

**GENETIC DIVERSITY OF APHID SPECIES ATTACKING
AMARANTH AND NIGHTSHADES IN DIFFERENT AGRO-
ECOLOGICAL ZONES OF KENYA AND TANZANIA**

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DECLARATION

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DEDICATION

I dedicate this research thesis to my parents, Mr. Elijah Kipnyargis and Mrs Esther Kipnyargis for the love and support that they accorded me during the enduring moments of this research.

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ACRONYMNS AND ABBREVIATIONS

BLAST	Basic Local Alignment Search Tool
COI	Cytochrome Oxidase I
DNA	Deoxyribonucleic Acid
HIV & AIDS Deficiency	Human Immunodeficiency Virus and Acquired Immune Disease
ICIPE	International Centre of Insect Physiology and Ecology
IPM	Integrated Pest Management
MtCOI	Mitochondrial Cytochrome Oxidase c I
NCBI	National Centre for Biotechnology Information
PCR	Polymerase Chain Reaction
AICc	Akaike Information Criterion corrected
BIC	Bayesian Information Criterion
GTR	General Time Reversible
BOLD	Barcode of Life Database
TAE	Tris-Ethylenediaminetetraacetate

ABSTRACT

Aphids are the major pests of vegetables leading to a significant yield loss in African indigenous vegetables including amaranth and nightshades. Information on the types of aphids that infest these vegetables and their genetic diversity in Kenya and Tanzania is scanty. This is an important diagnostic component in developing management strategies such as integrated pest management and early detection and control of invasive species. This study used a fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene region called the barcode region to characterize the species of aphids that attack amaranth and nightshades in different agro-ecological regions of Kenya and Tanzania. Individual aphid samples were collected in 22 localities of amaranth and nightshade growing zones of the two countries, representing low, mid and high altitude agro-ecological zones. Total DNA was isolated and amplified using universal barcoding primers targeting the 5' end of the COI barcode region. There was a strong homology ($\geq 98\%$ identity) in nucleotide sequences of the barcode region using the Basic Local Alignment Search tool for nucleotides (BLASTn) in the GenBank to four main species of aphids namely: *Myzus persicae*, *Aphis fabae*, *Aphis craccivora* and *Macrosiphum euphorbiae*. Further, three subspecies of the black bean aphid were identified as *A. fabae fabae*, *A. fabae ciirciacanthoidis* and *A. fabae solanella*. Intra-specific nucleotide diversity indicated that *M. euphorbiae* had no genetic diversity (0.0%); while *A. fabae* had the highest diversity (0.8%). The lowest inter-specific diversity was observed between *A. fabae* and *A. craccivora* (6.3%) while the highest was observed between *A. craccivora* and *M. persicae* (10.6%). The phylogenetic tree constructed using the maximum likelihood model showed each individual species clustering in robust clades irrespective of the host crop or the locality from which it was collected. This confirmed the BLASTn results. The principal coordinate analysis (PCoA) and the haplotype network analyses further confirmed these results by showing species clustering together in their space and haplotypes, respectively. Overall, COI successfully identified the species of aphid infesting amaranth and nightshades. This forms an important diagnostic tool for management strategies, early detection of newly evolving biotypes, deployment of resistant crop cultivars and containment of invasive species.

CHAPTER ONE

1.0 INTRODUCTION

1.1 Background information

Aphids are a group of phloem-feeding insects belonging to the Phylum *Arthropoda*, Order *Hemiptera* and Superfamily *Aphidoidea* (Blackman and Eastop, 2000). They have a documented species number of about 5200 (Favret, 2014) making them some of the successful insect pests invading both food and non-food crops in temperate and equatorial regions. Universally, aphids have been reported to cause over 70% loss in the production of crops (Aslam *et al.*, 2007). Directly, aphids pierce the stem and leaves of the plant using sharp mouthparts called stylets to obtain sap from the phloem tissues eventually destroying the plant through wilting (Blackman and Eastop, 2000). In the process, aphids indirectly inhibit crop production by transmitting up to 50% of the plant potyviruses (Gray and Banerjee, 1999). Moreover, aphids secrete a sugary substance called honeydew, which not only exposes the leaves to sun burns but also act as an attractant for secondary infection such as the sooty mold that covers the leaf surface preventing the physiological functions of the plant and reduce the aesthetic market appeal for the vegetables (Blackman and Eastop, 2000; Lee *et al.*, 2010).

Amaranth and nightshades are widely grown indigenous vegetables in many parts of East Africa where they play an important role in providing vital nutritional and economic benefits to the small holder farmers (Seeiso *et al.*, 2014). Unfortunately, they have received insufficient attention in mainstream food policies and were until recent times regarded as a poor man's food (Bosch *et al.*, 2009). Amongst other challenges, pests continue to be the predominant deterrents in their production. In Tanzania for example, arthropods, aphids include and nematodes contribute to a loss of 36% to 42% of amaranth and nightshade production (Keller, 2004).

Generally, the control mechanism of aphids on indigenous vegetables has been a challenge since the control methods have focused on the use of chemical control (Dewar, 2007). Consequently, a large group of aphids, over time, developed resistance. Chemicals also pose biodiversity disruption and make pest management an expensive affair. For instance, *Myzus persicae* (Sulzer), due to its ability to vector numerous plant phytopathogenic viruses has been subjected to heavy insecticide sprays which has led to development of resistant species (Devonshire *et al.*, 1998). Biological control would however, be environmental friendly but this requires extensive knowledge on their taxonomical and phylogenetic characters.

Aphid species diversity has also been suggested to be influenced by host-crop and environmental association especially due to the polyphagous nature of aphids that necessitates the need to adapt to the new host (Miller and Footitt, 2009; Peccoud *et al.*, 2010). The latest molecular clock calibration shows that aphid's main ancestor was in existence 84-99 million years ago. This is basically the same period when woody angiosperms began undergoing adaptive radiation (von Dohlen and Moran, 2000), suggesting that aphid adaptive diversification may have arisen as a result of genetic changes in their host plants. Agro-ecological zones are described by environmental heterogeneity through space and time. Since the availability and suitability of crops change in these environments throughout the year, aphids are likely to become polyphagous and mobile (Figueroa *et al.*, 2005; Brévault *et al.*, 2008). This may contribute to gene flow and subsequent proliferation of a new clone of aphids genetically distinct from the original population.

It is known that aphids are some of the most dynamic insects possessing high morphological plasticity (polyphenism) due to alternation of host crop and environmental changes. For example, species of the black bean aphids (*Aphis fabae*) are reported to exist in a complex of several unresolved subspecies (Béji *et al.*, 2013). This makes both identification and understanding of their genetic diversity a mystery. Again, aphids depict sexual dimorphism in which some reproduce parthenogenetically where female aphids produce other females (anholocycly); whereas others are

holocyclic where a single sexual phase is included in the reproductive cycle (Orantes *et al.*, 2012). In relation to host range, aphids can be moneoecious, where they complete their life cycle in one host while others are heteroecious where they spend some time in the primary host and move to secondary hosts depending on the weather conditions and the availability of either crop at a particular time of the year (Blackman and Eastop, 2000). This, in combination with their relatively small bodies, gives them the ability to fly to and conquer new frontiers and as such may change their genetic make up to adapt to such environments.

Characterizations of aphid species on world crops have primarily relied on the morphological characterization and host crop association (Dixon, 1998; Footitt *et al.*, 2008; Chen, 2012). However, this does discriminate such species of aphids with large populations and cryptic allometric relationship among body parts like members of the genus *Aphis*. Also, the large population of aphids means that many of the biotypes are distinguished from one another on some very minute characteristics which may not be picked by morphological method of identification (Komazaki *et al.*, 2010).

Advancement in molecular biology techniques has been adopted to help in the screening of germplasms, genetic diversity studies, testing accession stability and integrity and fingerprinting the taxonomy of otherwise cryptic species (Kameswara, 2004). This has helped in resolving ambiguities common in morphological markers and further enhanced the understanding of species phylogeography and population structures. Molecular markers are versatile tools that give objective analysis of data, give reproducible results and are not amenable to environmental influence. Besides, molecular markers occur frequently within the genome (Jonah *et al.*, 2011). Commonly used molecular markers include: Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), Amplified Fragment Length Polymorphism (AFLP), Microsatellites or Simple Sequence Repeats (SSRs), Single Nucleotide Polymorphisms (SNPs), mitochondrial DNA and Diversity Arrays Technology (DArT) (Liu and Cordes, 2004; Semagn *et al.*, 2006).

The mitochondrial cytochrome oxidase *c* subunit I (COI) gene is a eukaryotic marker lying in the control region of the mitochondria. Its 5' terminus has been used to characterize almost all animal species using universal primers (Herbert *et al.*, 2003). Because of this, it has been referred to as the standard barcode (Herbert *et al.*, 2003a, b; Hajibabaei *et al.*, 2007; Wang and Qiao, 2009; Rebijith *et al.*, 2013). The barcode region lies in the conserved control region of the mitochondria. This allows for reliable identification, to species and subspecies level, at any developmental stage of the pest life cycle, including the eggs and degraded samples of animal specimens (Arif and Khan, 2009). The barcode region has consequently been used to correctly identify and characterize more than 80% of animal species (Coeur d'Acier *et al.*, 2014), including aphids (Kinyanjui *et al.*, 2015). In addition, it has been used to define host crop and genetic differences in pests (Brunner *et al.*, 2004). Another property of mitochondrial DNA region is that it depicts a relatively high evolutionary rate that involves nucleotide substitution. The high mutation rate has been postulated to be due to its inaccurate DNA repair system and lack of gene regulating histone proteins (Bogenhagen, 1999). In addition, COI gene lacks recombination events and possess a robust resistance to molecular erosion (Castellana and Saccone, 2011; Chen *et al.*, 2012). This is mainly because it is maternally inherited hence evade recombination events (Taylor *et al.*, 2005). Mitochondrial DNA evolves 10-fold faster than the nuclear DNA (Arif and Khan, 2009). Besides, mitochondrial DNA is one of the genetic regions with highly efficient primers (Hebert *et al.*, 2004). As such, the barcode region has been used to clarify even the most cryptic of animal species (Smith *et al.*, 2006).

The species of aphids infesting the African indigenous vegetables in East Africa has not been subjected to detailed molecular study. Therefore, this study was undertaken to characterize aphid species attacking amaranth and nightshades in various agro-ecological zones of Kenya and Tanzania using universal barcode primers. Subsequently, the study describes the role of agro-ecological zones and host crop in aphid species diversity in the two countries. This will form an important diagnostic component for management strategies, early detection of newly evolving biotypes, deployment of resistant crop cultivars and containment of invasive species.

1.2 Statement of the problem and justification

Kenya and Tanzania are among the East African countries which grow African indigenous vegetables for consumption and economic purposes (Seeiso *et al.*, 2014). However, aphids cause significant loss in the production of amaranth and nightshades in Kenya and Tanzania through direct feeding and transmission of plant viruses. The liberalization of trade among the East African countries means pest will move alongside biological material. This therefore, requires the development of an anticipatory model with the capacity to rapidly and accurately identify taxa that are deemed invasive in a country for the purposes of quarantine and subsequent development of pest management strategy. Effective management of aphids heavily relies on timely and accurate identification of individual species attacking the particular crops and adequate knowledge of species genetic relationships. Unfortunately, pest identification and diversity using morphological characteristics has been extensively utilized, but this process is often time consuming, labour intensive, amenable to phenotypic plasticity and does not provide information on certain genes (Jacoby *et al.*, 2003). Morphological characters have also not resolved immature stages and closely related species with inseparable morphology. Finally, the deficiencies of morphological taxonomy approach necessitate the search of a new tool to accurately identify these species at molecular level. The barcode region is therefore chosen since it can identify samples to sub-species level at any developmental stage, has been used to characterize over 80% of animal species and has an established reference library. Consequently, DNA barcodes created for the aphids will act as molecular tags to aid in genetic diversity studies over time and identify new invading pests for appropriate management strategies.

1.3 Hypothesis

There is no significant genetic diversity of the aphid species attacking amaranth and nightshades in different agro-ecological zones of Kenya and Tanzania.

1.4 Objectives of the study

1.4.1 General objective

To determine the genetic diversity of aphid species infesting amaranth and nightshades in different agro-ecological zones of Kenya and Tanzania.

1.4.2 Specific objectives

1. To determine the species of aphids attacking amaranth and nightshades in Kenya and Tanzania using DNA COI barcode region.
2. To describe the genetic diversity of the aphid species attacking amaranth and nightshades in Kenya and Tanzania using barcode region.
3. To determine the relationship between agro-ecological zones/host crop and the genetic diversity of aphid species of amaranth and nightshades in Kenya and Tanzania.

CHAPTER TWO

2.0. LITERATURE REVIEW

2.1 Basic description of amaranth and nightshade

2.1.1 The amaranth

Amaranth is a small-seeded pseudo cereal vegetable belonging to the family Amaranthaceae, and genus *Amaranthus*. Amaranth derives its name from a Greek word “amaranth” with a significant meaning of ‘non-wilting’ (Mlakar *et al.*, 2010). This is due to the ability of some species to withstand adverse climatic conditions.

Amaranth is a short lived plant growing to a height of about 2m. It is grown for both its grains and leaves. At maturity, the crop flowers and produce tiny seeds that are black to dark brown, while grain types produces cream coloured seed (van Rosenburg *et al.*, 2007). This seed can remain viable for up to 40 years. It is a C4 photosynthetic crop and therefore requires less water and is adaptive to higher temperatures (up to 40°C), sunlight and drier conditions (Njume *et al.*, 2014). It comprises of a fairly wide variety of species (approximately 60 species) out of which many grow in the wild as weeds (Njume *et al.*, 2014). Amaranth is cultivated for food, feed, grain, vegetable and for ornamental purposes (Mlakar *et al.*, 2010).

