Wildlife of University of Cape Coast (UCC) for expert identification by an insect taxonomist (Dr. Rofela Combey).

3.5.1.2 Insect to Flower Visitation Rate and Fruit Set

To monitor insect to flower visitation rate, five inflorescences occurring on the same branch were tagged on each tree. The frequency of insect visits to the inflorescences was observed for 10 minute periods on a tree at three different periods of the day (6:00 – 8:00 am, 11: 00 am-1:00 pm and 4:00 – 6:00 pm). An insect to flower visit was defined based on Carr and Davidar (2015) as an insect visiting flower and touching the reproductive parts. It was however not possible to ascertain whether pollen was transferred in the process. Insect visiting shea flowers were broadly categorised into honey bee and stingless bees as it was not possible to identify insects in flight to



species level. Each tree had a total observation period of 240 minutes across the eight weeks of the flowering phase.



Plate 4: Flower visitors being collected with a sweep net

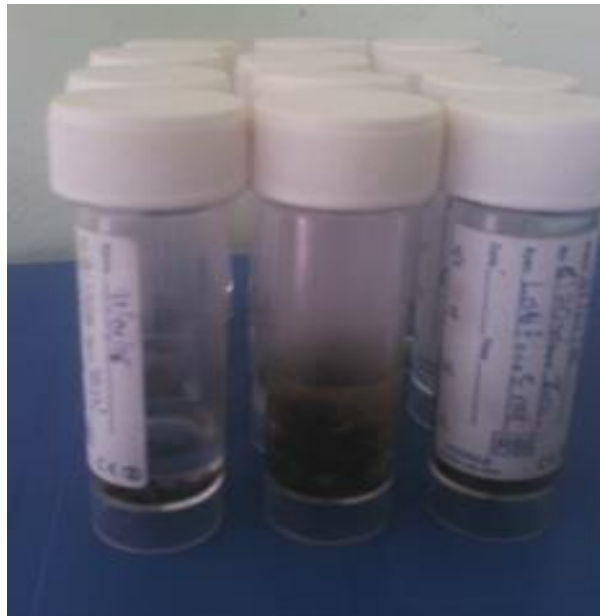


Plate 5: Collected specimen in temporary storage



3.5.1.3 Determination of Fruit Set and Yield

The number of fruit set on each tagged inflorescence was monitored and recorded weekly from the first fruit set on a tree till fruit maturity (Plate 6). These data were collected from the last week of March to June (9 weeks) to examine the effect of the various treatments on fructification. Fruits were harvested by hand plucking in June after the first ripe fruit fall was recorded. The number of fruits sustained to maturity in each experimental inflorescence was recorded before harvesting. Fruits were temporarily stored in labeled paper envelopes and transported to the Council for Scientific and industrial Research (CSIR) – Savannah Agricultural Research Institute (SARI) laboratory at Wa for further processing.

The fresh weight of fruits and nuts were determined with an electronic scale within 24 hours after plucking. Each fruit was weighed after which it was immediately depulped to remove the nut (seed). The fresh nut removed from a fruit was also weighed for fresh nut weight (Plate 7). The fresh nuts were then sun dried after weighing until a constant weight was attained in the 5th week after drying. Nuts were again weighed after drying for dry nut weight. The shells of the dry nuts were then cracked to remove the kernels from the nuts. Finally, each kernel was weighed for dry kernel weight.





Plate 6: Fruit set per inflorescence



Plate 7: Fresh shea nuts being weighed



3.6 Secondary Data

Secondary data was sought on the 2016 purchasing price per bag (85 kg) of shea kernel from five shea marketing companies in Ghana. The set marketing prices per bag of shea kernel at the Zini community market was also sought. These prices were used in determining the price range at which a bag of shea kernel was valued in monetary terms per the period of August, 2016. The purchasing prices of August were used because most women sell out their shea kernels around this period. The five shea marketing companies contacted were Star Shea Company Limited, Savannah Fruit Company Limited, Mother's Shea Company Limited, OLAM Company Limited and Kasajan Company Limited.

3.7 Data Analysis and Presentation

Numbers of the different flower visitors sampled from the two experimental sites were first entered on Microsoft (Ms) excel worksheet. Insect visitors were presented in bar charts to depict the abundance of the various insect pollinator species identified from the collected specimens.

To compare fruit set between the insect excluded and open pollinated treatments, average fruit set per inflorescence on each tree was calculated for both treatments. These data were then subjected to a paired t-test analysis using Genstat version 17. Similarly, to compare fruit set/yield between experimental sites, data on average fruit set per inflorescence on each tree were subjected to a simple t-test analysis. P-value threshold was set at 0.05.



Insect Pollinator Dependence (IPD) was calculated following the approach of Klein et al. (2007) by estimating the magnitude of fruit set or kernel yield (weight) reduction comparing experimental treatments with and without insect pollinators. Based on this approach, insect pollinator contribution was calculated as the fruit yield attributable to insect pollinator interaction with flowers thus fruit yield from open pollinated inflorescences excluding self pollination and or wind pollination yield.

IPD was estimated in terms of number of fruit set and kernel yield with the following formulae;

$$\text{IPD of fruit set} = \frac{FSOP - FSIE}{FSOP} \times 100 \quad 1$$

$$\text{IPD of kernel yield} = \frac{KWOP - KWIE}{KWOP} \times 100 \quad 2$$

Where FSOP is the total number of matured fruits produced from the open pollination treatment in a site, FSIE is the total number of matured fruits produced from the insect exclusion treatment in a site, KWOP= total dry weight of kernels produced from open pollination treatment in a site, KWIE= total dry weight of kernels produced from insect exclusion treatment in a site.

To establish the relationship between insect visitation rate and fruit set/yield, the mean number of insect visits to an inflorescence per hour was regressed against mean number of fruit set/nut weight per inflorescence in each tree. Visit/hour was computed following Carr and Davida (2015) by converting the total number of visits to the 5 tagged inflorescences for the total minutes of observation (240 minutes) into



visits per hour and dividing by 5 (number of inflorescences observed). Ms excel was used in plotting scatter plots to illustrate the relationship between the two variables.

The economic value of insect pollination was estimated per bag of shea nut (85 kg) by determining the monetary value of kernel yield attributable to insect pollination using the average purchasing price per bag of shea kernel. The monetary value was estimated with the formulae;

$$QAI = \frac{IPD}{100} \times 85 \text{ kg} \quad 3$$

$$EVI = QAI \times UP \quad 4$$

Where *QAI*= Quantity (kg) of kernel attributable to insect pollination, *EVI*= Economic value of insect pollination (GHC), *UP*= unit price of a kg of shea kernel.



CHAPTER FOUR

PRESENTATION, DISCUSSIONS AND ANALYSIS

4.1 Introduction

Insect pollination is essential for fruit set and yield of shea in the Guinea savanna zone of Ghana. This chapter covers data analysed and discussed on the insect pollinators of shea, the insect pollinator dependence of shea, the effect of insect pollination on the number of fruit set as well as the weight of nuts/kernels produced. The quantity of kernel yield (kg) attributable to insect pollination and the monetary value of insect pollination per bag of shea kernel were also estimated and discussed in this chapter.

4.2.1 Insect Pollinators of *V. paradoxa*

A total of 187 insect specimens were sampled from shea flowers in ten (10) sampling periods for five weeks of the flowering period. Although, all sampled flower visitors belong to the order Hymenoptera, the bees were the most dominant flower visitors. The finding of this present experiment is consistent with that of Lassen et al. (2016) who reported honeybee and stingless bee species as the primary insect pollinators of *V. paradoxa* in Burkina Faso. The study shows that *Hypotrigona* spp. was the most abundant (78%) flower visitor, followed by the *Apis mellifera* which recorded 14% (Fig. 5).



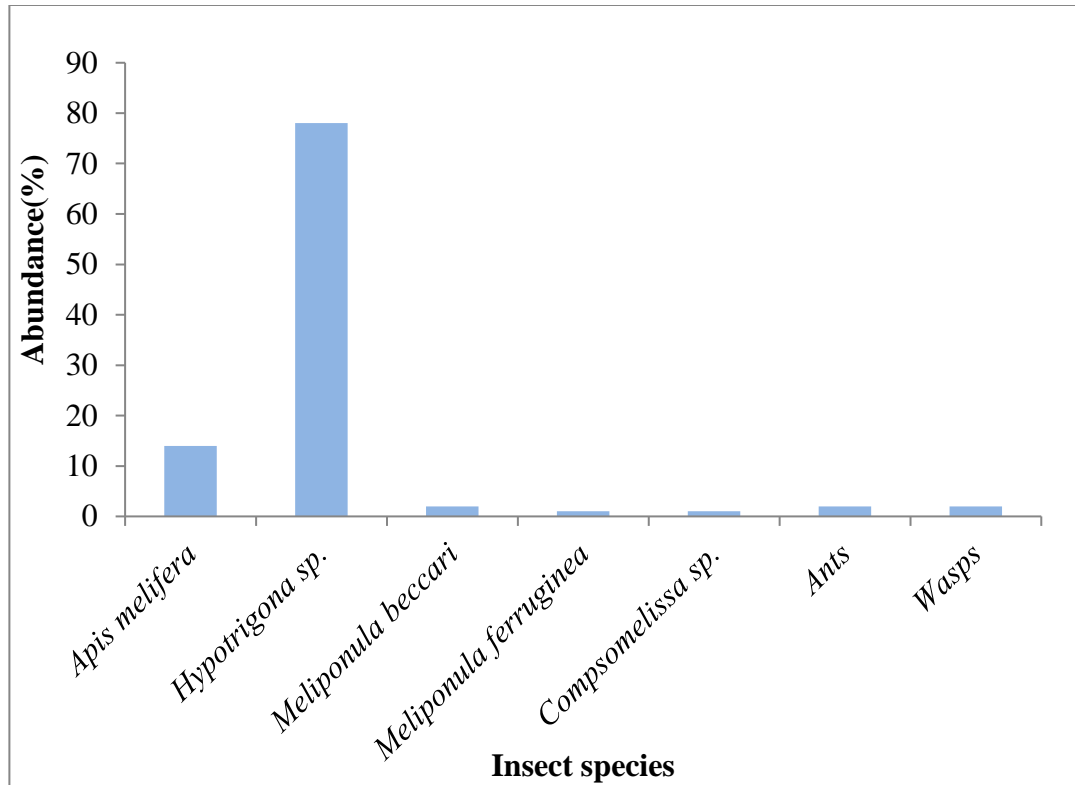


Figure 5: Percentage abundance of shea flower visitors

Meliponula ferruginea and *Compsomelissa* spp. were the least abundant flower visitors, which recorded 1% each (Fig. 5). Similar study by Kwapong (2014) also reported *Apis melifera*, *Hypotrigona* spp. and *Meliponula* spp. as the most frequent flower visitors of *V. paradoxa*. The study also recorded *Meliponula beccari*, ants and wasps (Fig. 5) among flower visitors of *V. paradoxa*. This finding also supports Abome (2002) and Okullo (2004) who reported wasps as pollinators of *V. paradoxa* in Burkina Faso and Uganda, respectively. The presence of ants on shea flowers were also reported by Okullo (2004) and Lassen et al. (2016). However, ants are not regarded as insect pollinators of shea as they do not come in contact with flower anthers during foraging (Okullo, 2004). They could be regarded as “nectar thieves” based on their foraging behaviour. On the contrary, Altshuler (1999) and Philpott et al.



(2006) argued that ants indirectly contribute to pollination by attacking pollinating insects to move more rapidly and therefore facilitates more pollen transfer.

Despite, the similarity of the identified pollinators with previous studies, there exist some variation in pollinator species diversity across shea parklands. For instance, carpenter bee (*Xylocopa* spp.) was not found in this study but Kwapong (2014) reported carpenter bee in the northern region of Ghana. Similarly, the identification of wasp in this experiment as a pollinator of *V. paradoxa* is contrary to Kwapong (2014) and Lassen et al. (2016) who did not record wasp as a flower visitor of *V. paradoxa*. Again some of the stingless bees species identified in this study (*Meliponula beccari* and *Meliponula ferruginea*) are also contrary to stingless bee species identified in Lassen et al. (2016). The present experiment conducted in Zini reported complete absence of beetles on shea flowers. This finding also contradicts that of Okullo (2004) who reported some beetles visiting the flowers of *V. paradoxa*.

This variation in pollinator species diversity across different shea parklands may be attributable to variation in pollinator habitat disturbances (Aluri, 1990; Okullo, 2004; Bartomeus et al., 2013; Norfolk & Gilbert, 2014). It is reported that wild insects require undisturbed habitats for nesting, rooting and foraging (Aluri, 1990). In the Guinea savannah zone of Ghana most natural habitats are gradually being converted into agricultural land (Tom-Dery et al. 2015) which could limit the natural habitats of pollinators. The intensity of these anthropogenic disturbances in parkland could play a role in determining insect community richness.



Contrasting effects of agriculture on insect community richness have been recorded; whilst agriculture negatively affected pollinator diversity in humid areas (Bartomeous et al., 2013), it contributed positively to pollinator diversity in arid areas (Gotlieb et al., 2011; Norfolk & Gilbert, 2014). In addition, Okullo (2004) reported urbanisation, overgrazing and population increase as some drivers of pollinator habitat destruction. The difference in pollinator species richness could also be attributed to variation in tree species diversity and abundance in shea parklands. Tree species richness was noted to have a positive relationship with insect species richness (Janganmohan et al., 2013). This relationship could even be stronger in pollinator species because insect pollinators require flowering plants to have a sustainable forage resource (nectar and pollen) all year round (Öckinger & Smith, 2007). Chimsah et al. (2013) reported substantial variation in tree species diversity across shea parklands in Ghana and this could have contributed to the differences in pollinator species diversity when compared with early studies.

The flowering period of some exotic tree species (*Mangifera indica* and *Eucalyptus* spp.) in the study area coincides with the flowering season of *V. paradoxa*. Flowering period overlaps in tree species could result in competition for pollinators among the flowering trees (Okullo, 2004). The degree of exotic tree species diversity and abundance in the area could have equally contributed to insect pollinator richness. There is rapid expansion of exotic tree plantations especially mango in the Guinea savannah (TDA, 2012) that will likely pose a threat to the availability of pollination services for *V. paradoxa* in the study area.