Amaranth originated from Central and South America where it was used by the Aztec community to perform some religious rituals such as eating amaranth mixed with human blood or popped and mixed with honey (Yarger, 2008). In fact, about 60 species of *Amaranthus* are native to America while the rest are distributed in Africa, Asia, India, China, Australia and Europe (Popa *et al.*, 2010). It is mostly used as a vegetable in Africa and Asia due to its unique spinach-like flavor, high yield capacity and the ability to grown in hot climate conditions (Popa *et al.*, 2010).

In East Africa, amaranth is known in Swahili as mchicha ((Vainio-Mattila, 2000). It is known that *A. spinosus* also called mbwache by the Sambia and *A. lividus* are the most

preferred vegetable species among the Sambia people living in the Western Usambara Mountains of Tanzania. On the other hand, *A. hybridus* is the most preferred of amaranth species among both the Eastern and Western inhabitants (Vainio-Mattila, 2000). The locals appreciate the inexpensive mode of preparation and their pleasant flavor.

2.1.2 The nightshade

Nightshades belong to the Solanaceae, a cosmopolitan family consisting of the world's popular fruits and vegetables such as tomatoes, potatoes, red and green peppers, egg plant, chillies as well as ornamental plants like *Petunia*, *Schizanthus* and *Lycium* species (Edmonds *et al.*, 1997).

African nightshade's taxonomy and nomenclature is quite complex due to its phenotypic plasticity, existence of polyploidy, frequent occurrence of spontaneous inter-specific hybridization and inconsistent use of local names (Ojiewo *et al.*, 2013).

They are annual or bi-annual and predominantly self-pollinating herbaceous plants growing up to 100 cm in height. The stem may be smooth or possess whitish hairs called trichomes (Njume *et al.*, 2014). They thrive well in soils rich in nitrogen and relatively light and warm climatic conditions which occur from the sea to the montane zones (Edmonds *et al.*, 1997). Optimum temperature ranges are 15-30°C for germination and 20-30°C for growth. An annual rainfall of 500-1200 mm is adequate for their growth (Ojiwe *et al.*, 2013). Their tender leaves are alternate in arrangement and bright green in colour; but purple colouration may be found as well (van Rosenberg *et al.*, 2007).

Nightshades are distributed throughout the world but with greater concentration in the warm temperate and tropical regions of Central and South America, Australia and Africa (Edmonds, 1978a). The centre of most diploid species of nightshades is Central

America; while most polyploids are mainly found in Africa and Europe (Ojiewe *et al.*, 2013). Polyploids can be exploited for exploitation of traits such as pest resistance.

In East Africa, local communities refer to this plant in various names. In Tanzania, it is referred to as *mnavu* among the Bonde and Mshambaa, *msogo* among the Bende and *mhaki* among the Kibena communities. The Ugandans generally call it *wsuggaenzirugavu*. In Kenya, it is called *managu* among the Agikuyu community, *isochot* among the Kalenjins and *ol'momoit* among the Maasai (Edmonds, 1997). In 2011, two species of *Solanum scubrum* (*nduruma*) and *olevolosi* were officially released by the World Vegetable Centre (AVRDC) into Tanzanian national seed catalogue. Vainio-Mattila (2000) reported that *Solanum nigrum* L. is the most preferred vegetable among the Eastern and Western inhabitants of the Usambara Mountains in Tanzania because of their flavor and consistent existence.

2.2 Health benefits of amaranth and nightshades

2.2.1 Amaranth

Amaranthus spinosus (*mbwache*) and *Amaranthus lividus* are the most preferred vegetable species among the Sambiaa people living in the Western Usambara Mountains of Tanzania. On the other hand, *A. hybridus* L. (*mchicha*) is the most preferred of amaranth species among both inhabitant of the Eastern and Western Usambara Mountains. The locals appreciate the inexpensive mode of preparation and their pleasant flavor (Vainio-Mattila, 2000).

Other than its ability to alleviate poverty and enhance food security, amaranth has sufficient amounts of proteins (17-19% of the dry weight), calcium, iron, folates, vitamins A, C and K. It is rich in amino acids lysine, arginine and histidine hence utilized in treating malnutrition in children (García *et al.*, 2011). Its dietary composition stimulates the body's immune system to retard the progression of HIV/AIDS virus (Ng'ang'a *et al.*, 2008). It has also been used to combat liver diseases, diabetes, hypertension and hemorrhage (Kim *et al.*, 2006).

2.2.2 Nightshades

In 2011, two species of *Solanum scubrum* (*nduruma*) and *Olevolosi* were officially released by the World Vegetable Centre (AVRDC) into Tanzanian national seed catalogue. Vainio-Mattila (2000) reported that *Solanum nigrum* L. is the most preferred vegetable among the Eastern and Western inhabitants of the Usambara Mountains in Tanzania because of their flavor and consistent availability. Apart from its use as a nutritive vegetable, Glew *et al.* (2009) reported that nightshade is boiled and its soup used to treat jaundice. In addition, it is used to treat open wounds, fever, eye diseases, heart diseases and skin diseases.

2.3 Pests attacking the indigenous African vegetables

Amaranth and nightshades are attacked by several arthropods pests which compromise their production. The various pests of amaranth are leaf defoliators, root pests and stem borers. The leaf eaters include aphids (Hemiptera: Aphidae) such as green peach aphid (*Myzus persicae*), black bean aphid (*Aphis fabae*), cowpea aphid (*Aphis craccivora*), the Hawaiian webworm (*Spoladea recurvalis*), *Psara basalis* (Aragón *et al.*, 1997). Amaranth is considered nematode tolerant and is thus recommended as a rotational crop to reduce nematode population for subsequent crops (Yarger, 2008). Nightshades on the other hand are generally attacked by black aphids, spider mites (*Tetranychus* spp.), lepidopterans and beetles (Van Rensburg, 2012).

Aphids destroy crops by sucking plant sap using their needle-like mouthparts called sytlet (Blackman and Eastop, 2000). Indirectly, aphids transmit plant viruses that cause various deformation and discoloration symptoms, and sometimes kill the plant. In addition, they secrete a sugary substance called the honeydew which attracts ants and

act as ingredient for the growth of black sooty mold other than reducing the aesthetic market appeal (Aslam *et al.*, 2007).

Globally, aphids are among the most economically important insect pests of crops because they rank high as invasive pests due to their ease of transport and parthenogenetic mode of reproduction (Footitt *et al.*, 2008). They are known to cause 70-80% of yield losses on different crops worldwide (Aslam *et al.*, 2007).

In Tanzania for example, arthropods, aphids include and nematodes contribute to a loss of 36% to 42% of amaranth and nightshade production (Keller, 2004). Information on aphid destruction scale on Kenyan indigenous is not known.

2.4 General characteristics of aphids

Aphids are a group of phloem-feeding insects belonging to the Phylum Arthropoda, Order Hemiptera and super-family Aphidoidea. They are a diverse group of insects comprising of over 4800 species (Armelle *et al.*, 2014), out of which 450 species colonize and affect food and fibre crops (Blackman and Eastop, 2007).

They are small soft bodied pear-shaped insects ranging in size from 1.59 mm as young aphid to 6.35 mm as adults (Ibraheem *et al.*, 2011). They are distinguished from other insects by the presence of a pair of tubular appendages of variable length known as cornicles that protrude from the posterior ends.

The diversity of aphids lies in their polymorphic nature and host alteration criterion. Many possess holocentric chromosomes. Aphids have the ability to alternate between parthenogenetic and sexual forms, migrating and non-migrating forms, winged (alatae) and wingless (apterae) forms and aestivating and hibernating forms (Kring, 1972). Their species can be heteroecious (alternating between primary and secondary hosts) or autoecious (complete life cycle on a single host), holocyclic (undergoing sexual and asexual reproduction) or anholocyclic (asexual only). Overall, holocyclic species transfer favourable genetic traits into the new generations hence potentiate their

adaptability response by increasing genetic diversity (Orantes *et al.*, 2012). A majority of aphids however, are autoecious, completing their entire life cycle in one host plant (Miller *et al.*, 2009). In addition, their small physique and ability to grow wings aids their dispersion over long distances (Armelle *et al.*, 2014). All these elements make them ideal models for studying evolution and ecology. Heteroecious aphids often migrate seasonally between primary and secondary hosts which may be in different agro-ecological zones resulting in gene flow. In Southern England, De Barro *et al.* (1995) reported an existence of diversity at micro-geographical level of *Metapolophium dirhodum* and absence of association between genotypes and host. This is contrary to the presence of high aphid gene flow in Europe as reported by the same study. The recent liberalization of trade among the East African states has posed a high risk of introduction of the aphids from different countries within the region and beyond especially in agriculture which is the main economic stay for all the countries in the block.

Aphids can to adapt to new conditions such as new plants hosts (Raymond *et al.*, 2001). In addition, since they are the major pests of crops, their genetic structure is presumably affected by extensive use of insecticides (Angela *et al.*, 2006). Many aphid species have developed resistance to various chemical groups of insecticides (Rubiano-Rodríguez *et al.*, 2014). For example, the green peach aphid, *Myzus persicae*, one of the aphids attacking Amaranthaceae and some Solanaceae, has been described to possess resistance towards insecticides. Insecticide resistance together with the complexity of the life cycle as well as several aspects of agro-ecological systems dramatically affects the genetic structure of aphids.

2.5 Aphids attacking amaranth and nightshades

Worldwide, aphids consist of about 5012 species (Favret, 2015). In Africa, some of the most prevalent aphid species include: Banana aphid (*Pentalonia nigronervosa*), Black bean aphid (*Aphis fabae*), Cabbage aphid (*Brevicoryne brassicae*), Citrus aphid (*Toxoptera citricidus*, *T. aurantii*), Green peach aphid (*Myzus persicae*), cow pea aphid (*Aphis craccivora*), Cotton aphid (*Aphis gossypii*), Russian wheat aphid (*Diuraphis*

noxia), Mango aphid (*Toxoptera odinae*), Maize aphid (*Ropalosiphum maidis*), Pea aphid (*Acyrtosiphum pisum*), Sorghum aphid (*Melanaphis sacchari*) (Blackman and Eastop, 2000).

In East Africa, some of the reported aphid species attacking indigenous vegetable are *M. persicae*, *A. fabae*, *A. craccivora*, *Brevicorryne brassicae* and *A. gossypii* (Kinyanjui *et al.*, 2015).

2.5.1 The Cowpea aphid (*Aphis craccivora* [Koch])

Aphis craccivora Koch (Hemiptera: Aphididae) are velvety black coloured aphids found mainly at the shoots of crops. Their apterae measure about 1.4-2.2 mm and alatae about 1.4-2.1 mm (Blackman and Eastop, 2000; Peterson *et al.*, 1998).

Cow pea aphid is a polyphagous pest that is known to transmit 30 persistent and non-persistent potyviruses (Berberet *et al.*, 2009; Blackman and Eastop, 2000). These viruses cause mosaic like symptoms like wilting of the young crops, and stunted growth and premature leaf senescence in the adult crops.

They are predominantly anholocyclic in life cycle where apterous females are produced parthenogenetically over several successive generations; while later stages yield males that are predominantly alate (Obopile and Ositile, 2010; Blackman and Eastop, 2000; Ofuya, 1997). Factors such as complex life cycle, polyphagy and polymorphism make morphological diagnosis of this pest a difficult task. The basic morphology of the cow pea aphid is as shown in Plate 1.

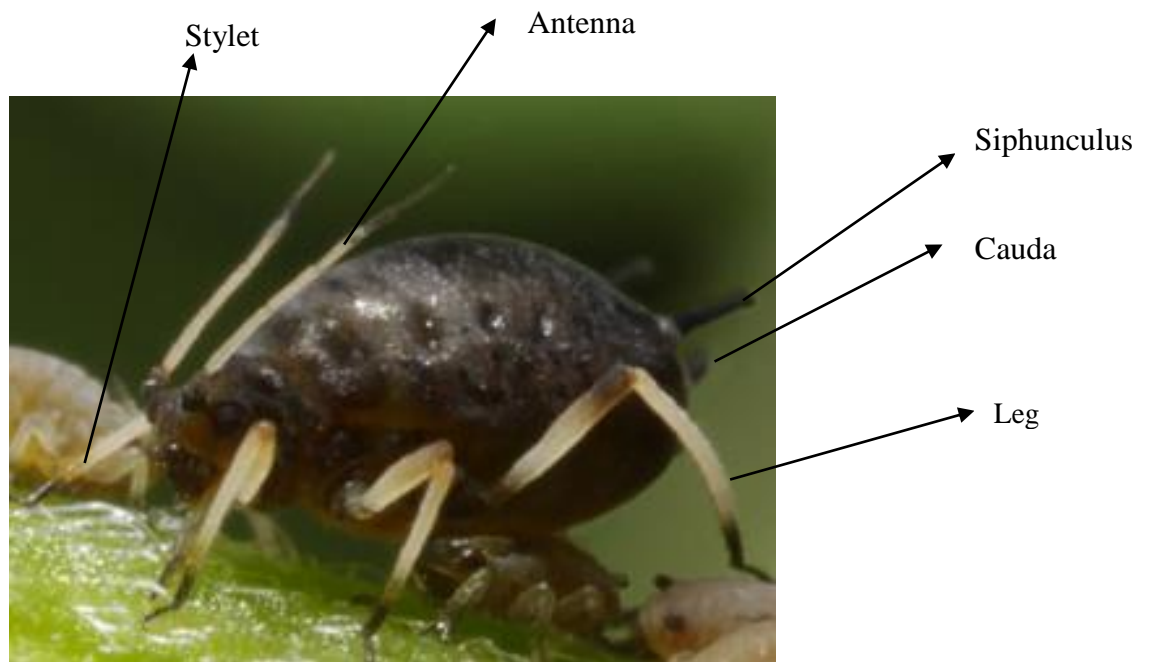


Plate 1: Cow pea aphid, *Aphis craccivora* (Claude Pilon, 2012)

2.5.2 The green peach aphid (*Myzus persicae* [Suzler])

The green peach aphid (Plate 2) has body colour that ranges from pale-yellow-green to whitish-green to red. The primary host crop are the peach trees; while alternative hosts are numerous where they transmit over 100 viruses both persistently and semi-persistently (Blackman and Eastop, 2000; Field *et al.*, 2003). Rebijith *et al.* (2013) found the green peach aphid on amaranthus crop in India, demonstrating their polyphagous nature. They exist both in asexual and sexual morphs (cyclical parthenogenesis) depending on the weather conditions (Field *et al.*, 2003). The green peach aphid's highly polymorphic nature and its ability to resist pesticides are some of the reasons why it is difficult to identify morphologically.

Studies on species of *Myzus persicae* and *Myzus nicotianae* in South Eastern United States using mitochondrial COII region and RAPD-PCR profiles reported low genetic diversity in both cases (Clements *et al.* (2000). This could indicate that the two species

are indeed very closely related and can only be distinguished via the barcode region. The same results were discovered when allozyme marker was used to study variation in *M. persicae* (Hales *et al.*, 1997). On the contrary, when microsatellite markers were used to study diversity in *M. persicae* populations of Eastern Australia, higher genetic divergence was observed (Wilson *et al.*, 2000). However, it is important to note that external factors such as host adaptability, resistance to chemical application and life cycle characteristics also play an important role in genetic changes of the green peach aphid.

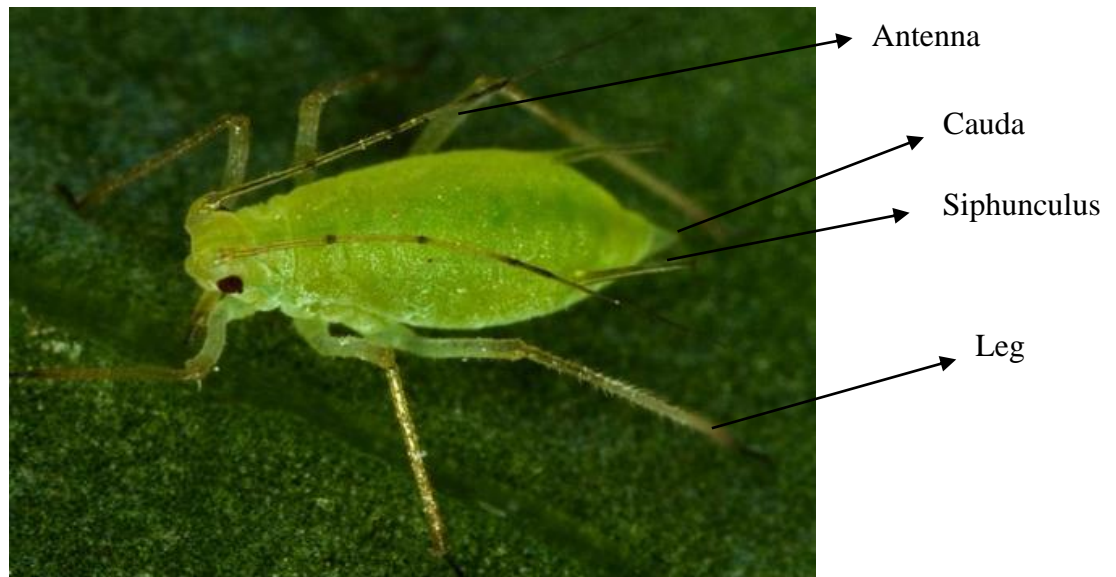


Plate 2: Green peach aphid, *Myzus persicae* (David Cappaert, 2010)

2.5.3 The black bean aphid (*Aphis fabae* [Scopoli])

The black bean aphid (Hemiptera: Aphididae; Plate 3) is a black-coloured aphid mainly found at the shoots of amaranth and nightshades aggregating in colonies and some having wax-like markings (Blackman and Eastop, 2000). They are highly polyphagous and holocyclic aphids causing significant damage to *Vicia faba* (Webster *et al.*, 2008; Béji *et al.*, 2015). *Solanum nigrum* was found to host *A. fabae* in India (Rebijith *et al.*, 2013). The existence of different morphs: *Aphis fabae fabae*, *Aphis fabae solanella* and *Aphis cirsiacanthoidis* makes the black bean aphid a very cryptic aphid for taxonomical studies using morphological techniques (Béji *et al.*, 2013). They coexist

together in their natural hosts and identification process using classical taxonomy is nearly impossible since the original classification relied on the ability of each subspecies to colonize their unique secondary host (Stroyan, 1984). *Aphis fabae*, in the colder regions, reproduces sexually on its primary host and asexually on its alternative regions. This means the genetic diversity on the two host could be affected.

Genetic diversity of the black bean aphid on faba bean and soybean has been studied using Random Amplified Polymorphic DNA-Polymerase Chain Reaction (RAPD-PCR) profiles (Béji *et al.*, 2013), mitochondrial cytochrome *c* oxidase I (COI) and the partial tRNA/COII region (Lee *et al.*, 2010; Kim *et al.*, 2010) and microsatellite genotyping on a few number of alleles (Vantaux *et al.*, 2011). On the contrary, no reported studies have been conducted to determine the genetic characterization of the black bean aphid infesting indigenous crops of East Africa.

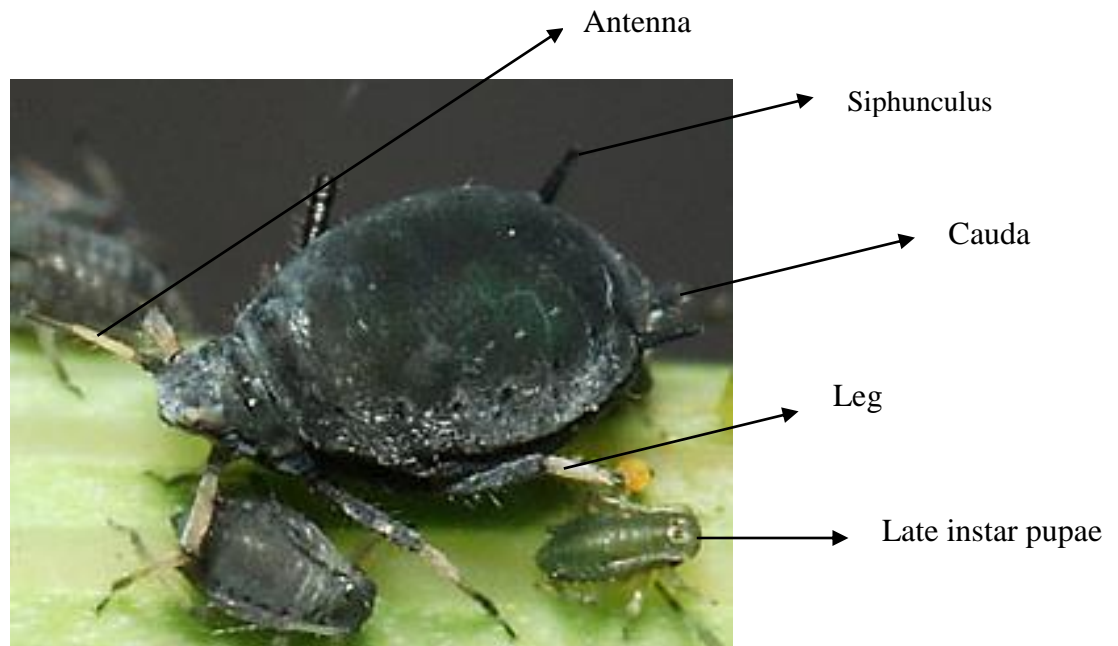


Plate 3: The black bean aphid, *Aphis fabae* (Influentialpoints, 2009)

2.5.4 The potato aphid (*Macrosiphum euphorbiae* [Thomas])

The potato aphid (Plate 4) ranges in size from medium to large and is characterized by pear-shaped body and its colour ranges between green to yellowish-pink (Blackman and Eastop, 2000). This gives it features that are similar to *M. persicae*. They have

been reported to depict holocyclic mode of reproduction (asexual and sexual modes of reproduction) depending on weather conditions seasons in North America and anholocyclic mode in the rest of the world (Blackman and Eastop, 2000; Alyokhin *et al.*, 2011). They exhibit host alternating character expanding host range to about 200 crops especially the Solanacea family (Borquel *et al.*, 2011), including nightshades. Furthermore, its prolific nature in reproduction and the vast number of crops that it infests cause significant damage to vegetables. It is indeed considered one of the most damaging aphids in the world which indirectly causes damage by vectoring 40 different viruses through the non-persistent route and five viruses persistently (Stufkens and Teulon, 2001).

Studies to enumerate the role of host and environment in the genetic diversity have been undertaken using RAPD (Raboudi *et al.*, 2011) and microsatellite markers (Raboudi *et al.*, 2012). In these studies, there was no significant genetic divergence reported when host crop and environment was put into consideration. There is need therefore to consider extra-nuclear genome such as the mitochondrial DNA regions to elaborate this further.



Plate 4: Green and brown morphotypes of the potato aphid, *Macrosiphum euphorbiae* (Claude Pilon, 2010)

2.6 Genetic diversity studies of aphids

Genetic diversity studies of aphids can be carried out using the nuclear and mitochondrial DNA. DNA markers have become a more efficient technique for determining diversity in aphid populations and species complexes. A notable percentage of genetic diversity of aphid populations arises due to mutation in the nuclear region or of a sensitive gene of mitochondrial cytochrome *c* oxidase subunit I (COI).

2.6.1 Allozyme markers

The principle of allozyme markers is that protein variants in an enzyme can be differentiated using gel electrophoresis according to the charge and sizes of the amino acids constituting the enzyme. To visualize the bands, gels are stained with enzyme specific stain that is conjugated with the enzyme substrate, cofactor and an oxidized salt (Johnson *et al.*, 1996).

In a study to demonstrate the diversity among the sexual and asexual forms of *Rhopalosiphum padi* in different regions of France, Delmotte *et al.* (2002) noted that allozymes showed little polymorphism among sampled sites. Similar results were reported in Russian wheat aphid in the United States except for 3 allozymes that showed polymorphism (Puterka *et al.*, 1993). In addition, allozyme markers have been used to infer the dominant mode of reproduction employed by populations of *R. padi* (Le Gallic, 1996). It is however notable that allozyme markers have a limited number of available markers, require fresh or frozen material and some loci show protein instability (Schlötterer, 2004).

Allozyme marker techniques have since been overtaken by the more advanced molecular marker techniques. Consequently, there is no reported case of its use in studying aphids of amaranth in amaranth and nightshades in East Africa.

2.6.2 Nuclear based DNA markers

Among the nuclear markers that have been used to study genetic diversity in aphid populations is the RAPD markers. Raboudi *et al.* (2011) using RAPD markers reported a greater genetic diversity among the 15 populations of the potato aphids (*Macrosiphum euphorbiae*) collected in different localities of Tunisia than within these populations. The same results were revealed for the study of 18 populations of *M. persicae* in Italy using RAPD markers (Angela *et al.*, 2006). However, there was low genetic diversity of populations of Canadian green peach aphids irrespective of the host crop or the sampling locality (Clements *et al.*, 2000).

Diversity also arises because the male X chromosome's gene region with spindle fibres attached to multiple sites along the chromosomes and ribosomal DNA is prone to many alterations (Blackman and Spence, 1996). These genes contain internally transcribed spacers (ITS 1 and ITS2) that are highly variable.

Nuclear DNA of aphids contains variable repeats known as microsatellites (Jarne & Lagoda 1996). They are mainly preferred nuclear markers because they infer genetic recombination, depict heterozygosity and can follow an individual clone from time to time (Sunnucks *et al.*, 1997). An experiment to study variation among the grain aphids *Sitovion avenae* in Southern England resulted in higher genic and genotypic variation when microsatellite markers were used to describe the role of geographic variation and host crop in genetic variability of cereal aphids (Sunnucks *et al.*, 1997). Among the sexual populations of the *Rhopalosiphum padi*, microsatellite markers revealed a high allelic diversity. However, the allozyme markers revealed low genetic diversity for the eight populations of the *R. padi* in France (Delmotte *et al.*, 2002).

A number of nuclear molecular tools have been used widely in identification of aphid species, PCR-RFLP (Valenzuela *et al.*, 2007), real-time PCR (Naaum *et al.*, 2012), random amplified polymorphic DNA (RAPD) and microsatellites (Helmi *et al.*, 2011).

2.6.3 Morphological markers

Aphids have been characterized by a number of key morphological features that are shared within species. The length and segmentation of the antennae is a major feature used in species identification (Liu and Sparks, 2001). Aphids also have a cauda and two-segmented tarsi with the second segment bearing two claws (Capinera, 2008). The shape and size of the cauda and the appearance of hairs on this structure are important characters used in species identification (Liu and Sparks, 2001). The winged forms are usually recognized by the venation and relative size of the front and hind wings. These taxonomically useful features are evident in most aphid species of economic importance though they may be modified, reduced or secondarily lost in some species (Blackman and Eastop, 2007).

Routine identification of aphid species based on their morphological characters suffers from several drawbacks. It is laborious, time-consuming and requires a lot of taxonomic expertise. It is also very difficult to accurately discriminate aphids due to their small size and the microscopic nature of some of their taxonomic characters (Lee *et al.*, 2011). In addition, evolutionary processes may lead to reduction, modification or complete loss of key morphological characters in some species, thereby complicating species identification and analysis of their relationships (Footit, 1997). As a matter of fact, morphological characters have proved unreliable in distinguishing closely related species, because of their remarkable morphology conservatism (Cocuzza & Cavalieri 2014). Further complications occur when these closely related species form large cryptic species complex and also when there are damaged specimens (Floyd *et al.*, 2009), often leading to erroneous identifications.

Accurate morphology-based identification of aphids is also hampered by their complex life cycles associated with parthenogenesis and polymorphism, which produces different morphological forms within a single species such as sex morphs, winged and wingless forms (Footit *et al.*, 2008). Moreover, aphids exhibit a wide range of continuous morphological variation in response to environmental factors, so that it is

difficult to identify them based on their morphological characters (Blackman and Eastop, 2007). Additionally, aphids have the capacity to undergo morphological adaptation in response to the physiological status of their host plants, quality of food plant, nutritional effects and natural enemy associations (Agarwala, 2007). Biological factors such as variation in developmental stages, individual growth rates and differences in number of nymphal instars, also contribute to morphological diversity among aphids, thereby complicating morphological-based identifications (Mehrparvar *et al.*, 2012).