The slight differences in composition of insect pollinator species as compared to early studies could also be an outcome of variation in microclimatic conditions of different shea parklands. The ability of the parkland to create conducive microclimate can influence insect pollinators. For instance Adjaloo (2012) reported higher insect species richness and abundance in relatively heavy shaded cocoa farms than widely spaced farms with little shade. This elucidates insect preference for microclimates with relatively low temperatures as compared to environments with high temperatures. The flowering period of *V. paradoxa* also coincides with the season of bushfires in the Guinea savannah zone of Ghana. Bushfires are noted for producing higher temperatures and smoke that tranquilises and make pollinators inactive (Millogo, 1989; Yidana, 2004). Hence the intensity of fires in the parkland could determine the diversity of insect pollinators.

Despite the differences in insect species richness, the relatively high pollinator species diversity for *V. paradoxa* (Fig. 5) affirmed the assertion of Okullo (2004) who indicated that *V. paradoxa* has a composite pollination syndrome (several insect species share pollination rewards). This could play a role in addressing the pollination inefficiencies associated with plants that have specialised pollination systems. Some plants produce floral structures (flowers that restrict access to all but a few pollinator species) that require specialised insects for reproductive success (Valle et al., 1990; Brew and Boorman, 1993). For instance cocoa is suggested to have a specialised pollination system in which pollinating insects belong to a single pollinator class and most often a few species of one insect family, tribe or genus (Goldblatt & Manning, 2005; Adjaloo, 2012).



The relatively high pollinator richness in this study could help in addressing the limitations of mis-match between insect body size and flower size, low nectar production and specialised pollen release mechanisms (Kearn & Inouye, 1997b). The diverse pollinators for *V. paradoxa* could also reduce the risk of pollination service losses in event of parasitic pest infestation of a specific bee species. This could sustain reproductive success in an eventual decline of a single pollinator species. This finding is supported by Karikari and Kwapong (2007) assertion that stingless bees can be explored as an alternative to honeybees for alleviating pollination service deficits. Stingless bee species are relatively more resilient to floral resource scarcity than honeybees hence the high abundance of stingless bees (Fig. 5) as shea flower visitors could be explored to help.

4.2.2 Weekly Trend of Insect Visitor Abundance on Shea Flowers

The highest number of flower visitors (29) was recorded in week 2 whilst the least (5) was recorded in week 5 (Fig. 6). However, the highest insect diversity (5) was recorded in week 1. The *Hypotrigena* spp. was the most abundant (48) among the morning flower visitors followed by the *Apis mellifera* (26) and the least been the *Meliponula ferruginea* (2). The abundance of most insect species decreased progressively from week 1 to week 5 of the flowering period (Fig. 6).

Although pollinator abundance also decreased progressively over the flowering period in the evening period, insect species diversity was relatively low (3) among evening visitors when compared to the morning flower visitors (Fig. 7). The highest number of flower visitors was recorded in week 2 whilst the least (5) was recorded in week 4



(Fig. 6). The *Hypotrigona* spp. was the most abundant whilst *Compsomellisa* spp. recorded the least abundance in the evening period (Fig. 7).

Hypotrigona spp. occurred as the most abundant flower visitor of shea in both morning and evening periods (Fig. 16). This finding is consistent with that of Lassen et al. (2016) who observed more stingless bees foraged on *V. paradoxa* fascicles than the honey bees. The 2% representation of wasps among flower visitors confirms Okullo (2004) who reported wasps, butterflies, sunbirds and bats as minor pollinators of shea. Similar study by Abome (2002) reported one wasp species among flower visitors of shea in Burkina Faso. The limited abundance of ants observed in this present experiment is consistent with that of Lassen et al. (2015) who reported few ants visiting shea flowers.

The relative abundance of an insect species and the amount of pollen carried are noted to be major determinants of pollinator species effectiveness in transporting pollen (Rader et al., 2009). Although, this study did not examine the amount of pollen carried by individual pollinating species, the occurrence of *Hypotrigona* spp and *Apis melifera* as the two most abundant flower visitors suggest they could be the key pollinators of *V. paradoxa* in the area. However, the larger body size of the *Apis melifera* could aid in more pollen transport than the *Hypotrigona* spp.

The progressive decline in pollinator species abundance from week two to five (Fig. 6 and 7) could be a response to flower attractiveness. Flowers become unattractive to insects when there is reduced pollen content, cessation of nectar and aroma production, change in flower colour, wilting or shedding of flower petals (Delaplane



& Mayer, 2000). Field observation revealed that shea flowers dried gradually after 100% flower bud opening in most trees. This withering was probably facilitated by the low humidity that characterises the Guinea savannah climate during harmattan period. This progressive decline in pollinator abundance is affirmed by Graham (1992) who asserts that bees forage continuously on flowers of the same species until they become unattractive.

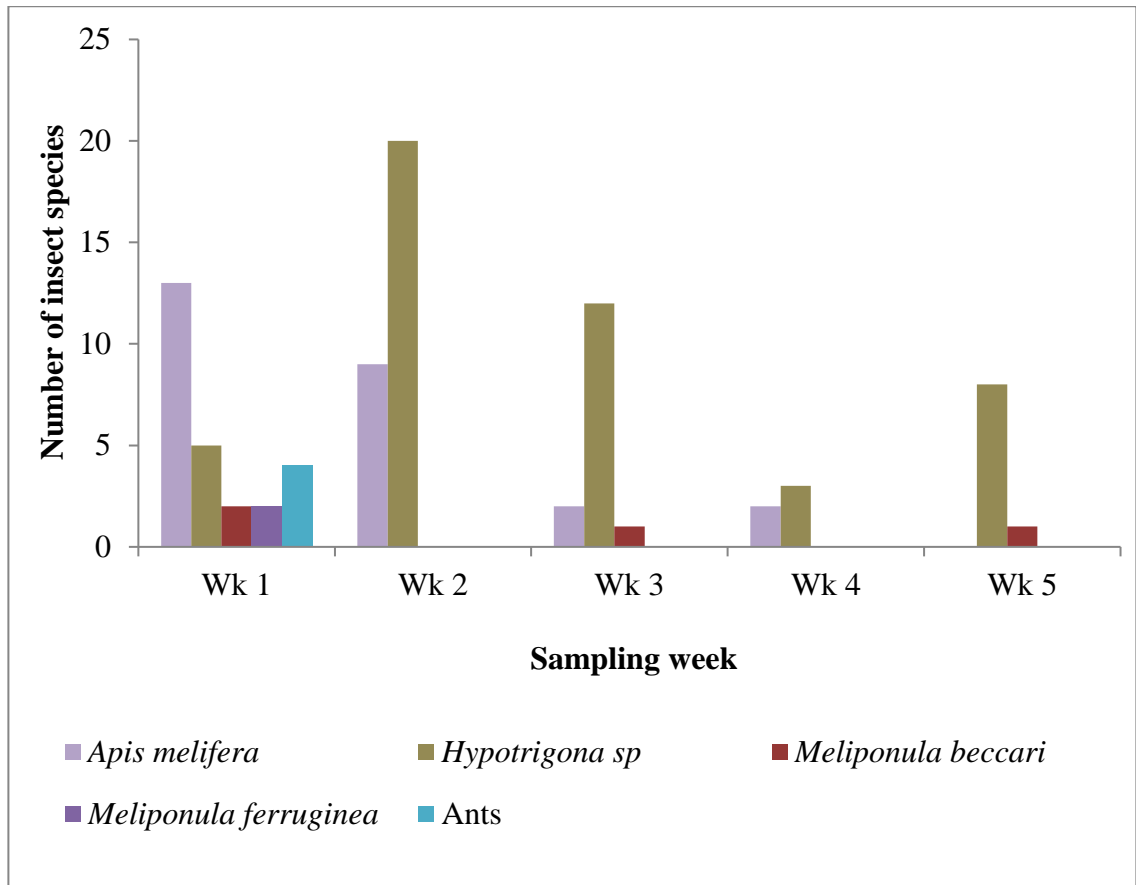


Figure 6: Insect species abundance on shea flowers in the morning period (6:00-8:00 am)

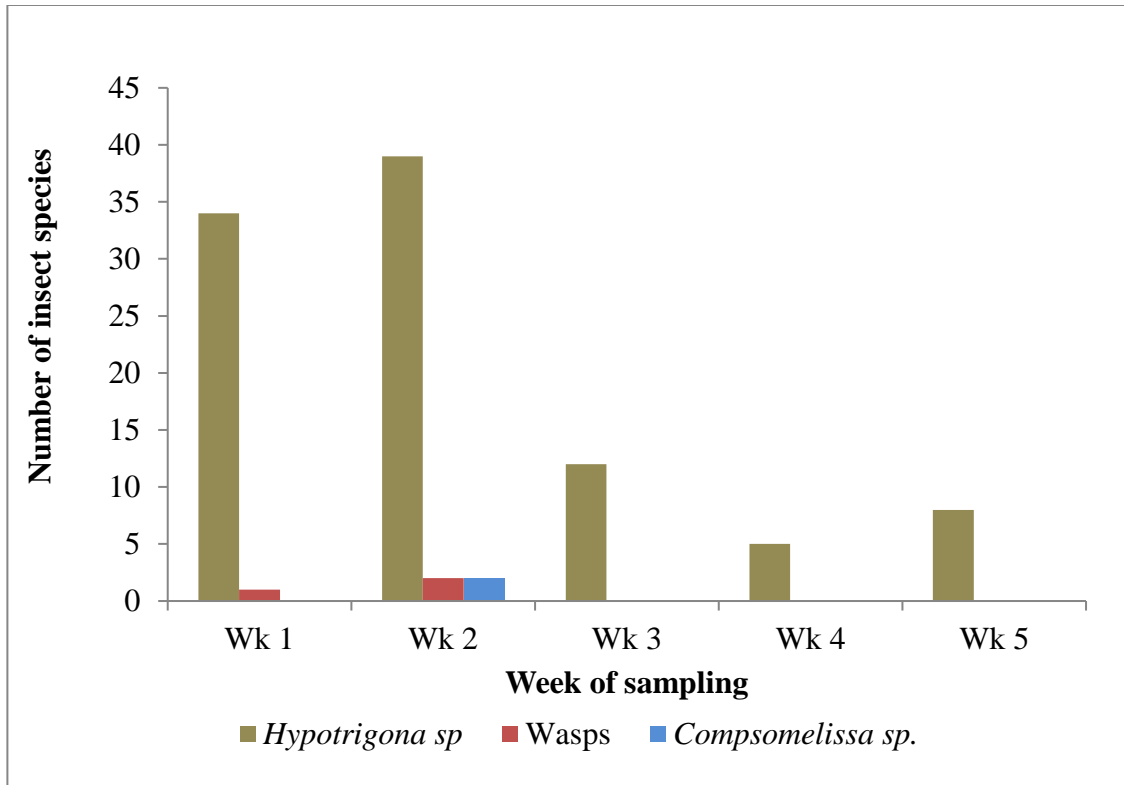


Figure 7: Insect species abundance on shea flowers in the evening period (4:00-6:00 pm)

4.3 Insect Pollinator Dependence of *V. paradoxa*

4.3.1 Number of Flowers per Inflorescence in *V. paradoxa*

The numbers of flowers or flower buds produced per inflorescence are presented in table 4 and 5 below. The mean number of flowers produced per inflorescence was 31.57 in site 1 and site 2 was 12.70. The number of flowers varied significantly between trees in both experimental sites (appendix 1 and 2). The highest number (64) of flowers per inflorescence was recorded in ZT3 whilst the least (5) was recorded in ZT13 (Table 4 and 5). Comparatively, the mean flower production between the two sites showed significant difference ($P = 0.001$).



The mean number of flowers per inflorescence in this study is low when compared with that of Yidana (2004) who reported 48 flowers per inflorescence in the northern region of Ghana. However, the mean number of flowers for site 1 (31.57) is consistent with that of Orwa et al. (2009) who reported that each inflorescence contains an average of 30 – 40 flowers.

The maximum number of flowers recorded per inflorescence in this experiment is greater than the maximum number of flowers reported in Lassen et al. (2016). There seem to be variations in number of flowers per inflorescence in shea across different geographical locations as findings of Maranz and Wiseman (2003), Orwa et al. (2009), Lassen et al. (2003) and the present study showed differences in flower production in their respective studies.

Table 4: Number of flowers/ flower buds per shea inflorescence in site 1

Tree	Open pollination			Insect exclusion			Mean
	Rep1	Rep2	Rep3	Rep1	Rep2	Rep3	
ZT1	48	26	37	30	28	35	34
ZT2	28	18	14	40	21	20	23.5
ZT3	53	43	38	53	46	64	49.5
ZT4	27	42	29	40	20	39	32.8
ZT5	55	27	34	18	21	19	29
ZT6	38	29	32	26	33	49	34.5
ZT7	29	43	41	22	39	33	34.5
ZT8	34	24	17	14	15	14	19.6
ZT9	23	18	42	30	25	23	26.8
Total	37.2	30	31.5	30.3	27.5	32.8	31.57



Table 5: Number of flowers/ flower buds per shea inflorescence in site 2

Tree	Open pollination			Insect exclusion			Mean
	Rep1	Rep2	Rep3	Rep1	Rep2	Rep3	
ZT10	27	13	19	34	24	17	22.3
ZT11	8	11	7	9	13	6	9
ZT12	5	14	8	7	11	16	10.1
ZT13	13	7	9	7	5	17	9.6
ZT14	9	12	15	7	6	18	11.1
ZT15	11	9	15	8	14	12	11.5
ZT16	13	10	18	9	17	15	13.6
ZT17	19	14	11	9	14	21	14.6
ZT18	15	8	10	12	13	17	12.5
Total	13.3	10.8	12.4	11.3	13	15.4	12.7

These variations can be attributed to the differences in environmental factors. The patterns of most phenological events such as flowering and leaf flush are known to be highly correlated with soil moisture and topography (De Bie et al., 1998; Law et al., 2000; Okullo et al., 2004). Marques et al. (2004) and Stevenson (2004) have also reported positive relationships between temperature and flowering in tropical plants. Flower production can also be triggered by the level of resource accumulation in a plant (Sakai et al., 2006). Variations in these biotic and abiotic factors across different shea parklands might have contributed to the pronounced differences in flower production.



4.3.2 Percentage Fertilisation of *V. paradoxa*

Successful fertilisation (percentage of inflorescences that produced at least one immature fruit) was higher in open pollinated inflorescences (62.97%) as compared to insect excluded inflorescences (25.92%). The means calculated indicated a significant difference between fertilisation under open pollination and insect exclusion ($P = 0.0013$) treatments. However, percentage fertilisation did not vary significantly between experimental sites ($P = 0.148$) although fertilisation differed slightly between sites in both treatments (Fig. 8).