2.6.4 Mitochondrial COI in diversity studies

Mitochondrial DNA (mtDNA) is a unique region used as a valuable tool in genetics and phylogeographic investigations (Herbert *et al.*, 2003). Eukaryotic genetic diversity studies utilize the region of mtDNA encoding sub-unit I of cytochrome *c* oxidase, one of the three mitochondrial DNA coding subunits in the respiratory chain of prokaryotes and eukaryotes. It is involved in catalyzing the oxidative phosphorylation in the mitochondria and is susceptible to high range of mutations (Lunt *et al.*, 1996). The amino acid residues in the reaction centres, which are highly conserved across species, do not cover the entire COI molecule. This allows room for considerable variations in some regions. In addition, mtCOI region has a higher rate of mutation, which results in significant variation in DNA sequences to distinguish closely related and cryptic aphid species (Leite, 2012). Mitochondrial DNA (Plate 5) is common across taxa and is strongly conserved across animals and existing in high copy numbers to allow annealing and subsequent amplification by the universal primers (Galtier *et al.*, 2009). This provides large area for ease of amplification during polymerase chain reaction (PCR). Moreover, mtCOI is haploid in nature and lacks introns, which facilitates sequence alignments of the amplified genes without much editing (Castellana and Saccone, 2011). Molecular markers that have been exploited in aphid species identification include mitochondrial cytochrome *c* oxidase subunit I (COI) and COII. COI gene lack recombination events and possess a robust resistance to molecular erosion (Chen *et al.*, 2012).

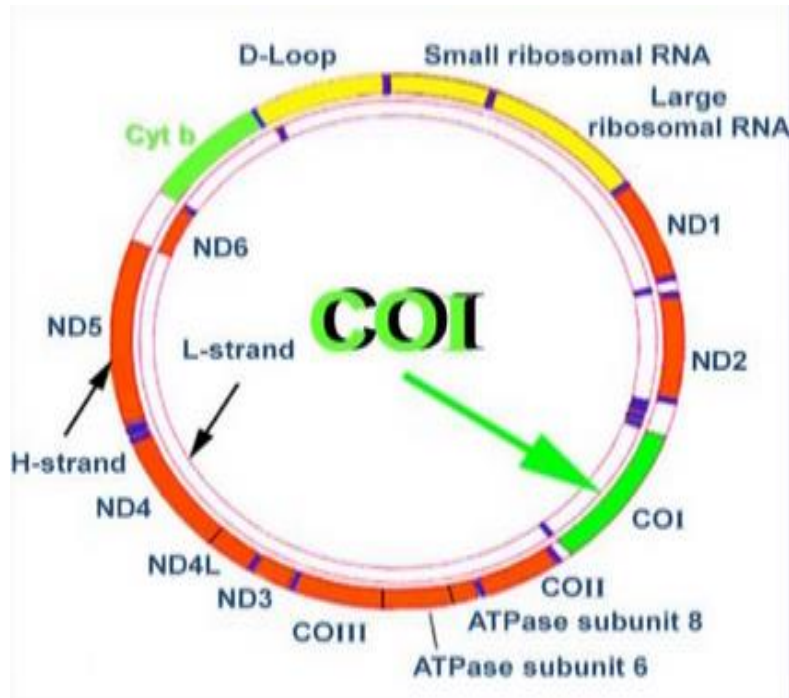


Plate 5: A general structure of the D-loop region of the mitochondrial DNA showing the COI locus. (Lende, 2015)

A consensus 648-bp region from the 5'-terminus of this molecule has been primed for eukaryotic species characterization, including insects. Meusnier *et al.* (2008) reported that the universal primers for the COI gene in eukaryotes amplified 94% of the insect population. Similarly, LCO-1490 and CHO-2198 primers by Folmer *et al.* (1994) were able to amplify 92.3% of the 457 aphid populations sampled from Korea (Lee *et al.* 2010).

In a study by Komazaki *et al.* (2010), each of 168 individuals of 7 species assessed contained 1,563 bp coding region; but 272 sites were variable among aphid species. This therefore makes the COI gene a model gene for determining genetic diversity among species.

The COI barcode gene region has been used widely to delineate as well as understand the genetic diversity of aphid species in relation to environmental variation. For example, it has been used to clearly distinguish the four subspecies of the black bean

aphid complex in Tunisia (Béji *et al.*, 2015), understand the genetic diversity of *Aphis gossypii* and other members of the *Aphis* genus in Japan (Komazaki *et al.*, 2010) and to perform phylogenetic analyses of the aphids in Greece (Papasotiropoulos *et al.*, 2013). However, similar studies on the aphid species attacking amaranths and nightshades in Kenya and Tanzania have not been carried out.

2.7 Factors affecting genetic diversity in aphid populations

Genetic diversification of aphid population aids them in adapting to new environments hence enhancing their survival in such new environments. Some of the factors that affect their diversification are discussed under the following topics.

2.7.1 Aphid-host association

Aphid species diversity is influenced by diverse host-crop association especially due to the polyphagous nature of aphids and reproductive isolation that occurs during migration from one host to another (Peccoud *et al.*, 2010; Rebijith *et al.*, 2013). For example, using morphological identification, Margaritopoulos *et al.* (1998) reported that the ultimate rostral segment in aphid species is known to vary with the host plant type and the physiological status of the plant. Similarly, under laboratory conditions, the body size and pigmentation of *M. persicae* were largely affected by the host plant type (Clements *et al.*, 2000).

Reports have also been put forth that aphids evolved in response to the conditions and changes in their host plant. In fact, the latest molecular clock calibration shows that aphid main ancestor was in existence 84-99 million years ago. This is basically the same period when woody angiosperms began undergoing radiation (von Dohlen and Moran, 2000). Subsequently, aphid interaction with host plant triggers resistance from the host. Over the years, response to plant defense mechanism has forced aphids to evolve in order to circumvent these host resistance. This allows them to survive by

feeding, growing and reproducing on their host plants. This becomes a forceful factor for aphids to develop host alternation, a factor that favours their proliferation because they diversify their feeding scope, evade enemies and develop a skill for competition for resources (Hales *et al.*, 1997).

2.7.2 Cultural factors

The ability of aphids to change their genetic make-up in response to unfamiliar cultural factors like pesticide application and the subsequent proliferation of resistant biotypes pose a threat to pest management strategies (Clements *et al.*, 2000). Aphids also, under stressful conditions develop wings (alate). With these wings and small body sizes and with the aid of wind, aphids can fly to other territories where they may cross-breed with the native species and donate pesticides resistant genes to these populations (Hales *et al.*, 1997). This phenomenon has been reported in the interaction between the *M. persicae* and *M. nicotianae* which interbreed freely to produce viable offsprings.

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1 Study sites and sampling technique

Sampling sites were categorized into low, mid and high agro-ecological zones. Classification into appropriate agro-ecological zones was done based on altitude (Corbett, 1998); where regions with elevation below 1000 m elevation were categorized as low altitude agro-ecological zones, regions with altitude ranging from 1000 m to 1799 m elevation were categorized as mid altitude agro-ecological zones; whereas regions with elevations above 1800 m above sea level were categorized as high altitude agro-ecological zones. Adult and late instar pupae of *Aphis craccivora*, *Myzus persicae*, *Aphis fabae* and *Macrosiphum euphorbiae* were sampled on cultivated amaranth and nightshades in each of six randomly selected Counties of Kenya in February, 2015 and five Provinces of Tanzania in May, 2015. The regions sampled in Kenya were: Mombasa, Kilifi, Embu, Kirinyaga, Kisii and Kiambu Counties while in Tanzanian the regions were: Arusha, Kilimanjaro, Morogoro, Tanga and Pwani (Table 1 and 2; Figure 1 and 2). In each region, two localities were randomly selected for sampling.

Sample collection was based on random sampling in each of the localities of each of the Counties and Provinces of Kenya and Tanzania, respectively. Sampling was done according to Lokeshwari *et al.* (2015) whereby collection was done on host crops situated at least 2 kilometres apart to eliminate chances of collecting clones from a single parthenogenetic female. Camel hair brush was used to sweep at least 20 (sample) adult and /or late instar pupae aphids naturally infesting amaranth and nightshades on the abaxial side of the leaf. They were killed by putting in 95% ethanol contained in 2 ml eppendorf tubes before being transported to the International Centre for Insect Physiology and Ecology (*icipe*), molecular pathology laboratory of the Arthropod Pathology Unit for genotyping. Additionally, other information such as weather condition, date of collection, locality, altitude, management practices such as pesticide

application and Global Positioning System (GPS) coordinates were recorded. The identified aphids were then photographed using the Leica LAS EZ4D stereo microscope (Leica Microsystems Inc., USA) at X25 magnification whereby pictures of the dorsal, lateral and ventral parts were taken.

Table 1: Aphid samples collected from various Kenyan agro-ecological zones

Species name	Analysis code	Host crop	County	Locality	Collection date	GPS Coordinates*
<i>Myzus persicae</i>	MpBo1,MpBo2, MpBo3,MpBo4, MpBo5	Amaranth	Kisii	Borabu	18-2-2015	00°79.929'S 035°01.373'E
<i>Aphis craccivora</i>	AcBo1, AcBo3,AcBo4, AcBo5	Amaranth	Kisii	Borabu	18-2-2015	00°79.929'S 035°01.373'E
<i>Aphis fabae</i>	AfBo2	Amaranth	Kisii	Borabu	18-2-2015	00°79.929'S 035°01.373'E
<i>Myzus persicae</i>	Mpkt1, Mpkt2,Mpkt3, Mpkt4	Amaranth	Kisii	Kitutu Masaba	18-2-2015	00°68.989'S 034°86.338'E
<i>Aphis craccivora</i>	AcKi2, AcKi3,AcK7, AcKi8, AcKi10	Amaranth		Kisauni Mombasa	10-2-2015	03°59.835'S 039°43.496'E
<i>Aphis craccivora</i>	AcNy1,AcNy3,AcNy4, AcNy6,AcNy7	Amaranth		Nyali Mombasa	10-2-2015	04°03.292'S 039°41.098'E
<i>Aphis craccivora</i>	AcLi1, AcLi2,AcLi4, AcLi5, AcLi6	Amaranth	Mombasa	Likoni	10-2-2015	04°05.641'S 039°38.926'E
<i>Aphis craccivora</i>	AcMt2,Acmt3, AcMt5, AcMt6, AcMt7	Amaranth	Mombasa	Mtongwe	10-2-2015	04°04.974'S 039°38.429'E
<i>Aphis craccivora</i>	AcMa1,AcMa2,AcMa4, AcMa5, AcMa6	Amaranth	Kilifi	Magarini	11-2-2015	03°08.598'S 040°06.431'E

<i>Aphis craccivora</i>	AcM11, AcM12, AcM13, AcM14, AcM15	Amaranth	Kilifi	Malindi	11-2-2015	03°09.858'S 040°05.248'E
<i>Aphis craccivora</i>	AcLa1, AcLa2, AcLa3, AcLa4, AcLa6	Amaranth	Kiambu	Lari	13-2-2015	00°59.182'S 036°37.152'E
<i>Aphis fabae</i>	AfLa1, AfLa3, AfLa7	Amaranth	Kiambu	Lari	13-2-2015	00°59.185'S 036°37.146'E
<i>Aphis fabae</i>	AfKr3, AfKr5, AfKr6	Nightshade	Kiambu	Karura	13-2-2015	01°12.188'S 036°43.059'E
<i>Aphis craccivora</i>	AcKr1, AcKr2, AcKr3, AcKr4, AcKr5	Amaranth	Kiambu	Karura	13-2-2015	01°12.179'S 036°43.063'E
<i>Myzus persicae</i>	Mpka1, Mpka2, Mpka3, Mpka6, Mpka7	Nightshade	Embu	Kangaru	20-2-2015	S0°28'27.95 37°34'49.23'E
<i>Aphis craccivora</i>	AcKa1, AcKa2, AcKa3, AcKa4, AcKa7	Amaranth	Embu	Kangaru	20-2-2015	00°50.696'S 037°45.820'E
<i>Macrosiphum Euphorbiae</i>	MeKm3, MeKm5	Amaranth	Embu	Kamiu	20-2-2015	00°52.448'S 037°46.549'E
<i>Aphis craccivora</i>	AcKm1, AcKm3, AcKm4, AcKm5, AcKm6	Nightshade	Embu	Kamiu	20-2-2015	00°52.458'S 037°46.556'E
<i>Aphis craccivora</i>	AcKb3, AcKb4, AcKb6, AcKb7, AcKb8	Amaranth	Kirinyaga	Kimbimbi	20-2-2015	00°63.059'S 037°35.064'E

*Global Positioning System coordinates were taken using Garmin eTrex® 20 (Garmin, USA)