The finding of this study shows higher fertilisation (62.97%) of open pollinated inflorescences as compared to insect excluded inflorescences. This conforms to the findings Lassen et al. (2016) who reported significant differences in fertilisation between bagged and open inflorescences. Variation in fertilisation (%) between the two treatments could be attributed to differences in pollination intensity as asserted by Field et al. (2012). The accessibility of open inflorescences to diverse insect pollinators in the parkland could have facilitated higher stigmatic pollen deposition. Differences in fertilisation success between the two sites could have been caused by the variation in pollinator abundance in the two sites. Since, Lassen et al. (2016) reported a positive correlation between fertilisation (%) and the number of honey bee colonies within 900 and 1000 m radii.



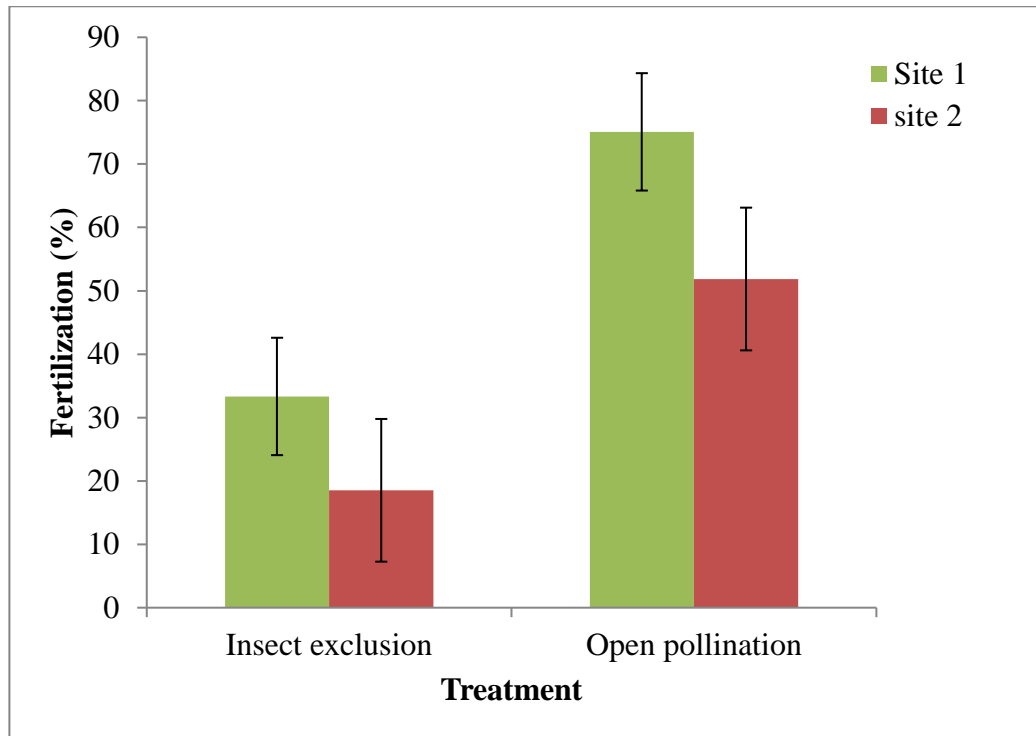


Figure 8: Fertilisation (%) of shea (under open pollination and insect exclusion treatments)

4.3.3 Fruit Production in *V. paradoxa*

Percentage fruit production (proportion of flowers which set matured fruits in each treatment) was higher in open pollinated flowers (6.5%) as compared to insect excluded flowers (1.5%) for both experimental sites (Table 6). However, fruit production was higher in site 1 among open pollinated flowers as compared to site 2 (Table 6). The mean number of matured fruits produced per inflorescence was also significantly higher in open pollinated inflorescences as compared to insect excluded inflorescences ($P = 0.001$) (Fig. 9). Mean number of matured fruit set per inflorescence also varied significantly between experimental sites in the open pollination treatment ($P = 0.013$). Open pollinated flowers in site 1 produced 2 fruits

per inflorescence whilst site 2 had 0.85 (Fig. 9). However, the number of fruit set per inflorescence from the insect exclusion treatment did not vary significantly between experimental sites ($P = 0.159$).

The 6.5% fruit production recorded from open pollination treatment (Table 6) is consistent with earlier findings by Okullo (2004), Yidana (2004) and Lassen et al. (2016) that reported large differences between the number of flowers initiated and percentage fruit set in *V. paradoxa*. For instance, the study conducted by Yidana (2004) reported 8.5% of initiated flowers producing matured fruits. On the contrary, the mean number of matured fruit set per inflorescence (1.42) from open pollination is higher than that of Lassen et al. (2016).

Table 6: Percentage fruit production (proportion of flowers that produced matured fruits) in shea

Experimental site	Insect exclusion (%)	Open pollination (%)
site 1	1.6	6.1
site 2	1.4	6.9
Total	1.5	6.5

In the opinion of Okullo et al. (2003b) the large number flower production in shea may reflect the need for a larger floral display for attracting and retaining diverse pollinators. According to van Schaik et al. (1993) the abundance of floral resources during this period attracts diverse insect pollinators with different foraging behaviour.



Some plant species produce excessive flowers on inflorescences as an advertisement for the attraction of pollinators but are unable to convert most of the flowers to fruits (McFarland, 1996). This could be the case of *V. paradoxa* since 70% of the flowers fall off the plant by the end of the flowering period prior to fruiting (Okullo, 2004; Lassen et al. 2016).

The low fruit production in shea could also be attributed to inadequate pollination services provided by natural agents in shea parklands. This was evident in the findings of Yidana (2004) and Okullo (2004) when flowers that were hand pollinated by outcrossing recorded a higher fruit set as compared to flowers that were open pollinated by natural agents in the parkland. An indication that shea is pollen limited. The overlap between *V. paradoxa* flowering period and that of some exotic tree species (*Mangifera indica* and *Eucalyptus* spp) in the savannah could have diverted bees and other potential pollinators away from *V. paradoxa* resulting in reduced pollination success. Okullo (2004) suggested soot and ashes from burning grasses could also clog stigmatic surfaces and restrict the germination of pollen tubes and the subsequent transportation of pollen to affect fertilisation in the ovary. The flowering period of *V. paradoxa* coincides with the harmattan season in the Guinea savanna zone; therefore the strong winds could facilitate the transportation of ashes.

Moreover, smoke together with the high temperatures that characterises the period of bushfires tend to have depressing and tranquilising effects on bees (Milogo, 1989) resulting in reduced pollinator activity in the flowering period of shea. These factors together could have contributed to the low percentage fruit production in the open pollinated inflorescences.



Notwithstanding, low fruit production is not unusual in flowering plants, this is a common phenomenon in many plants, where only a few of the flowers and ovules initiated develop into fruits and seeds (Lloyd, 1980; Stephenson, 1981; Bawa & Webb, 1984; Lee, 1988). For instance, the *nilotica* sub species aborted over 60% of the fruits even when flowers were sufficiently pollinated manually by pollen outcrossing (Okullo, 2004). This suggests that the low fruit set is not only an outcome of pollen limitation but resource limitation as well.

Klein et al. (2007) indicated that the positive effect of pollination on crop yield can be confounded when other variables that influence crop yield such as soil nutrients, macroclimate, water and pest and disease status are suboptimal. In *Vitellaria*, fruit production commences in the dry season when soil moisture level is still low, thereby limiting water and nutrient supply for fruit development. Osei-Amaning (1996) indicated that the seeds of shea are metabolically expensive to maintain, this could therefore limit the number of fruit set. Moreover, the overlap between fructification and leafing phases in shea is resource demanding, hence resource allocation for these two concurrent phenological events could have also limited fruit set in *V. paradoxa*.

Despite, the effect of resource and pollen limitations on fruit set, the 6.5% fruit production recorded from open pollinated flowers in this study is relatively low as compared to 8.5% reported by Yidana (2004) in the northern region of Ghana and 26% in Uganda (Okullo, 2004). The yield of *V. paradoxa* is known to fluctuate yearly (Boffa 1995; Elias, 2015). Hence, the level of fruit set for the study year could have accounted for this low fruit production. For instance, Lassen et al. (2016) recorded 1.45 fruits per inflorescence among open pollinated inflorescence in 2011 but in 2012



they recorded about 0.53 fruits per inflorescence in the same study area. This cyclical yield pattern of *V. paradoxa* could have contributed to the quantity of fruit set.

Okullo (2004) attributed annual fruit set variations in *V. paradoxa* to fires, pollinator availability, genetic factors and diversity in landuse practices across different parklands. For instance, Kafilatou et al. (2015) recorded longer and larger fruits on shea growing in cultivated and fallow lands than those in reserve forest lands. Similarly, Masters (2002) reported early fruiting and higher yields in cultivated fields than uncultivated lands. Some tree species also exhibit an alternate fruiting pattern where successful fruiting in a given year occurs at the expense of vegetative growth and the vice versa (Kelly & Sork, 2002).

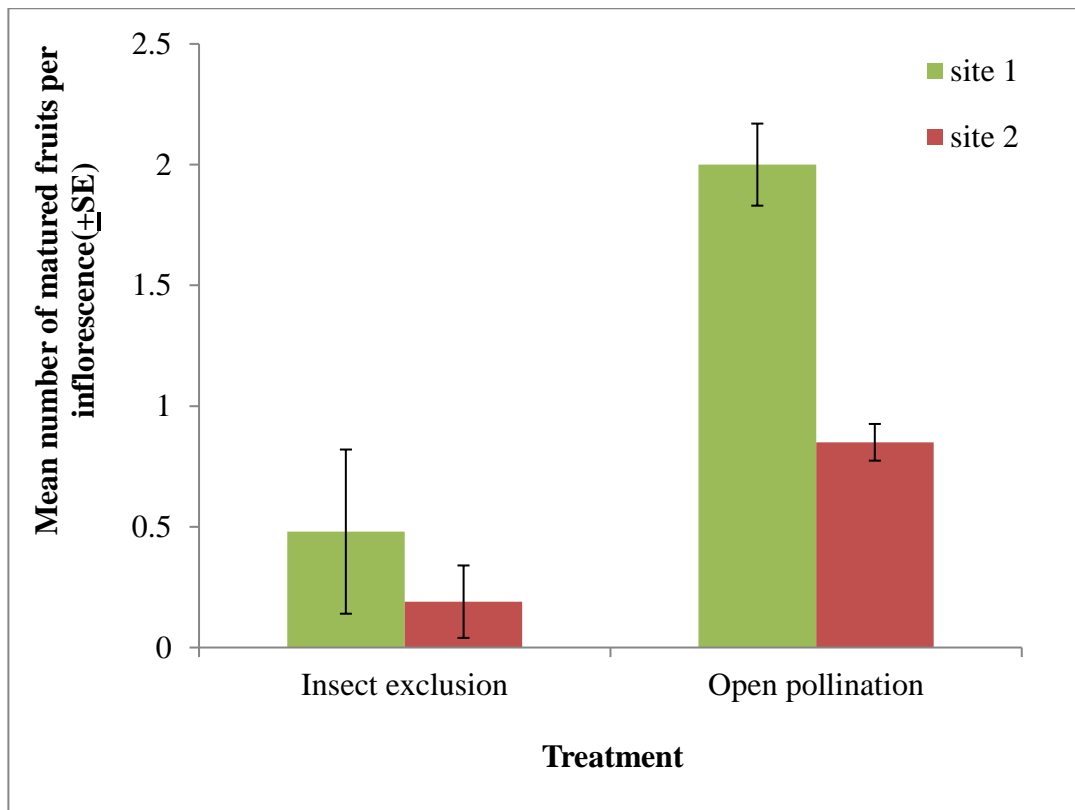


Figure 9: Mean number of matured fruits produced per inflorescence

Despite the general low fruit production in *V. paradoxa*, the study revealed high significant difference between matured fruit set per inflorescence from open pollinated flowers and insect excluded flowers. This finding conforms to that of Yidana (1991) and Hall et al. (1996) that reported that *V. paradoxa* relies heavily on cross pollination services. The yield of *V. paradoxa* can therefore be influenced significantly by the availability of insect pollinators (Okullo, 2003a). In the study of Lassen et al. (2016) the exclusion of only the larger bees (honeybee) from accessing shea flowers resulted in 35% reduced fruit yield an indication of heavy reliance on insect pollination. The internal colours of the inflorescence bract and the odoriferous yellow flowers of *V. paradoxa* are noted as major qualities of insect pollinated plants (Okullo, 2003b). Moreover, *V. paradoxa* pollen is known to be copious and sticky in nature (Yidana, 1994; Hall et al., 1996) and therefore adheres to insect visitors of shea flowers. The observed insect visits to the opened flowers could have contributed to the significantly higher yield of the open pollinated inflorescences.

The few fruit set recorded from the insect excluded inflorescences could be attributed to wind pollination (self and cross pollination). Shea produces hermaphrodite flowers, which show the existence of both types of sex organs in all flowers could facilitate both cross and self-pollination (Okullo 2004). Lassen et al. (2016) posit the contact between the protruding stigmas and the anthers with mature pollen on neighbouring flowers of the same fascicle could facilitate self pollination in shea. The occurrence of self pollination could be an adaptation response of shea to the limited pollination services in the environment. This can be supported by findings of Yidana (2004) who reported pollen limitation in *V. paradoxa*. However, fruit production in insect



excluded pollination treatment is not limited to shea, flowers of oil seed rape still produced some few seeds when insects were excluded from pollination (Bommarco et al., 2012; Stanley et al., 2013). The significantly low fruit set among insect excluded inflorescences conforms to Free (1993) who reported that the role of wind pollination is insignificant in deciduous fruit crops that require insect vectors for pollination.

The significant difference between mean fruit set per inflorescence in the two experimental sites could be attributed to variation in edaphic conditions. Availability of soil nutrients is known to influence flower abortion, intra and inter specific variations in fruit production (Breman & Kessler, 1995). The factors limiting fruit set may differ between sites, species and with time (Ayre & Whelan, 1989). Self pollination capacity of cultivars may as well vary from one location to another and also with age of tree (Free, 1993).

4.3.4 Weekly Trend of Fructification in *V. paradoxa*

The percentage fruit production was calculated weekly from the onset of fruiting phase to the 9th week of the fructification period (fruit maturity). Peak fruit production under open pollination occurred in 4th and 7th week after fruiting (WAF) for site 1 and 2, respectively. However, peak fruit production under insect exclusion occurred in 3WAF and 5 WAF for site 1 and 2, respectively (Fig. 10).

Fruit abortion occurred in both treatments considering the marginal decline in fruit production in the last three weeks of the fructification phase (Fig. 10). The occurrence of fruit abortion in shea was equally reported in the studies of Yidana (2004) and Okullo (2004). The inability of plants to sustain all fruits initiated fruits to maturity



could be attributed to diverse factors including resource limitation (Stephenson, 1981), fruit predation (Lee and Bazzaz, 1982) and strong winds. Okullo (2004) attributed higher fruit losses in the upper canopy of *V. paradoxa* trees to limited resources reaching the canopy, exposure to strong winds and fruit predation.

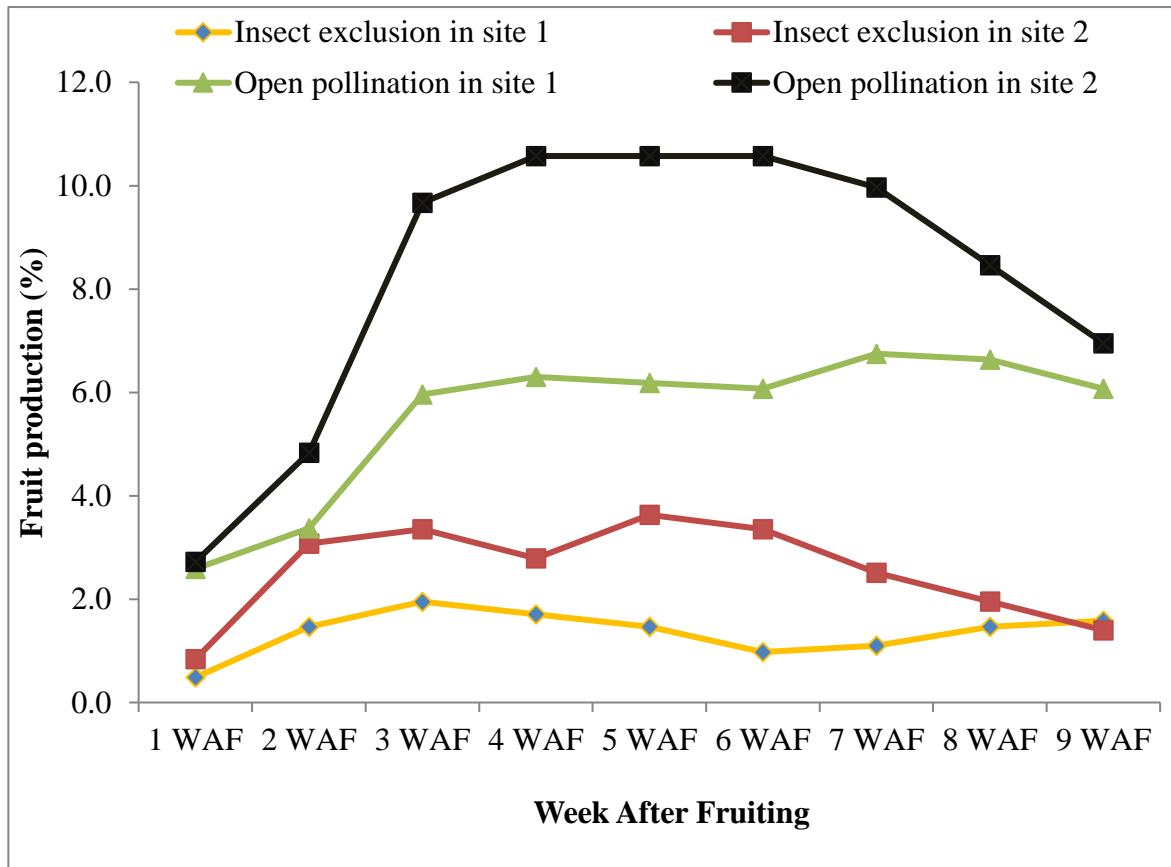


Figure 10: Fruit set pattern under open pollination and insect exclusion

4.3.5 Fruit and nut yield (weight) in *V. paradoxa*

The higher number of fruits in the open pollination treatment translated into a significantly higher fresh fruit weight per inflorescence ($P = 0.001$). Insect excluded flowers produced a significantly less fruit weight per inflorescence (14.42 g) as compared to open pollinated inflorescences (Fig. 11). Although the mean weight of



fruits per inflorescence varied significantly between treatments, the mean weight of a shea fruit did not vary significantly between treatments ($P = 0.130$) nor experimental sites ($P = 0.965$). However, fruits from open pollinated flowers weighed heavier (24.43 g) than fruits from insect excluded (20.46 g) flowers (Fig. 11).

The mean shea fruit weight recorded under both open pollinated and insect excluded treatments (Fig. 10) are higher than the maximum shea fruit weight recorded in the northern region of Ghana (Nyarko et al., 2012). The mean fruit weight recorded in this study also fell within the range (10.0 – 39.0 g) reported by Maranz & Wiseman (2003).

The mean nut weight for both treatments were found to be higher than nut weight recorded by Lassen et al. (2016) in 2011 but less than those recorded in the same study in 2012. This confirms the year to year variation in shea yield patterns within and across parklands (Hall et al., 1996). The mean dry kernel weight of both treatments fell within the 0.2 -10.4 g reported in Okullo (2004).



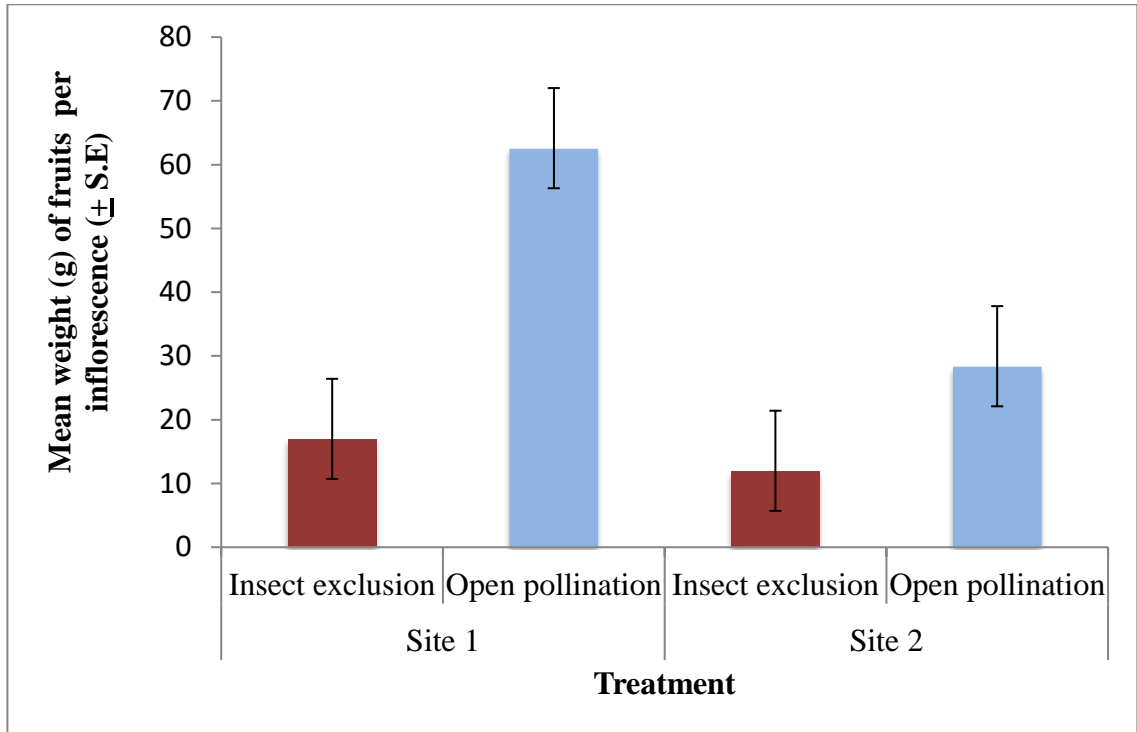


Figure 11: Mean fresh weight of shea fruits produced per inflorescence

The mean fresh weight of shea nuts produced per inflorescence varied significantly between treatments ($P = 0.045$) with open pollinated inflorescences producing heavier nuts (Fig. 12). However, the mean fresh weight of a single nut did not vary significantly between the two treatments ($P = 0.202$) although open pollinated flowers produced nuts with a relatively higher fresh weight (8.23 g) as compared to insect excluded flowers (7.15 g) (Fig. 13). The mean weight of dry kernels produced per inflorescence showed a significant difference between treatments ($P = 0.011$). Open pollinated inflorescences produced kernels with a significantly higher weight as compared to the insect excluded inflorescences in the two experimental sites (Fig. 14). However, the mean dry weight of a shea kernel did not vary significantly between



kernels produced from insect excluded flowers and those from open pollinated flowers ($P = 0.055$). Despite the insignificant differences in weight of a kernel for the whole experiment, a comparison of the two treatments in Site 1 showed a significant difference in mean weight (Fig. 15).

The insignificant difference in mean weight of a nut from the two treatments contradicts Lassen et al. (2016) who reported that nuts produced from open pollination were significantly heavier than nuts produced from insect exclusion. However, the reduced nut weight recorded in insect excluded inflorescences might be an outcome of inbreeding depression emanating from higher levels of self pollination (Galen et al., 1985; Kalisz, 1999). The inability of insect pollinators to forage on the flowers limited the chances of pollen outcrossing.

Moreover, the production of some growth hormones in plants is mediated by pollination (Klatt et al., 2013). For instance, in strawberry, fertilised achenes mediated the production of auxine which intend induced the accumulation of gibberellic acid (Csukasi et al., 2011).