Table 2: Aphid samples collected from various Tanzanian agro-ecological zones

Species name	Analysis code	Host crop	Province	Locality	Collection date	GPS Coordinates*
<i>Aphis fabae</i>	AfMm1,AfMm3, AfMm5, fMm6,AfMm7	Nightshade	Morogoro	Mvomero	11-5-2015	06°57.609'S 037°31.936'E
<i>Aphis fabae</i>	AfMg1,AfMg6,AfMg8	Nightshade	Morogoro	Morogoro Rural	11-5-2015	06°50.088'S 037°47.213'E
<i>Aphis craccivora</i>	AcMg1,AcMg2, AcMg3,AcMg5,AcMg7	Amaranth	Morogoro	Morogoro Rural	11-5-2015	06°49.627'S 037°48.151'E
<i>Aphis craccivora</i>	AcBg1, AcBg2, AcBg3, AcBg4, AcBg5	Amaranth	Pwani	Bagamoyo	12-5-2015	06°26.849'S 038°54.434'E
<i>Aphis craccivora</i>	AcMu1, cMu2,AcMu3, AcMu5	Amaranth	Tanga	Muheza	13-5-2015	05°10.600'S 038°48.002'E
<i>Aphis fabae</i>	AfLt4, AfLt6	Nightshade	Tanga	Lushoto	14-5-2015	04°50.831'S 038°20.178'E
<i>Aphis craccivora</i>	AcLt1,AcLt2,AcLt3, AcLt4, AcLt5, AcLt6	Amaranth	Tanga	Lushoto	14-5-2015	04°50.879'S 038°20.129'E
<i>Aphis craccivora</i>	AcMs1,AcMs2, AcMs3,AcMs4, AcMs5	Nightshade	Kilimanjaro	Moshi	15-5-2015	03°23.288'S 037° 31.981'E
<i>Aphis craccivora</i>	AcMs2b,AcMs3b, AcMs4b, AcMs6b	Amaranth	Kilimanjaro	Moshi	15-5-2015	03°23.288'S 037° 31.981'E

<i>Aphis craccivora</i>	AcHa3,AcHa4, AcHa5, AcHa6,AcHa7	Amaranth	Kilimanjaro	Hai	15-5-2015	03°17.464'S 037° 10.310'E
<i>Aphis craccivora</i>	AcH1, AcH2, AcH3, AcH4,AcH5	Nightshade	Kilimanjaro	Hai	15-5-2015	03°17.464'S 037° 10.310'E
<i>Aphis craccivora</i>	AcMe1,AcMe2, AcMe3,AcMe4	Amaranth	Arusha	Meru	16-5-2015	03°19.667'S 036° 59.685'E
<i>Aphis craccivora</i>	AcMer2,AcMer3, cMer4,AcMer5,AcMer6	Amaranth	Arusha	Meru	16-5-2015	03°19.667'S 036° 59.685'E
<i>Aphis craccivora</i>	AcAs1, AcAs2,AcAs3, AcAs5,AcAs8,AcAs9, AcAs10	Nightshade	Arusha	Arusha	16-5-2015	03°18.333'S 036° 41.677'E
<i>Aphis craccivora</i>	AcMmr2,AcMmr3, AcMmr4,AcMmr5,	Nightshade	Arusha	Mt. Meru	16-5-2015	03°17.787'S 036° 41.740'E
<i>Aphis craccivora</i>	AcMm1,AcMm2, AcMm5,AcMm6	Amaranth	Arusha	Mt. Meru	16-5-2015	03°18.122'S 036° 41.957'E
<i>Aphis craccivora</i>	AcTe3,AcTe6, AcTe7,	Nightshade	Arusha	Tengeru	16-5-2015	03°23.123'S 036° 48.463'E

*Global Positioning System coordinates were taken using Garmin eTrex® 20 (Garmin, USA)

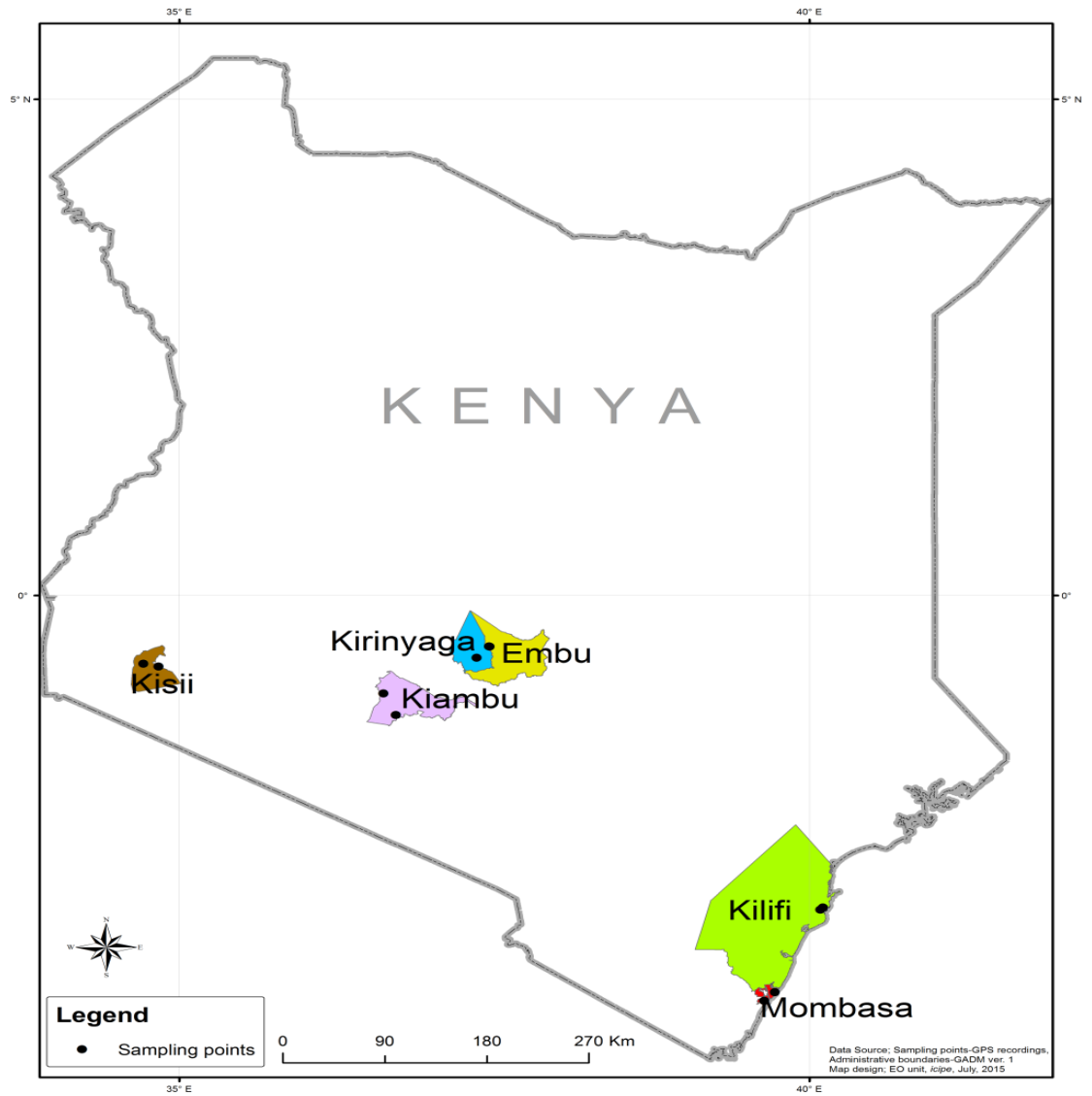


Figure 1: Map of Kenya showing aphid sampling sites. (Geo-Information Unit, ICIPE)

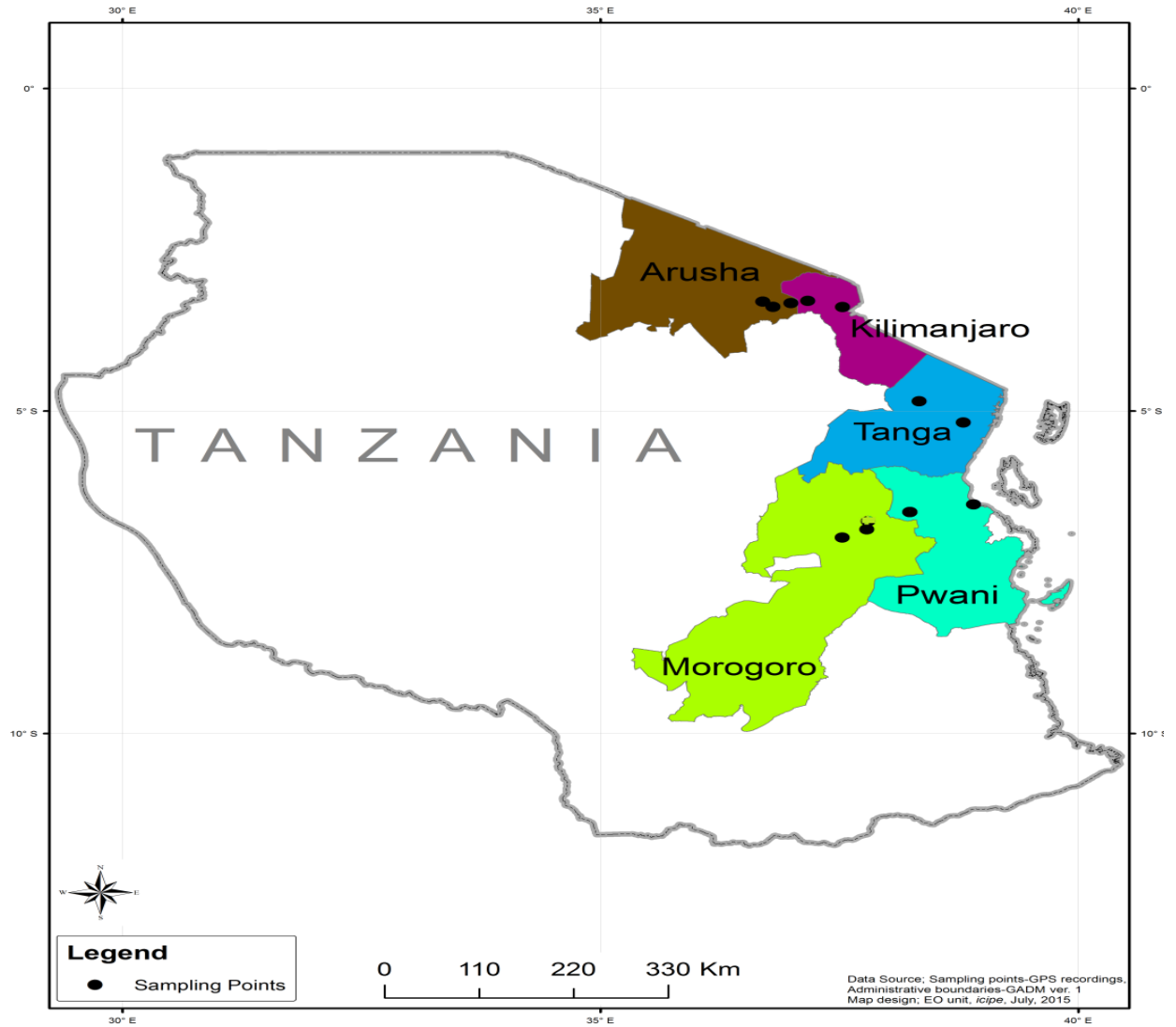


Figure 2: Map of Tanzania showing aphid sampling sites. (Geo-Information Unit, ICIPE)

3.2 DNA extraction, quantification and quality check

Five individual aphids from a sampled site and host crop was surface sterilized in 3% sodium hypochlorite, rinsed three times with distilled water and placed in a sterile 1.5 ml microcentrifuge eppendorf tube. Total DNA extraction from an individual aphid was done by grinding with a sterile mini pestle. Subsequent extraction steps were done using ISOLATE II genomic DNA kit (Bioline, UK- <http://www.bioline.com/sg/isolate-ii-genomic-dna-kit.html>) according to the manufacturer's standard protocol. The concentration and purity of DNA was determined using Nanodrop 2000/2000c spectrophotometer (Thermo Fisher Scientific, USA) using 2 µl of each sample. Absorbance ratio at A260/A280 nm determined the purity of the samples. A high quality DNA should have an absorbance ratio at 260/280 nm of between ~1.8 and 2 (Wilfinger *et al.*, 1997). DNA concentration of each sample was also measured in ng/µl. The concentrations of isolated DNA samples were brought to 15 ng/µl by addition of PCR water before they were stored in racks at -20°C until further downstream processes were conducted. The voucher specimens from the original samples were deposited under the author's name in the -80°C chamber at the Arthropod Pathology Unit of ICIPE, Duvivile Campus, Nairobi, Kenya.

3.3 PCR amplification of the barcode region

The 5'- terminal portion of the mitochondrial cytochrome *c* oxidase sub unit I (mtCOI) gene was amplified using universal primers LCO 1490 Forward (5'-GGTCAACAAATCATAAAGATATTGG-3') and reverse primer- HCO 2198 (5'-TAAACTTCAGGGTGACCAAAAAATA-3) (Folmer *et al.*, 1994). Amplification was performed by PCR where 10 µl reaction volume containing: 5.375 µl of DNase/RNase free PCR water (Bioline, UK), 2 µl of 5X MyTaq reaction buffer (containing deoxynucleotide triphosphates), 0.5 µl of each primer, 0.5 µl of 25mM MgCl₂, 0.125 µl of 0.625U of MyTaqTm DNA polymerase (Bioline, UK) and 1 µl of 15-50 ng/µl of crude DNA extract. PCR amplification was done in Arktik thermocycler (Thermo Fisher Scientific, USA) under the following optimized conditions: initial denaturation of 95°C for 2 minutes; followed by 40 cycles of 30 seconds denaturation at 95°C, 45

seconds annealing state at 50.6°C and elongation state for 1 minute at 72°C. There was final elongation of 10 minutes at 72°C for maximum extension of DNA; and a 10°C hold.

3.4 Gel electrophoresis of PCR products

A 1% agarose gel was prepared according to Lee *et al.* (2012). Agarose powder (0.7 g) was dissolved in 70 ml Tris Acetate EDTA (TAE) buffer by boiling in a microwave oven for 1 minute. Agarose was allowed to cool to about 50° C and 6 µl Ethidium bromide added to the gel and gently shaken. While the agarose was cooling, the gel tray was prepared by sealing the open edges of a clean, dry glass tray with autoclave tape so as to form a mold to avoid leakage and for the tray to accommodate the desired thickness of the gel. The warm agarose solution was then be poured into the gel tray in which a comb was inserted to form sample slots. The gel was allowed to set for 30 minutes before removing the autoclave tape, and immersing the gel in the electrophoresis tank containing 1X TAE buffer.