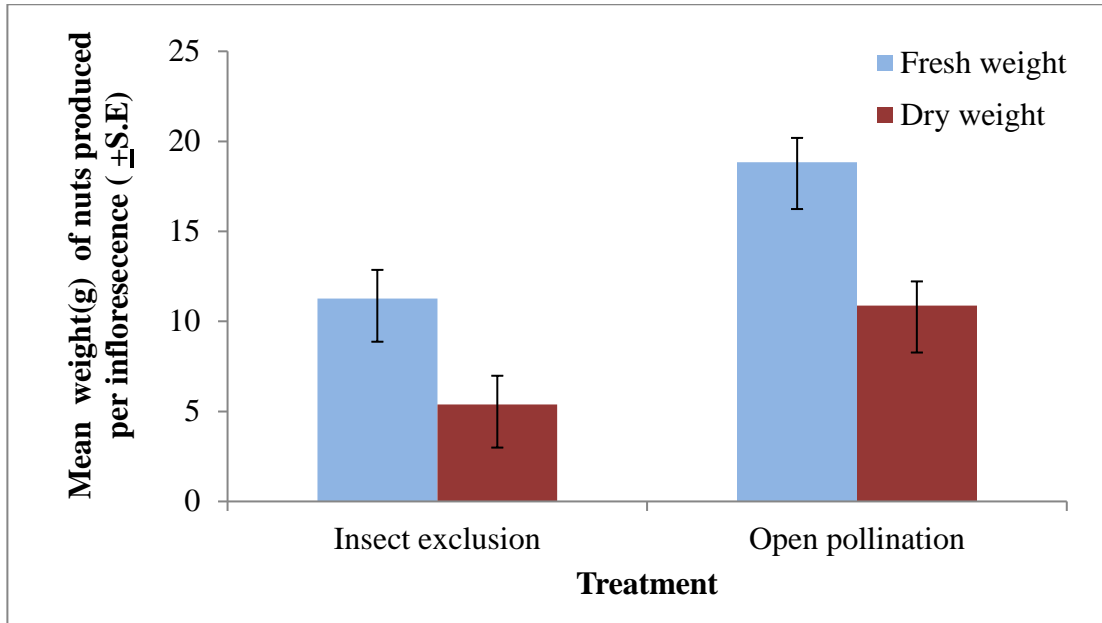


Figure 12: Mean weight of shea nuts produced per inflorescence

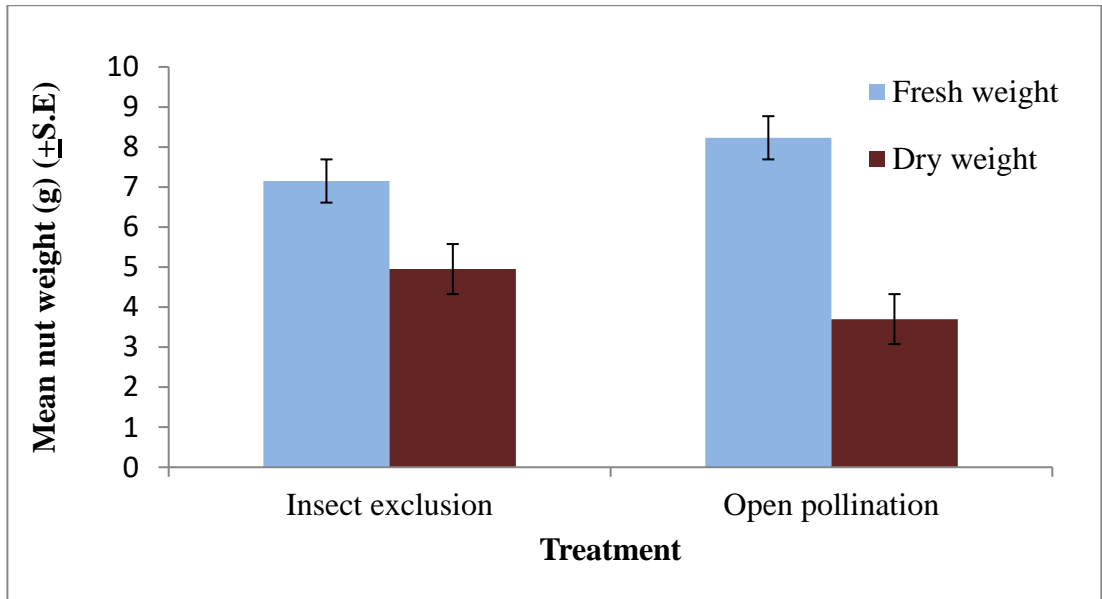


Figure 13: Mean weight of a shea nut

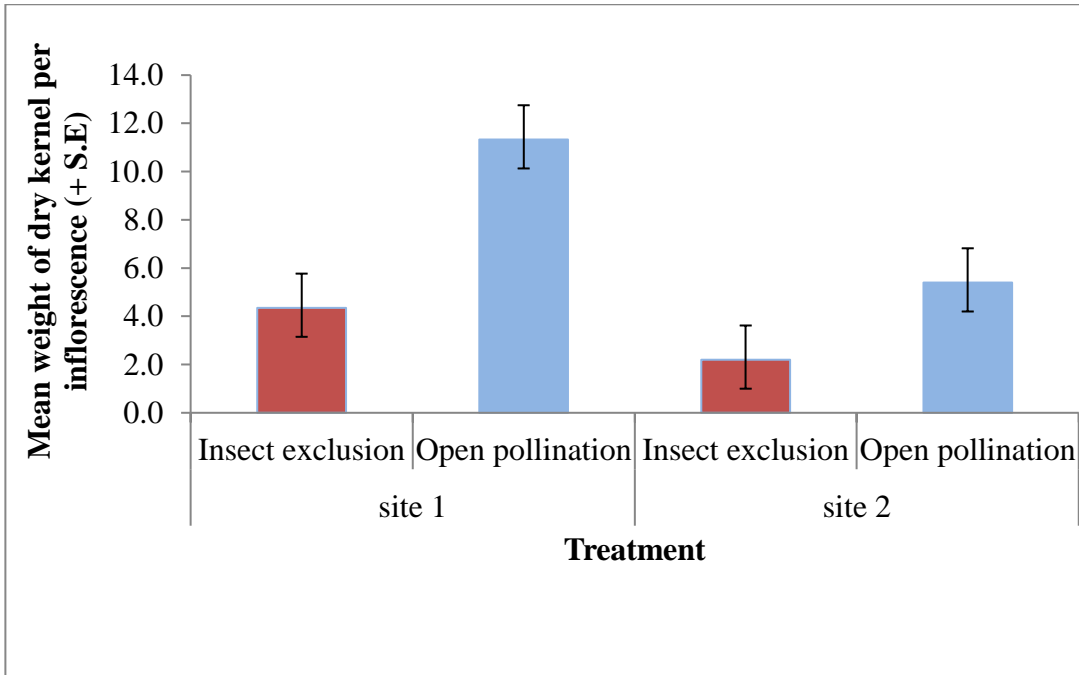


Figure 14: Mean weight of dry shea kernels produced per inflorescence

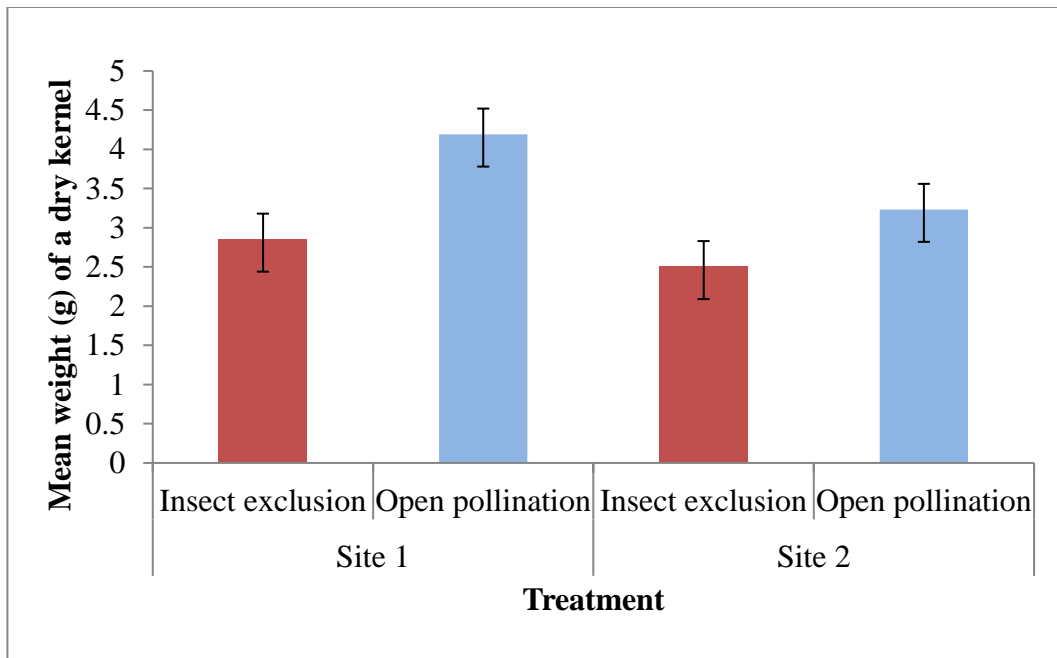


Figure 15: Mean weight of a dry shea kernel



These hormones facilitate fruit growth by enhancing cell progeny and size which results in an increased fruit weight (Roussos et al., 2009). Some of the fruits produced from open pollination had two solitary seeds. The presence of two seeds in some fruits of the open pollinated flowers could have also contributed to the higher weight in open pollination.

The positive effect of pollination on yield was reported in many other food crops. For instance, insect pollinated strawberry fruits were found to be 11.0% heavier than wind pollinated fruits and 30.3% heavier than self pollinated fruits (Klatt et al., 2013). Stanley et al. (2013) reported oil seed rape produced from open pollination had a significantly higher seed weight per pod than insect excluded pods. Coffee and blueberry had an increased fruit set and size under insect pollination services as compared to insect exclusion (Klein et al., 2003a; Isaacs and Kirk, 2010; Klatt et al., 2013).

A decline in insect pollination services could therefore have corresponding economic losses as a result of reduced nut weight. On the contrary, Lassen et al. (2016) revealed a higher germination percentage among the relatively lighter shea seeds than heavy seeds. Lighter seeds have relatively faster water absorption (Kikuzawa & Koyama, 1999) which is an important quality for germination. The production of lighter seeds from wind/self pollinated inflorescences could therefore be an advantage in terms of propagation

Although fruit quality was not examined in this study, insect pollination can influence the quality of fruit/seed yield. Bartomeus et al. (2014) reported higher oil content with



less chlorophyll in oil seed rape exposed to open pollination as compared to seeds that were produced from insect excluded flowers. Strawberry that was adequately pollinated by honeybees produced heavier and firmer fruits with less sugar-acid-ratio and longer commercial shelf life as compared to wind pollinated plants Klatt et al. (2013).

4.3.6 Percentage Insect Pollinator Dependency of *V. paradoxa*

The Insect Pollinator Dependency (IPD) of shea was estimated at 77% for fruit set and 73% for dry kernel yield (weight). Thus, the exclusion of insect pollinators from accessing shea flowers resulted in a 77% decrease in the number of fruit set and 73% decrease in dry kernel weight as shown in tables 7 and 8, respectively. IPD also varied slightly between the two sites, with site 1 recording less fruit set and kernel yield dependence on insect pollination.

The percentage pollinator dependence recorded in this study suggests *V. paradoxa* is a high pollinator dependent species based on Klein et al. (2007) categorisation of pollinator dependence levels. About 18.7% of crops in the developing world are known to fall within this category of high animal pollinator dependence (Aizen et al., 2009). There was variation in levels of pollinator dependence between the two sites. This finding is consistent with that of Carr & Davidar (2015) that reported variations in pollinator dependencies. This could be attributed to variation in site conditions. Variation in pollinator dependency between sites also occurred in oil seed rape comparing the findings of Stanley et al. (2013) and Bartomeus et al. (2014).



Table 7: Insect pollinator dependency of shea fruit set

Site	FSOP	FSIE	FSAI (FSOP-FSIE)	%IPD (FSAI/FSOP*100)
1	54	13	41	76
2	23	5	18	78
Mean	38.5	9	29.5	77

FSOP = total number of matured fruits produced from open pollination in a site, FSIE = total number of matured fruits produced from insect exclusion in a site, FSAI = number of fruits attributable to insect pollination in a site, IPD = % fruit set dependence on insect pollination.

Table 8: Insect pollinator dependency of shea kernel yield

Site	KWOP	KWIE	KWAI (KWOP - KWIE)	%IPD (KWAI/KWOP * 100)
1	79.6	25.6	54.0	68
2	45.2	10	35.2	78
Mean	62.4	17.8	44.6	73

KWOP=total weight (g) of kernels produced from open pollinated inflorescences, KWIE= total weight of kernels produced from insect excluded inflorescences, KWAI=kernel weight attributable to insect pollination, IPD= % of kernel yield dependent on insect pollination



Pollinator dependency may as well vary within different varieties of the same crop species (Breeze et al., 2016). Hence, the variation in genotypic characteristics of individual tree species might have contributed to the difference. Aside this, the intensity of air circulation can influence wind pollination and this could as well influence the insect pollinator dependence.

The paucity of information on pollinator dependence estimates for *V. paradoxa* supports calls (Cook et al., 2007; Klein et al., 2007) for an intensive review of insect pollinator dependence of commercially important crops of the world. Although some authors argued that insect pollinator dependent crops represent a relatively small volume of staple food consumption at a global scale, high pollinator dependent species provide disproportionately large economic returns to the local and international market (Richards, 2001; Ghazoul, 2005).

For instance, a loss of insect pollination services for shea might not have a significant impact on global food consumption but the livelihoods of about 16.2 million people would be affected in Africa (Glew & Lovett, 2014). Narrowing the importance of pollination service to their contribution to global staple consumption would appear to have minimal economic importance and tends to obscure local phenomena (Alizen et al., 2009). A pollinator dependent species is valued five times larger than a non-pollinator dependent crop (Gallai et al., 2009).

The high insect pollinator dependence of *V. paradoxa* implies that a decline in insect pollinators will have devastating effects on the fruit set and yield. However, unfriendly



ecosystem practices such as indiscriminate burning, habitat conversion and pesticide use in the area poses a threat to the conservation of pollination services.

4.4.0 Relationship between Insect Visitation Rate and Fruit Set/ Yield of *V. paradoxa*

4.4.1 Insect to Flower Visitation Rate

The rate of insect visits to inflorescences varied between experimental trees with ZT4 recording the highest (4.2) visits/ hour whilst ZT12 recorded the least (0.7) as shown in table 9. Comparison of insect visitation rate between experimental sites also indicated that site 1 recorded a significantly higher mean rate of 2.56 visits/ hour as compared to site 2 which recorded a mean of 1.82 visits/ hour ($P = 0.026$). Moreover, visitation rate varied significantly between the two major insect pollinator groups ($P = 0.00014$). Stingless bees had a significantly higher (1.8) visits/ hour as compared to honeybees that recorded 0.41 visits/ hour (table 9). This finding is similar to that of Lassen et al. (2016) who reported 1.3 stingless bees per fascicle and 0.5 honey bees per fascicle in the morning session. The higher visitation rate of stingless bees could be due to their significantly higher abundance (Fig. 5) as compared to the honey bee species.

A similar trend occurred in cocoa agroforestry where the most abundant insect pollinator group (midges) recorded the highest visitation rate (Adjalloo, 2012). Although the honeybees exhibited a more aggressive foraging behaviour, the long foraging period of stingless could have also accounted for their significantly higher



visit rates. For instance, some stingless bees visited flowers around mid day when honey bees were completely absent on shea flowers.

Moreover, the stingless bees hovered around the same inflorescence or branch for longer periods with limited movement across branches or trees. The shorter distances covered could also contribute to their higher visitation rate although this is noted for enhancing more self pollination than cross pollination (Okullo, 2004). However, short foraging ranges of the stingless bees reduces the problem of competition with other plant species for pollinators (Albano et al., 2009), because flight range of smaller bee species is often less than 200 m whilst honey bees frequently forage several kilometers away from the nest (Beekman & Ratnieks, 2000).

Insect visitation rate also differed between the two experimental sites with site 1 recording significantly higher visits as compared to site 2. The existence of a fallow land adjacent site 1 might have helped conserve more pollinators at a close proximity to the site. Lee et al. (2001) detected that uncultivated areas and shrubbery around farmlands serve as important buffers for insects in the mix of insecticides use.

Landuse in the vicinity of the parkland could also play a significant role in shaping insect visitation rate. For instance, Bartomeus et al. (2014) deduced that honey bee visits were often higher in more complex landscapes than simple landscapes.

Variation in insect visitation rate between experimental trees (Table 9) confirms the findings of early authors (Abrol, 1992; Wolf et al., 1999) who reported similar findings in other plants. This could probably be an outcome of variation in floral rewards. Insects primarily visit flowers for either pollen or nectar with nectar known



to be the most prioritised floral reward for bees (Dafni, 1992; Free, 1993). The sugar concentration in nectar can influence the attractiveness of a flower to insect visitors (Knopper et al., 2016).

Honeybees specifically prefer visiting flowers with a sugar nectar concentration of 30 – 50% (Abrol, 1992). In watermelon, nectar sugar concentration varied significantly between cultivars (Wolf et al., 1999) hence variation in genotypic characteristics of shea could influence sugar nectar concentration in flowers. This could have explained the differences in the insect visitation rate among experimental trees of the same site.

Aside nectar sugar concentrations, insect visits could be influenced by composition of plant allelochemicals. In some plants, allelochemicals serve as chemosensory cues for attracting insect pollinators (Pham-Delegue et al., 1990). The chemical composition of flower volatiles is a determinant of flower attractiveness to bees through olfactory signals (Wolf et al., 1999). Other factors that might have contributed to the variation in visitation include tree proximity to a bee colony (Lassen et al., 2016) and the amount of flowers initiated by a tree (McFarland, 1996). Massive flowering in trees serve an advertisement for attracting more insect species to flowers. For instance, Schmitt (1983) detected that bees selectively foraged more in areas of higher flower densities. Hence, trees with inflorescences containing larger number of flowers could be attracting more pollinators than less dense ones.



Table 9: Visitation rate (visits/ hour) of insect pollinators to a shea inflorescence

Visits per hour				
Site	Tree	Honeybees	Stingless bees	Total
1	ZT1	0.5	2.4	2.9
1	ZT2	0.3	1.7	2.0
1	ZT3	0.4	2.0	2.4
1	ZT4	1.6	2.7	4.2
1	ZT5	0.2	1.9	2.0
1	ZT6	0.4	1.9	2.3
1	ZT7	0.3	2.3	2.5
1	ZT8	0.5	1.9	2.3
1	ZT9	0.2	2.4	2.6
2	ZT10	0.6	1.8	2.3
2	ZT11	0.8	1.3	2.1
2	ZT12	0.2	0.6	0.7
2	ZT13	1.1	1.1	2.1
2	ZT14	0.3	1.6	1.9
2	ZT15	0.4	2.1	2.4
2	ZT16	0.2	1.4	1.5
2	ZT17	0.2	2.0	2.2
2	ZT18	0.4	1.2	1.6
Mean		0.4	1.8	2.2



4.4.2 Daily Pattern of Insect Visitation to *V. paradoxa* Flowers

Insect visitation rate also varied across the different periods of the day with both pollinator groups (honey bees and stingless bees) recording higher visitation rates in the morning session (6:00-8:00 am). The least visitation rates were recorded in mid day with only stingless bees visiting flowers at a rate of 0.21 visit/ hour. Visitations again peaked up in the evening as the heat of the sun reduced with honey bees recording a visitation rate of 0.038 and stingless bees recording 0.91 visit/ hour (Fig. 16).

Flower visitors exhibited different foraging behaviour on flowers of *V. paradoxa*. *Apis mellifera* generally foraged in the morning and were the earliest visitors arriving on the flowers by the break of dawn (around 6:00 am). They foraged actively on flowers until the heat of the sun intensifies. The visitation rate of *Apis mellifera* to shea flowers reduced with increasing sun heat intensity. Decline in *Apis mellifera* activity on flowers often starts from 7:40 am and were not seen on flowers after 9:00 am. Some few *Apis mellifera* were observed hovering around flowers just before sun set (5:30 – 6:00 pm) though this was extremely rare.

The foraging habit of *Apis mellifera* reported in this study is very similar to the findings of Okullo (2004) who observed foraging behaviour of *V. paradoxa* pollinators in Uganda. The occurrence of *Apis mellifera* as the earliest flower visitor in the morning could be influenced by its specific floral resource demand. This can be supported by Lassen et al. (2016) who observed that *Apis mellifera* gathered only pollen for the first 30 minutes and subsequently gathered pollen and/ or nectar for the preceding 30-60 minutes.



Aside the honeybee, all other flower visitors sought for nectar only (Okullo, 2003) this could also suggest that shea pollen is often released at the break of dawn. This exclusive pollen collection could facilitate more pollen transport and subsequently pollination success. The early foraging habit of *Apis mellifera* is not limited to shea, H'oehn et al. (2008) indicated that larger body sized bees generally visit flowers earlier (during cooler morning hours) as compared to smaller body sized bees. The foraging behaviour of *Apis mellifera* observed in this study learn support from that of Stone (1994) that indicated that some species of the Hymenoptera have specific daily durations of foraging activity.

Stingless bees (*Hypotrigona* spp.) on the other hand stayed on flowers for almost the whole day but with very little presence around mid day. They visited flowers in the morning but not as early as the *Apis mellifera*, the stingless bees again recorded some visits to flowers in the evening period (4:00 – 6:00 pm) when the heat from the sun begun to decline. However, some stingless bee species (*Meliponula beccari* and *Meliponula ferruginea*) were recorded foraging on shea flowers in the morning only. Although the stingless bees foraged similar to the honeybee (crawling across flowers or flying across branches), stingless bees were less active and foraged less vigorously as compared to the honeybees. The stingless bees stayed on one flower/inflorescence for relatively longer periods before moving to another.

The high visits of stingless bees (*Hypotrigona* spp) in the morning period observed in this study agrees with Mathiasson et al. (2015) that reported the peak daily activity of *Hypotrigona* spp. in the morning hours. The resumption of stingless bee visits in the evening was observed in Okullo (2004) as well. According to Chagnon et al. (1993)



the less active foraging habit of small sized bees tends to facilitate more pollen transfer within the same flower as compared to the active large sized bees. Therefore, the foraging habit of stingless bees might be enhancing more self pollination than cross pollination.

The variation in daily foraging periods of the flower visitors could have been influenced by their respective morphology (Pereboom & Biesmeijer, 2003), physiology or time of pollen release from main food sources (Stone, 1994). Climatic conditions (temperature and humidity) are also known to play a role in determining foraging and nesting activities of insects (Levings and Windsor, 1982; Feener and Schupp, 1998; Klein et al., 2003b; Ofori-Frimpong et al., 2007). For instance, Mathiasson et al. (2015) observed that stingless bee behaviour can be influenced by the daily weather conditions of the area.

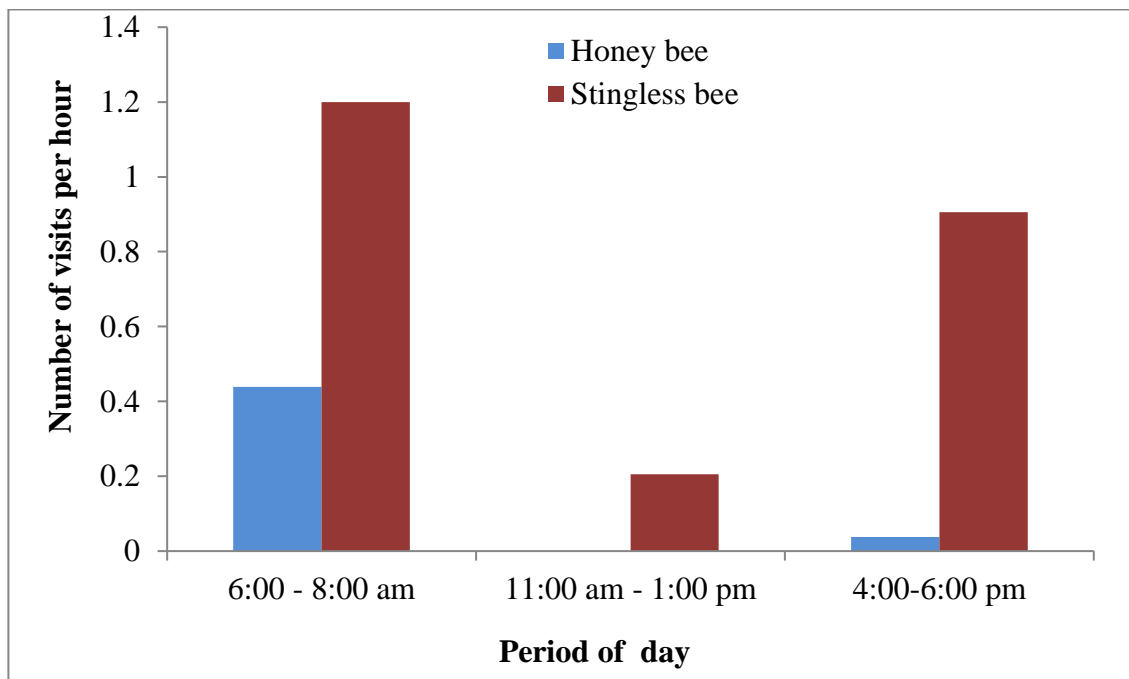


Figure 16: Visitation rate across different periods of the day

4.4.3 Weekly Trend of Insect Visitation to *V. paradoxa* Flowers

Visitation rate did not only vary across different periods of the day but also varied weekly throughout the flowering period. Insect visitation rates for both sites peaked in the second week when flowers were still fresh with 70 – 90% flower bud opening. Visitation however began to decline progressively after week 3 with the least visitation rate recorded in week 8 for both experimental sites (Fig. 17).

The weekly trend of insect visitation observed in this study (an upsurge of insect visits in the first and second week followed by a progressive weekly decline in insect visitation rate for the rest of the flowering season) (Fig. 17) could be a response to flower resource availability in shea. In some plant species, nectar production reduces as flower ages (Southwick & Southwick, 1983).

Field observations revealed that shea flowers recorded the highest insect visits at 70 - 90% bud opening when flowers were still fresh and perhaps had more floral rewards. Peaked flower nectar production is known to occur during anther dehiscence (Masierowska, 2003) thereby presenting more floral rewards. This explained the upsurge in insect visitation rate in the first two weeks of the flowering period (Fig. 17). However, visitation began to decline a week after 100% flower bud opening when flowers that opened earlier had started withering hence became less attractive to insects. Flowers generally become unattractive to insect pollinators when there is less pollen, cessation of nectar and aroma production, wilting, permanent closure or shedding of petals (Delaplane & Mayer, 2000).



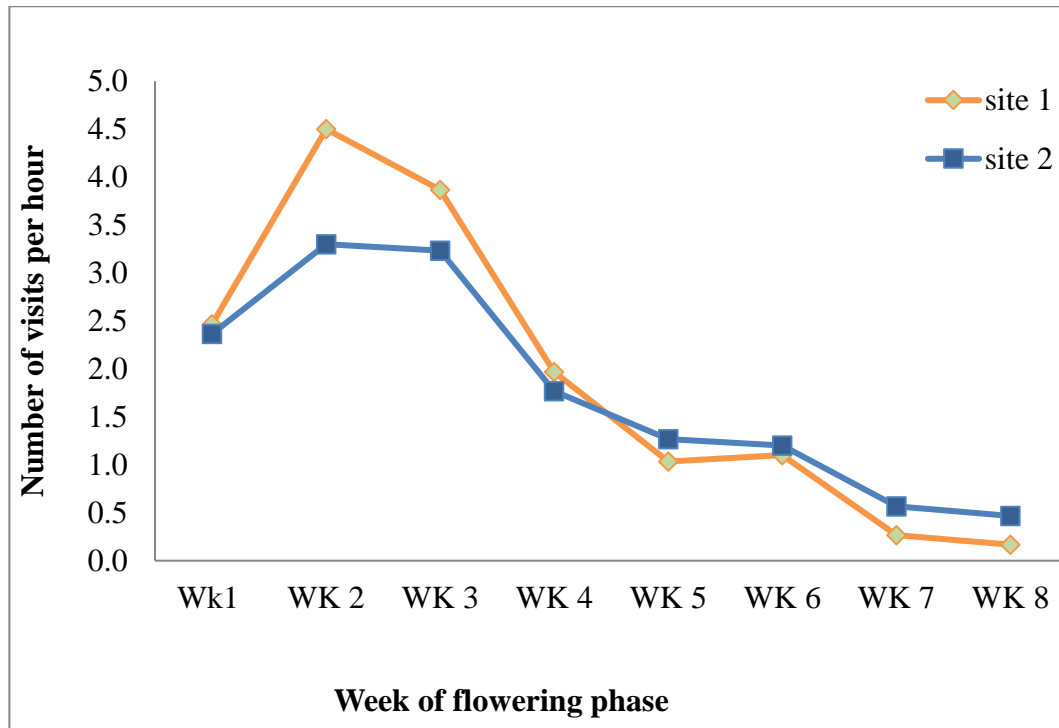


Figure 17: Insect visitation rate to shea inflorescence in the flowering phase

4.4.4 Insect to Flower Visitation Rate and Fruit Set in *V. paradoxa*

The relationship between insect visitation rate and fruit set was examined using the mean insect visits to an inflorescence per hour and the mean number of matured fruits produced per inflorescence. ZT13 was excluded because the branch on which visitation was observed got broken by a windstorm in the 4th week of fructification and hence did not have data on matured fruit set. Figures 18, 19 and 20 present the relationship between insect visitation rate and mean number of matured fruits per inflorescence. Total insect visitation rate positively affected the number of fruit set ($Y = 0.239 + 0.636X$; $R^2 = 0.35$) (Fig. 18). Fruit set increased steadily among inflorescences that had higher insect visits. A similar trend was observed when

visitation rate of the two main pollinator groups (honeybee and stingless bee) were plotted individually against the number of fruit set per inflorescence. The number of honey bee visits affected fruit set positively ($Y=1.348+0.725X$; $R^2=0.098$) (Fig. 19). Similarly, stingless bee visits also affected fruit set positively ($Y=0.001 + 0.914X$; $R^2=0.376$) (Fig. 20). In all cases insect visitation rate had a positive effect on the number of fruit set.

The positive relationship recorded between insect visitation rate and fruit set (Figures 18, 19 and 20) confirms early authors (Maynard, 1992; Adlerz, 1996; Wolf et al., 1999) that reported positive correlations between the number of bee visits and the fruit/ seed set in other plants. Flowers that recorded more insect visits had a higher tendency of receiving more viable pollen from the multiple visits. The amount of pollen received in the stigma is a major determinant of seed set in many plants (Elmstrom & Maynard, 1990; Maynard, 1992; Straka & Starzomski, 2014).

Moreover, some plant species have specific pollen requirements for fruit development which depends on a minimum number of insect visits. For instance, a normal fruit development in water melon requires a minimum of 10 bee visits to the flower (Maynard, 1992). In the veestar cultivar of strawberry a minimum of 4 insect visits are required to effect pollination (Chagnon et al., 1993). Therefore, inflorescences that recorded a higher insect visitation rate could have received more pollen to meet the minimum pollen requirement for a fruit set.

Despite the positive relationship between insect visits and fruit set, Klinkhamer et al. (1994) indicated that an increase in insect pollinator visitation rate does not always



result in an increased seed set. In some plants, it may rather result in lower seed set due to higher levels of selfing, clogging of stigmatic surfaces with self-pollen and may end in reduced pollen export (Klinkhamer et al., 1994). For instance, Norfolk and Gilbert (2014) observed no significant difference in seed set of wild plants in agricultural gardens over those in the surrounding natural environment though insect visitation rate was significantly higher in the gardens than the natural environment.