The resultant PCR products were loaded with a 6X loading dye into preformed wells in the 1% agarose gel. To avoid cross sample contamination, a single sterile pipette tip was used to load each sample onto agarose gels. PCR products were separated via an optimized electrophoresis process at 80 volts for 40 minutes. For base pair scoring, PCR products were ran alongside 1 kb DNA ladder (Fermentas, Thermo Fisher Scientific, USA). In addition, a negative control tube with all the PCR reagents except the DNA template was included in every set of reaction. The gel was then viewed under KETA GL imaging system (Wealtec Corp., USA) and photographs of all gels were taken.

3.5 PCR product purification and sequencing

To purify the PCR products, 2 to 3 PCR reactions each of 30 µl reaction volumes were prepared before electrophoresis in 2% agarose gel. A 2% agarose gel was prepared by dissolving 3.85 g in 250 ml Tris Acetate EDTA (TAE) followed by procedure outlined

in section 3.4. Electrophoresis was run at optimized electrophoretic conditions of 80V for 1 hour for clear band separation. Amplified DNA bands of at least two to five randomly selected aphid individuals per site per host crop were excised from the gels using sterile scalpels and purified using ISOLATE II PCR and gel kit (Bioline, UK) according to the manufacturer's protocol. The purification protocol is found at <http://www.bioline.com/sg/isolate-ii-pcr-and-gel-kit.html>. They were packed in 1 ml vials and sent for bi-directional sequencing using the amplification primers at Macrogen Inc. Europe (Amsterdam, Netherlands). Sample packaging protocol used in this study is as shown in appendix 1.

3.6 Phylogenetic analyses of the barcode region

Nucleotide chromatograms of the sense and antisense sequences were subjected to quality assessment by editing manually using Chromas Lite 2.0 (Technelysium Pty Ltd, Queensland, Australia). This helped to confirm the absence termination codons and miscalls. Subsequently, Jalview (Waterhouse *et al.*, 2009) further helped to view sequence alignments and perform trimming to a consistent sequence number of 662 base pairs. The sequences generated in this study are as shown in Appendix 2. The nucleotide sequence homology searches were performed through the Basic Local Alignment Search Tool for nucleotides (BLASTn) algorithm (Zhang *et al.*, 2000) hosted at the National Centre for Biotechnology Information (NCBI) (<http://www.ncbi.nlm.nih.gov/>) for species identification. ClustalX 2.1 (Thompson *et al.*, 1997) generated multiple sequence alignments using Clustal W algorithm. The software jModelTest 2 (Darriba *et al.*, 2012) was used to determine the best fitting evolutionary model for the phylogenetic tree analysis. TrN+G model was chosen based on the Akaike Information Criterion corrected for small sample (AICc) and the Bayesian Information Criterion (BIC) as the best fitting model to be used under General Time Reversible (GTR) substitution model with gamma-distributed rate variation across sites in 5 discrete number of gamma categories. Maximum Likelihood phylogenetic tree analysis was conducted in MEGA 6 under a general time reversible

GTR+GAMMA substitution model. In order to assess robustness of the clades, bootstrap values for node support were calculated for 1000 pseudoreplicates.

The matrix of inter-species genetic distances and the Maximum Likelihood (ML) estimation of transition/transversion bias were estimated using Tamura-Nei model in MEGA 6.0 (Tamura and Nei, 1993). This model assumes that transversions occur at the same rate, but that rate is allowed to be different from both of the rates for transitions. It distinguishes between the two different types of transition (Adenine <-> Guanine); is allowed to have a different rates to (Cytocine<->Thymine) (Tamura and Nei, 1993).

To produce the number of samples with unique sequences (haplotypes), haplotype data file and to calculate monomorphic, polymorphic, the number of sites with a minimum of 2 nucleotide that are present at least twice (parsimony informative sites) and haplotype diversity (Hd), the software DNA Sequence Polymorphism (DnaSP v 5.10.01) (Librado and Rozas, 2010) was used. The Nexus haplotype data file produced was then transferred to Network 5.0.0.0 (Fluxus Technology Ltd.) to generate the haplotype network under the median-joining algorithm (Bandelt *et al.*, 1999).

Principal coordinate analysis (PCoA) plot was generated by GenAlEx 6.502 (Peakall and Smouse, 2012) using the interspecific genetic distance values generated in Mega 6. Sequences were deposited at the GenBank (NCBI) and submitted to the Barcode of Life Database (BOLD).

CHAPTER FOUR

4.0 RESULTS

4.1 Nanodrop results

The quality of the DNA extracted from the aphid species showed a high quality DNA. The concentrations ranged from 18.2 to 216.7 ng/μl and a purity level of about 2.0 to 2.23. A representative sample for the spectrophotometric results is as shown in Table 3.

Table 3: Nanodrop results of a representative sample of aphids collected in Kenya and Tanzania

Sample ID	Nucleic Acid Conc.	Unit	A260	A280	260/280	260/230	Sample Type
AfMm1	48.4	ng/μl	0.969	0.483	2	2.24	DNA
AfMm2	18.2	ng/μl	0.363	0.174	2.08	-7.81	DNA
AfMm3	116.3	ng/μl	2.326	1.089	2.14	3.15	DNA
AfMm4	66.9	ng/μl	1.338	0.651	2.06	3.63	DNA
AfMm5	58.3	ng/μl	1.167	0.567	2.06	2.82	DNA
AfMm6	77.4	ng/μl	1.547	0.741	2.09	2.54	DNA
AcBg1	54.1	ng/μl	1.082	0.515	2.1	2.64	DNA
AcBg3	38.4	ng/μl	0.769	0.365	2.11	8.92	DNA
AcBg4	86.8	ng/μl	1.737	0.806	2.15	3.91	DNA
AcBg6	86.7	ng/μl	1.734	0.807	2.15	3.66	DNA
AcH1	81.5	ng/μl	1.63	0.75	2.17	4.29	DNA
AcH3	98.9	ng/μl	1.978	0.91	2.17	3.39	DNA
AcH5	88.1	ng/μl	1.763	0.813	2.17	3.57	DNA
AMer1	64.4	ng/μl	1.288	0.583	2.21	4.36	DNA
AcMer2	76.9	ng/μl	1.539	0.717	2.14	3.75	DNA
AcMer3	69.4	ng/μl	1.389	0.653	2.13	2.98	DNA
AcTe3	216.9	ng/μl	4.339	2.002	2.17	2.87	DNA
AcTe4	87.7	ng/μl	1.754	0.811	2.16	3.22	DNA
MpKa1	94.2	ng/μl	1.884	0.861	2.19	3.37	DNA
MpKa2	67.4	ng/μl	1.348	0.632	2.13	3.42	DNA
MpKa3	108.4	ng/μl	2.168	0.973	2.23	3.8	DNA
MpKa4	58.2	ng/μl	1.164	0.541	2.15	3.44	DNA
MeKm5	54.5	ng/μl	1.09	0.503	2.17	3.64	DNA
MeKm5	83.3	ng/μl	1.667	0.767	2.17	3.41	DNA

4.2 PCR Amplification of the barcode region

PCR amplification yielded a uniform band at about 700 bp region among the *A. craccivora*, *A. fabae*, *M. persicae* and *M. euphorbiae* in Kenya and Tanzania. The bands below 200 bp indicate primer dimers (Figure 3). Negative control entailed all the reagents of PCR minus the DNA template. A representative gel image as scored by the standard base scoring ladder for *A. craccivora* and *A. fabae* in Kenya and Tanzania is as shown in Figures 3 and 4, respectively.

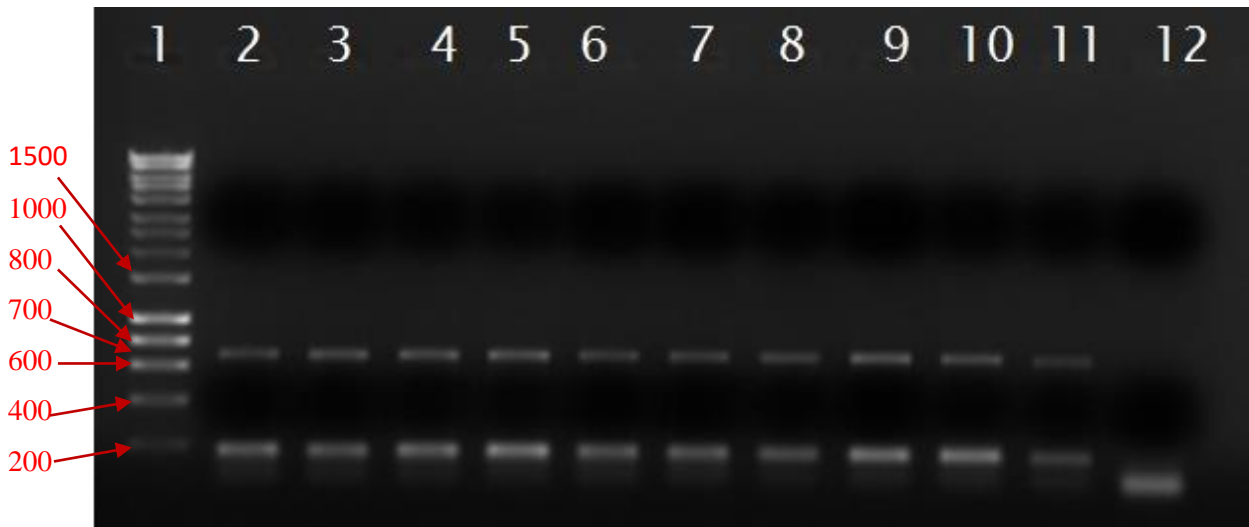


Figure 3: 1% agarose gel showing banding patterns of COI region for *Aphis craccivora* (Ac) collected in Kisauni (Ki), Mombasa County, Kenya.

Lanes **1** = 1kb HyperLadder™ (Bioline, UK), **2** = AcKi1, **3** = AcKi2, **4** = AcKi3, **5** = AcKi4, **6** = AcKi5, **7** = AcKi6, **8** = AcKi7, **9** = AcKi8, **10** = AcKi9, **11** = AcKi10, **12** = Negative control.



Figure 4: 1% agarose gel showing banding patterns of COI region for *Aphis fabae* (Af) collected in Mvomero (Mm), Morogoro Province, Tanzania.

Lanes **1** = 1kb HyperLadder™ (Bioline, UK), **2** = AfMm1, **3** = AfMm2, **4** = AfMm3, **5** = AfMm4, **6** = AfMm5, **7** = AfMm6, **8** = AfMm7, **9** = AfMm8, **10** = AfMm9, **11** = AfMm10, **12** = Negative control.

4.2 DNA isolation from agarose gels

The gel image for 30 µl PCR product for gel excision is as shown in Figure 5.

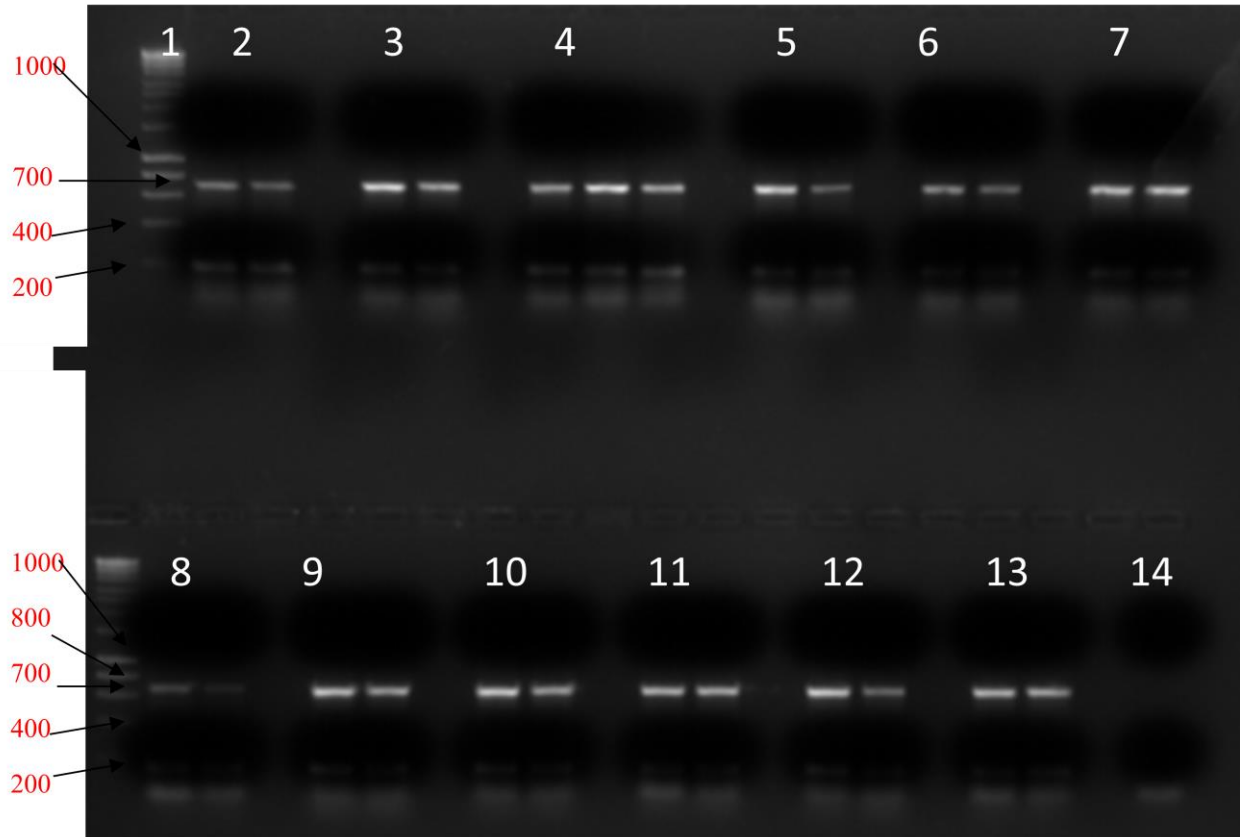


Figure 5: 2% agarose gel before purification of COI region of *Aphis craccivora* (Ac) and *Aphis fabae* (Af) for purification.

Lanes **1** = 1kb standard ladder (Bioline, UK), **2** = AcKi1, **3** = AcKi2, **4** = AcKi6, **5** = AcKi8, **6** = AcKi9, **7** = AfNy1, **8** = AfNy2, **9** = AfNy3, **10** = AfNy4, **11** = AfNy5, **12** = AfNy6, **13** = AfNy7, **14** = Negative control.

4.3 Sample and BLAST results

The complete data set consisted of 165 samples collected on amaranth and nightshades in both countries. Their respective sample codes and barcode nucleotide sequences are as shown in Tables 1 and 2 and Appendix 2, respectively. The search for the aphid species done using homology against the GenBank sequences using BLASTn

algorithm positively identified four main types of aphid species on the two host crops. They are: the cowpea aphid, *Aphis craccivora* Koch, the black bean aphid *Aphis fabae* Scopoli, green peach aphid, *Myzus persicae* Sulzer and the potato aphid, *Macrosiphum euphorbiae* Thomas. Of the total samples collected (Table 4), *A. craccivora* composed the highest sample (82%), followed by *M. persicae* Sulzer (10.1%), *A. fabae* (8.2%) and *M. euphorbiae* (0.7%). The total number of aphids collected in Kenya was 88 while in Tanzania was 77. Members of the genus *Aphis* represented the largest sample collected.

The distribution of aphid samples across agro-ecological zones is as shown in Table 4. Except for absence of *M. persicae* and *M. euphorbiae* in Tanzania, *A. fabae* and *A. craccivora* were collected in both countries. *Aphis fabae* and *M. euphorbiae* were found on amaranth; whereas *A. fabae*, *A. craccivora* and *M. persicae* were found on both crops (Tables 1 and 2). However, *M. persicae* and *M. euphorbiae* were not collected in Tanzanian samples. Generally, aphids did not depict host-specificity.

Nucleotide sequences were run under BLASTn algorithm using highly similar sequences (Megablast) where all samples were subjected to homology search in the GenBank. Table 5 shows the distribution of the samples for BLASTn results of the aphids collected. The search hits showed at least 98% similarity meaning that sequence identities was correct.

Table 4: Distribution of aphid species based on agro-ecological zones in both Kenya and Tanzania

Agro-ecological zone	Aphid type	Number sampled
High altitude	<i>A. craccivora</i>	31
	<i>A. fabae</i>	7
	<i>M. persicae</i>	9
	<i>M. euphorbiae</i>	0
Mid Altitude	<i>A. craccivora</i>	57
	<i>A. fabae</i>	8
	<i>M. persicae</i>	4
	<i>M. euphorbiae</i>	2
Low Altitude	<i>A. craccivora</i>	45
	<i>A. fabae</i>	0
	<i>M. persicae</i>	0
	<i>M. euphorbiae</i>	0
Total		165

Table 5: Basic Local Alignment Search Tool homology search results for a representative aphid samples collected in Kenya and Tanzania

CODE	Aphid type from the GenBank (NCBI)	QUERY COVER	E-VALUE	IDENTIFICATION	REFERED ACCESSION
AcNy1	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcNy3	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcNy4	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AfLa7	<i>Aphis fabae fabae</i>	100%	0.0	98%	AB506722.1
MpBo1	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
MpBo3	<i>Myzus persicae</i>	100%	0.0	99%	KM577343.1
MpBo4	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
MpBo5	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
AfMm1	<i>Aphis fabae solanella</i>	100%	0.0	99%	AB506722.1
AfMm3	<i>Aphis fabae solanella</i>	100%	0.0	100%	AB506722.1
AfMm5	<i>Aphis fabae solanella</i>	100%	0.0	100%	AB506722.1
AfMm6	<i>Aphis fabae solanella</i>	100%	0.0	100%	AB506722.1
AcBg1	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcBg4	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
MeKm3	<i>Macrosiphum euphorbiae</i>	100%	0.0	99%	KR044470.1
MeKm5	<i>M. euphorbiae</i>	100%	0.0	99%	KR044470.1
AfKis8	<i>A. fabae circiicanthoidis</i>	100%	0.0	100	JX507414.1
AfBo2	<i>A.fabae circiicanthoidis</i>	100%	0.0	98%	JX507414.1
AfMg6	<i>A.fabae fabae</i>	99%	0.0	99%	KR037186.1
AcKis10	<i>Aphis craccivora</i>	100%	0.0	99%	AB506714.1
AcKis19	<i>Aphis craccivora</i>	100%	0.0	99%	AB506714.1
MpKa1	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
Mpka2	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
Mpka3	<i>Myzus persicae</i>	100%	0.0	100%	KM577343.1
AcAs1	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcAs2	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcAs3	<i>Aphis craccivora</i>	100%	0.0	100%	AB506714.1
AcKr1	<i>Aphis craccivora</i>	100%	0.0	99%	AB506714.1
AcKr2	<i>Aphis craccivora</i>	100%	0.0	99%	AB506714.1
AcKr4	<i>Aphis craccivora</i>	100%	0.0	99%	AB506714.1

4.5 Barcode Sequences analyses

Partial sequencing of the mtCOI gene yielded about 700 bp sequences. Manual editing and trimming of the primers LCO 1490 and HCO 2198 annealing sites resulted in a uniform 662 bp region which was used for analysis. Out of the 662 bp region, 552 were invariable, 110 sites were polymorphic while 99 were parsimony informative sites.

The average nucleotide composition for all the aphids was Thymine = 40.8%, Cytosine=13.7%, Adenine=35.0% and Guanine=10.6%. Generally, there was reported bias towards Adenine-Thymine constituting 76.1%. No deletions and insertions were detected and therefore sequence divergence analysis was based on substitution.

The estimated Transition/Transversion bias (R) is 1.36. Substitution pattern and rates were estimated under the Tamura-Nei (1993) model (+G). A discrete Gamma distribution was used to model evolutionary rate differences among sites (5 categories, [+G], parameter = 0.1923). The nucleotide frequencies are A = 34.96%, T/U = 40.82%, C = 13.65%, and G = 10.57%.

Maximum composite likelihood (Tamura *et al.*, 2004) estimate of the pattern of nucleotide substitution (Table 6) shows the probability of substitution (r) from one base (row) to another base (column).

Table 6: Maximum composite likelihood estimate of the pattern of nucleotide substitution for the partial COI gene region of all aphids collected in Kenya and Tanzania

	A	T	C	G
A	-	4.72	4.72	15.57
T	4.72	-	15.57	4.72
C	4.72	15.57	-	4.72
G	15.57	4.72	4.72	-

For simplicity, the sum of r values is made equal to 100. Rates of different transitional substitutions are shown in **bold** and those of transversional substitutions are shown in *italics*. The nucleotide frequencies are 25% (A), 25% (T/U), 25% (C), and 25% (G). The transition/transversion rate ratios are $k_1 = 7.306$ (purines) and $k_2 = 11.427$ (pyrimidines). The overall transition/transversion bias is $R=5.656$, where $R = [A * G * k_1 + T * C * k_2] / [(A+G) * (T+C)]$.

The phylogenetic tree was used to draw the evolutionary history as inferred using the nearest neighbor in maximum likelihood method is shown in Figure 6. The evolutionary distances computed using the substitution model is in the units of the number of base substitutions per site in 1000 pseudoreplicates. The node support values are shown for samples with nodes above 50%. The analysis involved 165 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated, resulting in total of 662 positions the final dataset.

The phylogram shows samples of the same species clustering together systematically in distinct clades independent of the locality collected or the host crop. For example, AcBg1-AcBg5, which are *A. craccivora* samples collected on amaranth in Bagamoyo, low-altitude agro-ecological zone of Tanzania, clustered together strongly (99% support bootstrap value) with AcKm1- AcKm6, which are *A. craccivora* samples collected on nightshade in Kamiu, a mid-altitude agro-ecological zone of Kenya. This was the case for all other species sampled in this study. The tree topology shows two primary clades where *A. fabae* and *A. craccivora*, belonging to the same genus, separated from the first clade and regrouped themselves into their own distinct species clades; while *M. persicae* and *M. euphorbiae* branched off to compose the second paraphyletic clade with a strong bootstrap support value of 99%. Members of the *A. craccivora* collected on amaranth in Karura area of Kiambu County of Kenya further formed a subclade from an almost predominantly monophyletic cowpea aphid with a bootstrap support value of 65%. Similarly, the black bean aphid also depicted the

subclading of the three subspecies (the *Aphis fabae fabae*, *A. fabae cirsiacanthoidis* and *A. fabae solanella*) delineating into their various subclades from the original node.

The molecular clock test (Table 7) was performed by comparing the maximum log-likelihood values for the given topology with and without the molecular clock constraints under General Time Reversible (GTR) model. As expected, the value with the clock hypothesis was smaller than the value without the clock hypothesis. The null hypothesis of equal evolutionary rate throughout the tree was rejected at a 5% significance level ($P = 5$).

Table 7: Results from a test of molecular clocks using the Maximum Likelihood method

	lnL	Parameters	(+G)	(+I)
With clock	-297710.773	172	n/a	n/a
Without clock	-1628.855	335	n/a	n/a

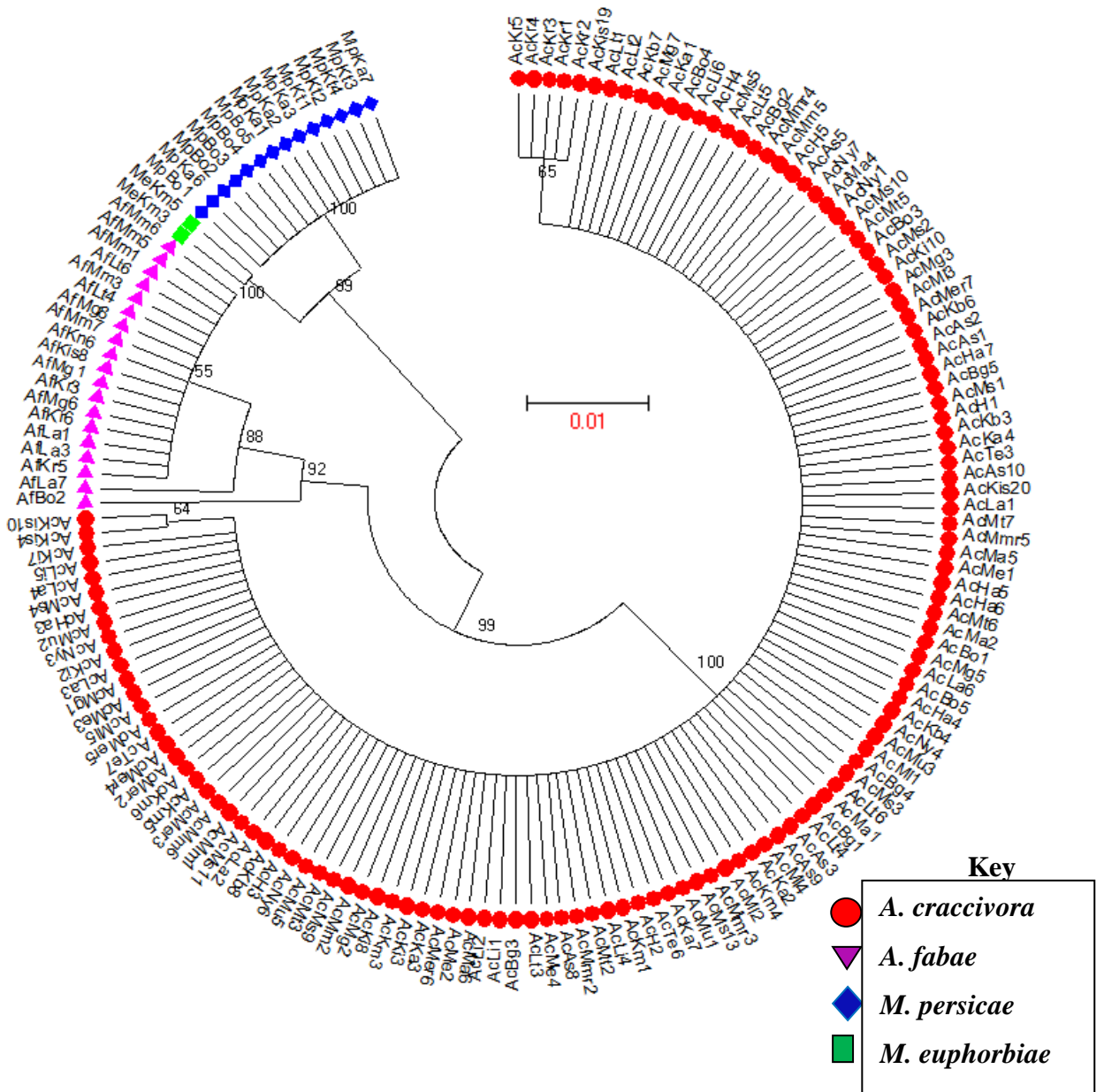


Figure 6: The maximum Likelihood phylogenetic tree of the aphid species collected in Kenya and Tanzania generated using GTR model under 1000 pseudoreplicates in MEGA 6.0.

AfBo2 represents *Aphis fabae ciirciacanthoidis* sample number 2 collected in Borabu, AfLa7 represents *Aphis fabae solanella* sample number 7 collected in Lari, Kiambu . The rest of Af samples represents the *Aphi fabae fabae* samples.

AcKr1 to AcKr5 represents a sub-clade of the *Aphis craccivora* samples collected in Karura, Kiambu.

The conspecific sequence divergence generated in MEGA 6.0 ranged from 0.0% to 0.8% with the maximum distance observed in the species of *A. fabae*. The average conspecific nucleotide sequence divergence (Table 8) of *A. fabae*, *A. craccivora*, *M. persicae* and *M. euphorbiae* was 0.8%, 0.1%, 0.1% and 0.0%, respectively. The relatively low divergence demonstrates that there is no significant intra-specific diversity of aphids infesting these two vegetables.