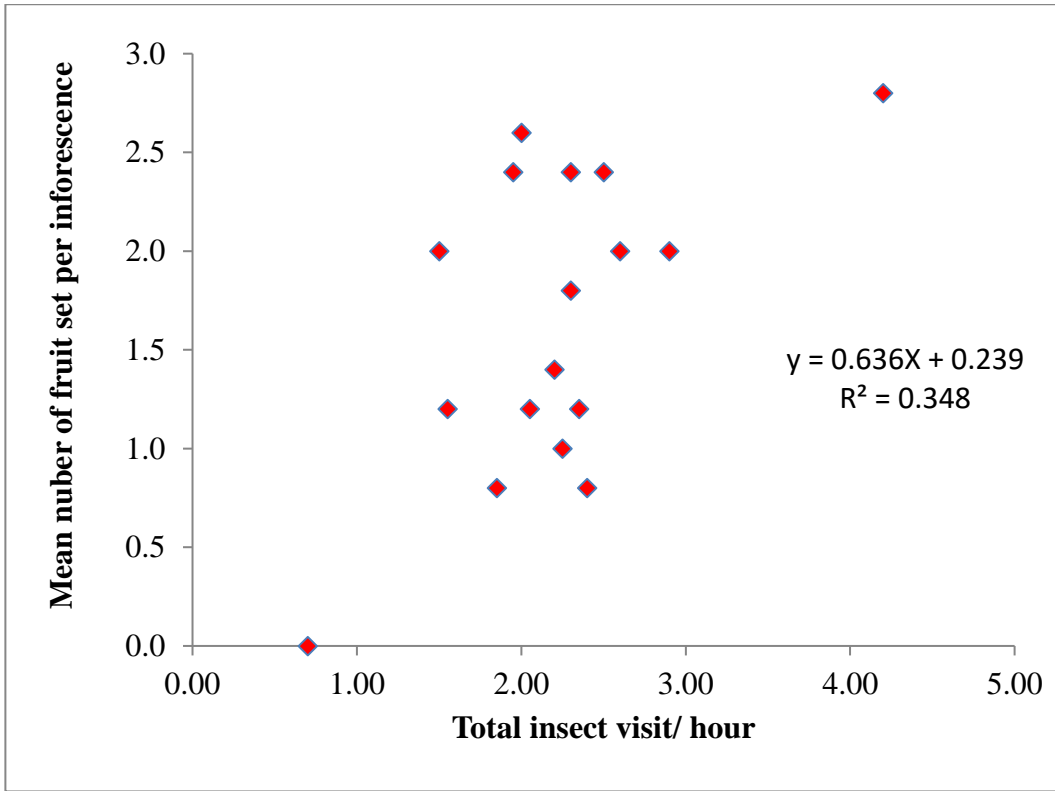


Figure 18: Relationship between pollinator visitation rate and mean fruit set



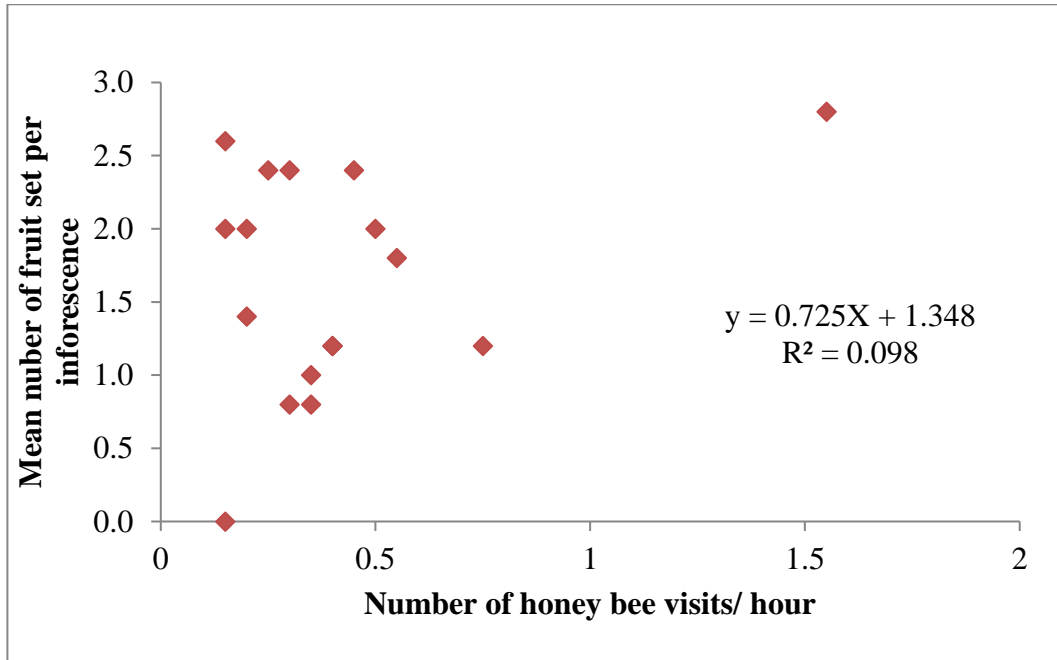


Figure 19: Relationship between honey bee visitation rate and mean fruit set

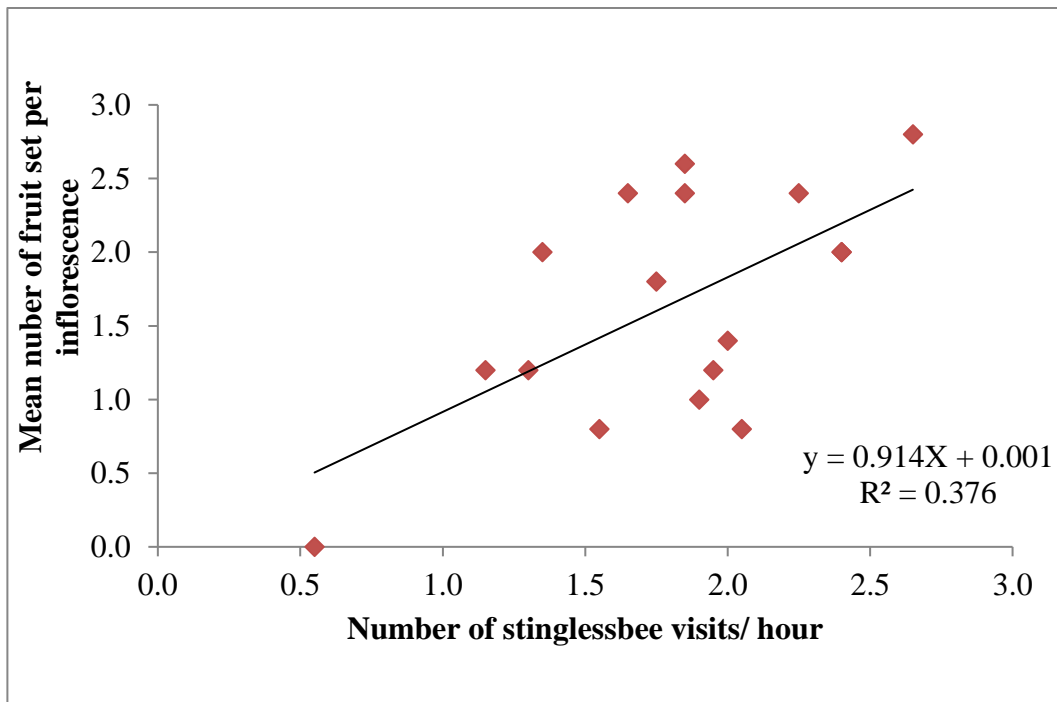


Figure 20: Relationship between stingless bee visitation rate and mean fruit set

4.4.5 Insect Visitation Rate and Nut Yield of *V. paradoxa*

Figures 21, 22 and 23 present the relationship between insect visitation rate and mean weight of dry nuts produced per inflorescence. Total insect visitation rate positively affected the mean weight of nuts ($Y = 0.563 + 7.2846X$; $R^2 = 0.35$) (Fig. 21). Nut weight increased steadily among inflorescences that had higher insect visits. A similar trend was observed when visitation rate of the two main pollinator groups (honeybee and stingless bee) were plotted individually against the nut weight per inflorescence. The number of honeybee visits affected nut weight positively ($Y = 11.90 + 11.59X$; $R^2 = 0.193$) (Fig. 22). Similarly, stingless bee visits also affected nut weight positively ($Y = 0.310 + 9.091X$; $R^2 = 0.386$) (Fig. 22). In all cases insect visitation rate had a positive effect on nut weight.

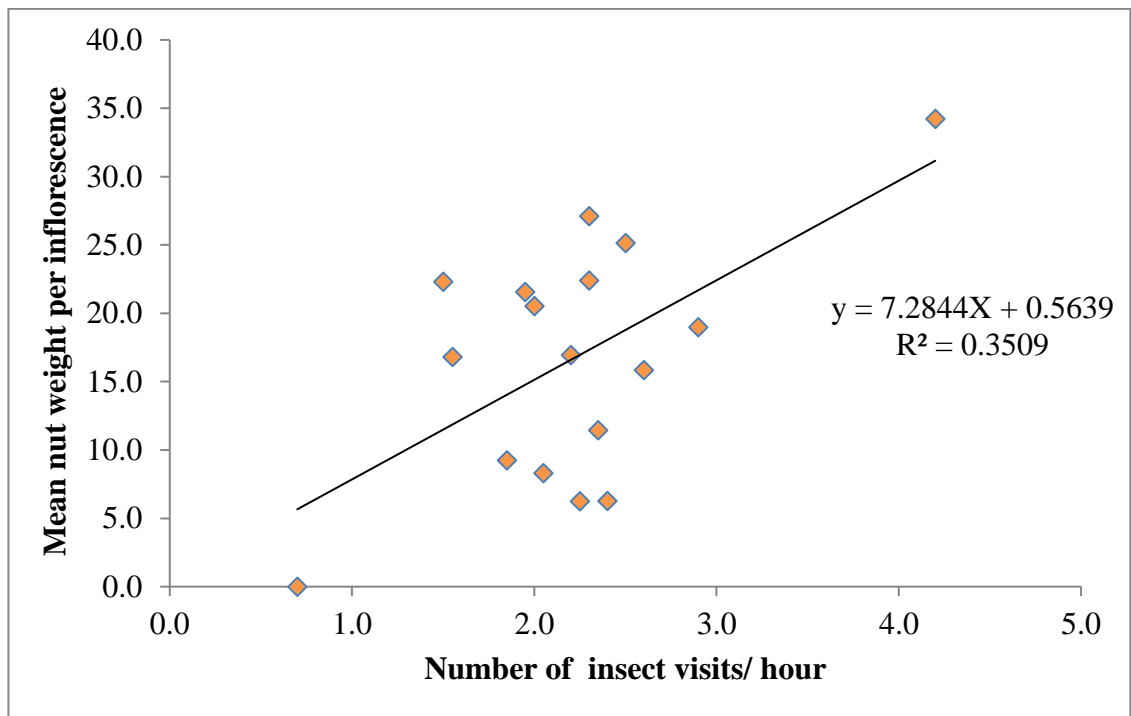


Figure 21: Relationship between pollinator visitation rate and nut yield



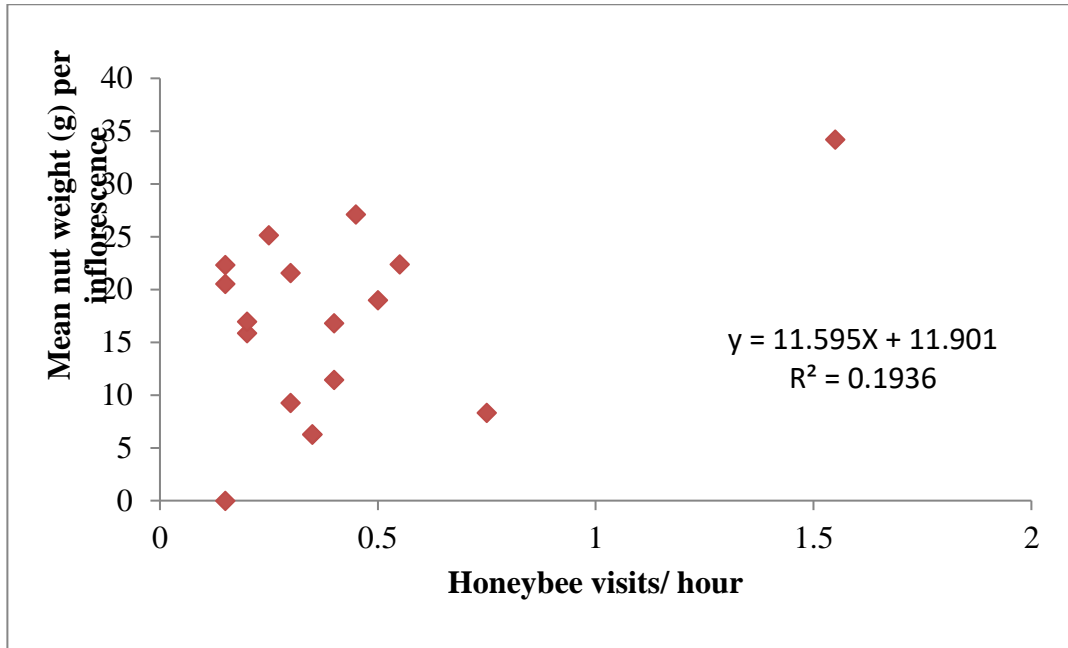


Figure 22: Relationship between honey bee visitation rate and nut weight

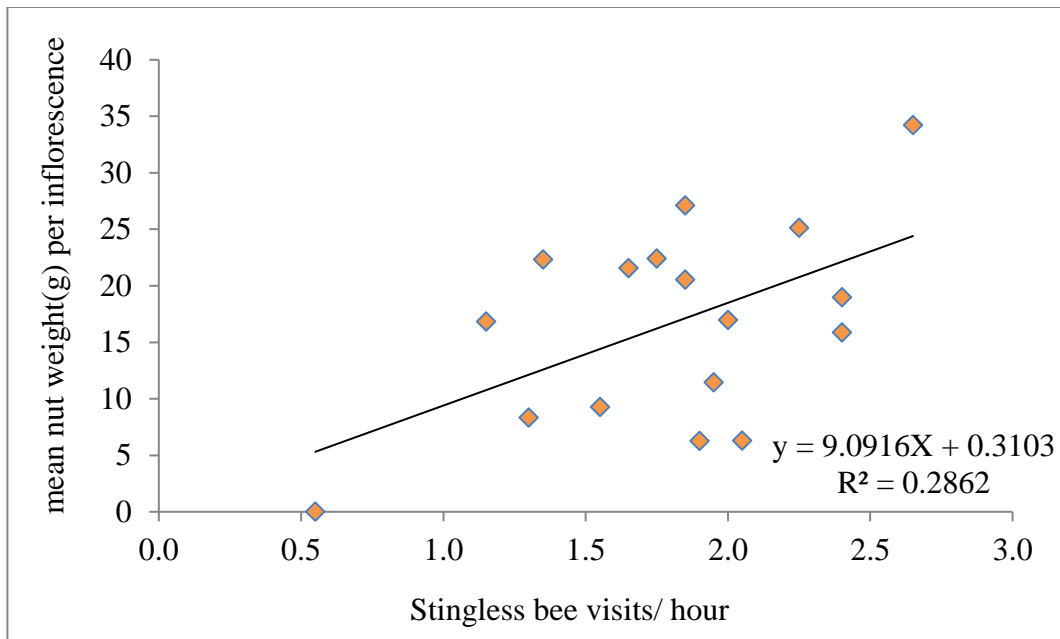


Figure 23: Relationship between stingless bee visits and nut weight

4.5 Economic Value of Insect Pollination in *V. paradoxa*

The purchasing price per bag of dry shea kernel varied from one company to another (Table 10). The price of a bag of shea kernel ranged from GHC 90.00 to GHC 105.00 in August, 2016. The least price was recorded in the Zini market. The average price was estimated at GHC 100.00. Thus, the monetary value of a bag of kernel stood at GHC 100.00 per August, 2016.

Table 10: Purchasing price per bag of shea kernel per the month of August, 2016

Price source	Purchasing Price (GHC)
Star Shea Company Limited	105.00
Savannah Fruit Company Limited	100.00
Mother's Shea Company Limited,	105.00
Kasajan company Limited	100.00
OLAM Ghana	100.00
Zini community market	90.00
Average	100.00

The economic value of the contribution of insect pollinators to the yield (dry kernel) of shea was estimated at GHC 73.21 per bag (85 kg). The economic value of insect pollination in site 2 was more than that of site 1 because of the variation in the pollinator dependence (Table 11). This finding confirms the assertion of Zebrowska (1998) that an increase in yield does not only reflect productivity but translates in to substantial amount of income for crop farmers. Estimates of economic value of



pollination can vary from one region to another in response to produce prices, production cost, labour and other factors of production (Breeze et al., 2016).

Although Allsopp et al. (2008) suggests a more accurate estimation of economic value of pollination services should consider the cost of replacement of wild pollinators with managed ones or cost of replacement with mechanical pollination services. There currently exist neither managed bee keeping nor mechanised pollination in the study area. Therefore, all estimates were based on the economic value of the quantity of the response variable (kernel yield) attributed to insect pollination.

Table 11: The monetary value (GHC) of insect pollination per bag of shea kernel (85kg) in August, 2016

Site	EVB (GHC)	UP(GHC)	QAI(kg)	EVI (GHC)
1	100	1.18	57.80	68.20
2	100	1.18	66.30	78.23
Mean	100	1.18	62.05	73.21

EVB=Economic value of a bag of shea kernel, UP= Unit price of a kg of shea kernel, QAI= Quantity (kg) of kernel attributable to insect pollination, EVI= Economic value of insect pollination (GHC).

Unfortunately, quantity of kernel yield might not represent economic value completely because economic standpoint focuses on produce quality as well (Ferguson & Watkins, 1992). For instance, the contribution of insect pollination to shelf life alone added US\$ 0.32 billion to the commercial value of strawberry. A more comprehensive



study on economic value could consider the quality of butter extracted from the kernels that were pollinated by insects since shea butter is the most important economic product of *V. paradoxa*.



CHAPTER FIVE

SUMMARY, CONCLUSION AND RECOMMENDATIONS

5.1 Summary

This study assessed the effect of insect pollination on the reproductive performance (fruit set and yield) of *V. paradoxa* in cultivated fields of the Guinea savannah zone of Ghana in 2016. The study also identified the insect pollinators of *V. paradoxa* in the Guinea savanna zone. The monetary value of insect pollination per bag of shea kernel was also estimated per the month of August, 2016.

A total of six insect species belonging to the order hymenoptera were identified as pollinators of *V. paradoxa* out of 187 flower visitors that were collected in the study. The *Hypotrigena* spp. was the most abundant among the collected specimens whilst *Compsomellisa* spp. and *Meliponula ferruginea* were the least abundant. Flower visitor abundance on flowers varied across different periods of the day as well as flowering phase. *Apis mellifera* exclusively foraged on flowers in the early morning hours (6:00 – 8: 30 am) whilst the stingless bees foraged on flowers for almost whole day but with limited presence in mid day (11: 30 am – 1:00 pm). *Apis mellifera* foraged more actively than the stingless bee species. Flower visitor diversity was also higher in the morning periods as compared to the other periods of the day.

The insect pollinator dependence of *V. paradoxa* yield was estimated at 73%. The pollinator dependency of site 2 was slightly higher than that of site 1. Insect pollination had a significant effect on the number of fruit set in *V. paradoxa*. The number of fruit set on flowers that had access to insect pollination was four times higher than those that did not have access to insect pollination. In terms of yield, the



weight of fruits produced from insect pollinated flowers and also the dry weight of nuts/ kernels produced from insect pollinated flowers were significantly higher than those produced from insect excluded flowers.

Insect to flower visitation rate varied between pollinator groups. The stingless bees had a significantly higher flower visitation rate than the honey bees. Insect visitation rate to *V. paradoxa* flowers also varied between trees. The rate of insect visits to a *V. paradoxa* inflorescence had a positive relationship with the number of fruit set as well as yield. The two main pollinator groups (honey bee and stingless bee) had positive effects on fruit set when visitation rate of each group was plotted against the fruit set.

The monetary value of the contribution of insect pollinators to the yield (kernel weight) of *V. paradoxa* was estimated at GHC 73.21 per bag (85 kg) of shea kernel that had a total monetary value of GHC 100.00 per the month of August, 2016. The monetary value of insect pollination in site 2 was more than that of site 1 because of the variation in the pollinator dependencies of the two experimental sites.

Overall, insect pollination had a positive effect on fruit set and yield because *V. paradoxa* is more dependent on cross pollination than self pollination. The open pollinated flowers that had substantial insect visits received more viable cross pollen which is a prerequisite for fertilization in insect pollinated plants.



5.2 Conclusion

The flower visitors of *V. paradoxa* are relatively diverse with the stingless bee been the most abundant visitor. Most insects visited flowers in the early morning period than any other period of the day. However, the flower visitors exhibited different foraging behavior. This difference in foraging behavior of flower visitors could possibly help in compensating/complementing each other's pollination.

Insect pollination significantly influenced fruit set and yield of *V. paradoxa* and therefore contributed immensely to the economic returns. A positive relationship exists between the rate of insect visits to a flower and the number of fruit set. Therefore, a decline in insect pollinators will not only affect the yield of *V. paradoxa* but will also translate into reduced income for the rural population that depends on shea for livelihood.

Hence the conservation of insect pollination as an ecosystem service is critical for the sustainability of shea yield. Insect pollination of *V. paradoxa* could be enhanced by creating conducive and undisturbed habitats for insect pollinators around shea parklands. Moreover pollination services could be enhanced by keeping bees on cultivated shea parklands to provide insect pollination services at a close proximity to the trees.



5.3 Recommendations

Based on the findings of this study the following is recommended;

1. Farmers should incorporate pollinator – friendly practices into contemporary landuse to help conserve pollinators in shea parklands. Some of these practices include reduced pesticide use and reservation of forest patches to serve as habitats for pollinators in shea parklands.
2. Farmers should adopt agrisilvi-pastoral systems especially beekeeping on shea parklands as way of providing managed pollination services at a close proximity of the trees.
3. Major stakeholders in environmental conservation such as the Environmental Protection Agency, Forestry Commission and Civil Society Organisations should educate the general public on the need to conserve insect pollinators in shea parklands of the Guinea savanna.
4. The study concentrated on effect of pollination on the quantity of fruit set and yield. It is therefore recommended that future studies should examine the effect of pollination on the quality of yield output especially fruit taste and oil quality. Also studies should be done on the effect of the other variables that influence fruit set such as soil moisture and nutrients to help disentangle the contribution of insect pollinators from the other variables that influence fruit set and yield in shea.
5. Again the economic value of the contribution of insect pollination to the annual income of a shea nut collector should be estimated to help establish a direct link between pollination and rural livelihoods.



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APPENDICES

Appendix 1: ANOVA table for mean flower production per inflorescence between trees in site 1

Source of variation	d.f	S.S	M.S	F	P-value	F crit
Between Groups	8	3492.03	436.50	5.066471	0.00016	2.1521
Within Groups	45	3877	86.155			
Total	53	7369.03				

Appendix 2: ANOVA table for mean flower production per inflorescence between trees in site 2

Source of Variation	d.f	S.S	M.S	F	P-value	F crit
Between Groups	8	784.3704	98.0463	4.968562	0.00019	2.152133
Within Groups	45	888	19.73333			
Total	53	1672.37				

Appendix 3: T-test comparing number of flowers per inflorescence between sites

	Site 1	site 2
Mean	31.57778	12.7
Variance	72.97944	16.335
Observations	9	9
Pooled Variance	44.65722	
Hypothesized Mean Difference	0	
Df	16	
t Stat	5.992545	
P(T<=t) one-tail	9.39E-06	
t Critical one-tail	1.745884	
P(T<=t) two-tail	1.88E-05	
t Critical two-tail	2.119905	



Appendix 4: T-test comparing fertilization (%) between treatments

	open pollination	Insect exclusion
Mean	62.97222	25.92778
Variance	1031.693	1118.926
Observations	18	18
Pearson Correlation	0.216305	
Hypothesized Mean Difference	0	
Df	17	
t Stat	3.82785	
P(T<=t) one-tail	0.000673	
t Critical one-tail	1.739607	
P(T<=t) two-tail	0.001347	
t Critical two-tail	2.109816	

Appendix 5: T-test comparing mean fertilization (%) between sites

	site 1	site 2
Mean	74.07778	51.86667
Variance	772.0994	1142.748
Observations	9	9
Hypothesized Mean Difference	0	
Df	15	
t Stat	1.522736	
P(T<=t) one-tail	0.074313	
t Critical one-tail	1.75305	
P(T<=t) two-tail	0.148626	
t Critical two-tail	2.13145	



Appendix 6: Paired T-test comparing mean fruit set between the two treatments

	Open pollination	Insect exclusion
Mean	1.422778	0.331667
Variance	1.068151	0.194909
Observations	18	18
Pearson Correlation	0.599556	
Hypothesized Mean Difference	0	
Df	17	
t Stat	5.471048	
P(T<=t) one-tail	2.07E-05	
t Critical one-tail	1.739607	
P(T<=t) two-tail	4.14E-05	
t Critical two-tail	2.109816	

Appendix 7: T-test comparing mean fruit set per inflorescence under open pollination between the two sites

	site 1	site 2
Mean	1.997778	0.847778
Variance	1.136119	0.389794
Observations	9	9
Pooled Variance	0.762957	
Hypothesized Mean Difference	0	
Df	16	
t Stat	2.792892	
P(T<=t) one-tail	0.006516	
t Critical one-tail	1.745884	
P(T<=t) two-tail	0.013031	
t Critical two-tail	2.119905	



Appendix 8: T-test comparing mean fruit set per inflorescence under insect exclusion pollination between the two sites

	site 1	site 2
Mean	0.48	0.183333
Variance	0.279975	0.0847
Observations	9	9
Pooled Variance	0.182338	
Hypothesized Mean Difference	0	
Df	16	
t Stat	1.473795	
P(T<=t) one-tail	0.079969	
t Critical one-tail	1.745884	
P(T<=t) two-tail	0.159939	
t Critical two-tail	2.119905	

Appendix 9: T-test comparing fresh Fruit weight per inflorescence between treatments

	Open pollination	Insect exclusion
Mean	45.40111	14.42
Variance	872.5767	267.5985
Observations	18	18
Hypothesized Mean Difference	0	
Df	17	
t Stat	4.844104	
P(T<=t) one-tail	7.6E-05	
t Critical one-tail	1.739607	
P(T<=t) two-tail	0.000152	
t Critical two-tail	2.109816	



Appendix 10: T-test comparing single fruit weight between the two treatments

	Open pollination	Insect exclusion
Mean	24.42796	20.45769
Variance	2.870231	2.172811
Observations	2	2
Pooled Variance	2.521521	
Hypothesized Mean Difference	0	
Do	2	
t Stat	2.500281	
P(T<=t) one-tail	0.064794	
t Critical one-tail	2.919986	
P(T<=t) two-tail	0.130	
t Critical two-tail	4.302653	

Appendix 11: T-test comparing single fruit weight between the sites

	site 1	site 2
Mean	22.52296	22.365
Variance	19.25676	1.49645
Observations	2	2
Pooled Variance	10.3766	
Hypothesized Mean Difference	0	
Df	2	
t Stat	0.049037	
P(T<=t) one-tail	0.482673	
t Critical one-tail	2.919986	
P(T<=t) two-tail	0.965346	
t Critical two-tail	4.302653	



Appendix 12: Mean fresh weight of nuts produced per inflorescence

	Open pollination	Insect exclusion
Mean	18.83714286	11.27272727
Variance	208.0429916	78.49018182
Observations	35	11
Hypothesized Mean Difference	0	
Df	28	
t Stat	2.091601144	
P(T<=t) one-tail	0.022833057	
t Critical one-tail	1.701130908	
P(T<=t) two-tail	0.045666114	
t Critical two-tail	2.048407115	

Appendix 13: T-test mean weight of dry nuts per inflorescence

	Open pollination	Insect exclusion
Mean	11.46061	5.666666667
Variance	83.94559	27.49380952
Observations	33	15
Hypothesized Mean Difference	0	
Df	43	
t Stat	2.769487	
P(T<=t) one-tail	0.004127	
t Critical one-tail	1.681071	
P(T<=t) two-tail	0.008255	
t Critical two-tail	2.016692	



Appendix 14: Mean fresh weight of a single nut

	Open pollination	Insect exclusion
Mean	8.227108844	7.153030303
Variance	10.02143075	4.279934343
Observations	35	11
Hypothesized Mean Difference	0	
Df	26	
t Stat	1.306928425	
P(T<=t) one-tail	0.101339392	
t Critical one-tail	1.705617901	
P(T<=t) two-tail	0.202678784	
t Critical two-tail	2.055529418	

Appendix 15: Mean weight of dry kernels per inflorescence

	Open pollination	Insect exclusion
Mean	8.315625	4.03076923
Variance	48.30394153	13.7273077
Observations	32	13
Hypothesized Mean Difference	0	
Df	40	
t Stat	2.675191406	
P(T<=t) one-tail	0.005384106	
t Critical one-tail	1.683851014	
P(T<=t) two-tail	0.010768212	
t Critical two-tail	2.02107537	



Appendix 16: Mean dry weight of a nut

	Open pollination	Insect exclusion
Mean	4.950998	3.7
Variance	4.709286	3.88
Observations	31	13
Hypothesized Mean Difference	0	
Df	25	
t Stat	1.864104	
P(T<=t) one-tail	0.037046	
t Critical one-tail	1.708141	
P(T<=t) two-tail	0.074092	
t Critical two-tail	2.059539	

Appendix 17: Mean dry weight of a single kernel

	Open pollination	Insect exclusion
Mean	3.784185	2.739744
Variance	3.496238	2.166368
Observations	33	13
Hypothesized Mean Difference	0	
Df	28	
t Stat	2.000455	
P(T<=t) one-tail	0.027617	
t Critical one-tail	1.701131	
P(T<=t) two-tail	0.055233	
t Critical two-tail	2.048407	



Curriculum Vitae

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