Table 8: Mean intra-species diversity of the four sampled species of Kenya and Tanzania

Aphid type	Intra-species divergence (%)
<i>A. fabae</i>	0.8
<i>A. craccivora</i>	0.1
<i>M. persicae</i>	0.1
<i>M. euphorbiae</i>	0.0

The inter-specific divergence (Table 9) showed that the genetic distance among the aphids sampled ranged from 6.3% (between *A. fabae* and *A. craccivora*) to 10.6% (between *A. craccivora* and *M. persicae*) with an average total divergence of 8.61%.

Table 9: Estimates of evolutionary distances between four species of aphids sampled in Kenya and Tanzania

	<i>A. fabae</i>	<i>A. craccivora</i>	<i>M. persicae</i>	<i>M. euphorbiae</i>
<i>A. fabae</i>	-			
<i>A. craccivora</i>	0.063	-		
<i>M. persicae</i>	0.093	0.106	-	
<i>M. euphorbiae</i>	0.087	0.083	0.085	-

The principal coordinate analysis (PCoA) plot generated from the distance divergence matrix (Table 9) is shown in Figure 7. The first and second axes accounted for 60.97% and 39.03% of the variations, respectively. It enabled examination of genetic relationship among the different aphid species. The results showed that aphids of the same species clustered in their distinct space as is qualified by the inter-species nucleotide divergence. *A. fabae* and *A. craccivora* formed a closer relationship on one side of the plane while *M. euphorbiae* and *M. persicae* formed a different group in the opposite side of the plane.

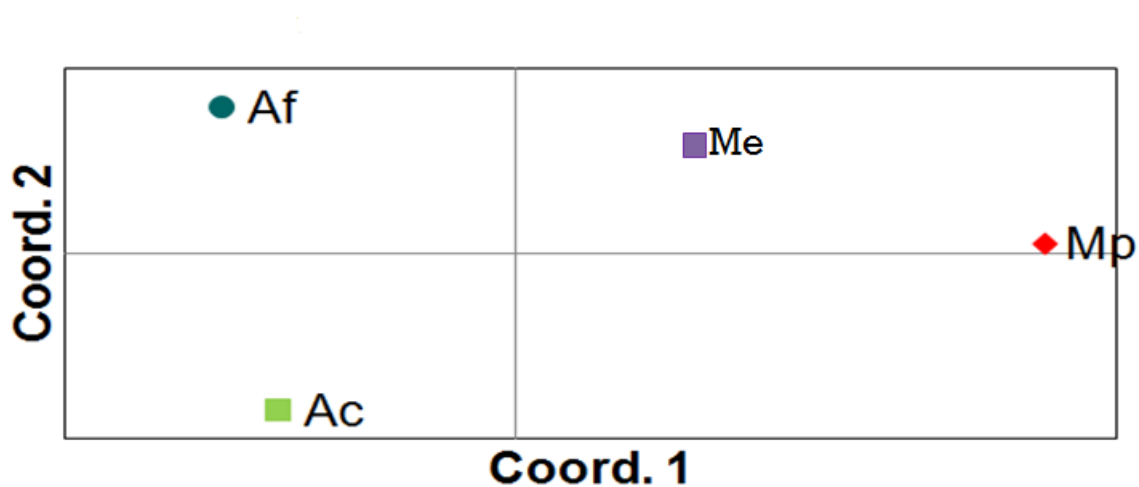


Figure 7: Principal Coordinate Analysis plot generated in GenAlEx 6.502 for the inter-specific distance matrix for the four aphid species collected in Kenya and Tanzania.

Af = *Aphis fabae*, Ac = *Aphis craccivora*, Me = *Macrosiphum euphorbiae*, Mp= *Myzus persicae*

Furthermore, haplotype network (Figure 8) generated 4 numbers of haplotypes using DnaSP with a haplotype diversity (Hd) values of 0.464 with a standard deviation of haplotype diversity of 0.048 and a variance of 0.0023. The median-joining algorithm

revealed a clear separation of the various species of aphids in to their clusters in accordance with the number of substitutions between each haplotype.

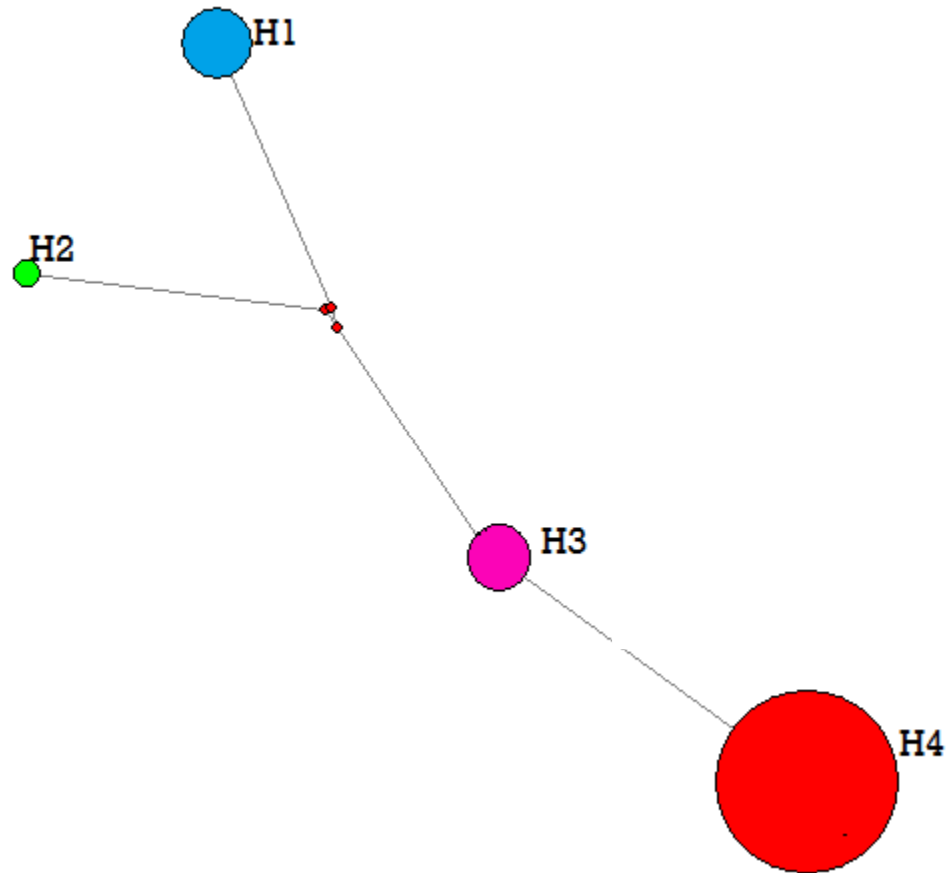


Figure 8: The haplotype network of the four aphid species from Kenya and Tanzania as generated by the software Network 5.0.0.0. The size of each haplotype confers to the number of the samples represented in that particular group.

H1= *Myzus persicae*, **H2** = *Macrosiphum euphorbiae*, **H3** = *Aphis fabae*, **H4** = *Aphis craccivora*

The network shows how close or far away the collected aphid species are from each other. The illustration shows that *A. craccivora* (H4) and *A. fabae* (H3) are closely related while *M. persicae* (H1) and *M. euphorbiae* (H2) are closer to each other in their relative genetic changes.

CHAPTER FIVE

5.0 GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

5.1 Discussion

The universal Folmer *et al.* (1994) primers successfully amplified the ≈ 650 bp barcode region of the mitochondrial COI of the collected aphid species. Basic Local Alignment Search Tool (BLAST) for nucleotides managed to obtain similarity of the aphids from the GenBank with high confidence level ($\geq 98\%$), indicating that the tool is reliable in comparing DNA barcodes to sequence database. The analyses of partial sequence of cytochrome *c* oxidase I (COI) gene showed that it can be applied for DNA fingerprinting of aphids. This would not otherwise have been a difficult task using morphological characterization. The general relative abundance of the members of the genus *Aphis* tallies with world's record of most abundant and cryptic group of aphids in the subfamily Aphidinae (Papasotiropoulos *et al.*, 2013; Coeur d'acier *et al.*, 2014). However, the absence of *M. persicae* and *M. euphorbiae* Tanzania need to be investigated further particularly during dry season in order to confirm the results depicted in this study. Rainy season that was experienced throughout the sampling frame during the sampling period may have contributed to their wash-off or a condition of overwintering which is a common characteristic of this type of aphid. This is supported by the contrary presences of the same aphid type in Kenya whose sampling was done in a hot and dry weather.

Lack of host specificity of the sampled aphids indicates their polyphagous nature as reported by Blackman and Eastop (2000). Living organisms increase their genetic diversity in order to successfully colonize and establish diverse habitats. In the event, organisms such as aphids develop certain features that aid them in adapting to their new habitats. For example, using morphological identification method, the ultimate rostral segment in aphid species is known to vary with the host plant type and the physiological status of the plant (Margaritopoulos *et al.*, 1998). Similarly, under

restricted conditions, the body size and pigmentation of *M. pesicae* is known to be affected by the host plant (Clements *et al.*, 2000).

The nucleotide bias towards Adenine-Thymine is similar to reports on other studies relating to the use of mtCOI in genetic diversity of aphids (Kim *et al.*, 2011; Wang *et al.*, 2011; Chen *et al.*, 2012; Papasotiropoulos *et al.*, 2013, Rebijith *et al.*, 2013; Kinyanjui *et al.*, 2015). This is important as it lowers the amount of energy required to break the DNA double helix during replication (Mitchel, 1997). The greater intra-specific genetic divergence (0.8%) value as expressed by *A. fabae* is explained by different morphotypes of this type of species sampled in this study. This result is in agreement with the previous studies that showed low genetic divergence in the aphids of *A. fabae* complex in Tunisia from different geographical zones (Béji *et al.*, 2015).

One of the major goals of this study was to check whether agro-ecological zones and hosts crop play a role in the mtCOI sequence diversity. The results from this study showed low genetic distance among and between the species of aphids collected. Moreover, various species clustering largely together in their clades irrespective of the host crop, country or the locality of collection (Figure 6), indicating that diversity was not because of agro-ecological zone or host crop. This further confirmed the results of the homology search in the GenBank. These clades were clearly separating one species from its nearest neighbour indicating that species identification using homology search in the GenBank was correct. This result was further supported by the PCoA and haplotype networks that showed samples of the same species grouping together irrespective of the locality or the host crop. However, the cowpea aphids collected from Karura in Kiambu County of Kenya formed their own subclade with a relatively strong support value of 65%. This may suggest that *A. craccivora* exist in cryptic nature.

The overall mean inter-species divergence of 8.61% obtained in the study is substantive to warrant delineation between the various species of aphids collected from Kenya and Tanzania (Kinyanjui *et al.*, 2015). The lowest inter-species divergence (6.3%) was found between the samples of *A. fabae* and *A. craccivora* (Table 9). This is probably because they belong to the same genus, *Aphis*, and with almost indistinguishable

morphological characters. *Aphis fabae* complex depict black or bluish-green colour and dorsal sclerites on the abdominal segment as the distinct morphometric traits found in its members. *Aphis craccivora* on the other hand possess a shiny black to gray black in colour with a shiny dorsal shield (Balckman and Eastop, 2000). On the other hand, the greater sequence divergence between *M. persicae* and *A. craccivora* is in agreement with the studies undertaken by Kinyanjui *et al.* (2015) whose study generated the largest genetic distances between the two species in Kenya. This is no surprise because the two species belong to different genus. Besides, their morphological features are quite distinct.

The intra-species divergence values showed that *M. euphorbiae* had no genetic distance (0.0%). This may however be attributed to the low level of samples collected rather than the differences in their genetic diversity. Raboudi *et al.* (2005), using microsatellite markers produced a varying rate of genetic variability among the 200 samples of *M. euphorbiae* sampled in Tunisia.

Indeed, the samples of *A. fabae* showed paraphyletic distribution in the nearest neighbour phylogenetic tree, where individuals separated into three sister species clusters of *Aphis fabae*, *A. fabae cirsiacanthoidis* Scopoli and *Aphis fabae solanella* Theobald. They were separated against one another (Figure 6) by an insignificant genetic distance (0.1%). These members of the black bean aphid are similar in colour and other morphological features. According to Béji (2013), *A. fabae* complex has been postulated to constitute a group of at least five subspecies which because of their phenotypic plasticity are morphologically indistinguishable. They coexist together in their natural hosts and identification process using classical taxonomy is nearly impossible since the original classification relied on the ability of each subspecies to colonize their unique secondary host (Stroyan, 1984). Even though these groups of black bean aphid separated themselves in the phylogenetic tree, there was an insignificant (0.9%) genetic distances among them. This may suggest that their genetic uniqueness may have been due to a weak speciation pressure or differentiation into these subspecies might have occurred in the recent years for detectable substitution to

be noticed. The two subspecies of the black bean aphid (*A. fabae fabae* and *A. fabae solanella*) for example, are separated pre-zygotically by the differences in sex pheromones which prevent mating (Thieme and Dickson, 1996). Females of *A. fabae solanella* release pheromones quite fast as compared to *A. fabae fabae* whose females release the mating pheromone about an hour later when both subspecies are placed under a light controlled environment (Thieme and Dickson, 1996). This form of assortative mating may have been responsible for sympatric speciation between them; hence making mating a cumbersome process. Besides, *A. f. fabae* was previously reported to possess a more pronounced phenotypic plasticity than *A. f. solanella* and *A. f. cirsiacanthoidis* (Béji *et al.*, 2015).

The phylogenetic construction revealed that aphid species clustered together in their distinct clades independent of the geography or host crop (Figure 6). This confirmed the lack of geographical or host crop genetic diversity of aphids attacking amaranth and nightshade in Kenya and Tanzania. This was supported further by aggregation of species into their distinct clades in the phylogenetic tree and clustering together of various aphid species into their haplotype and coordinates in haplotype network and principle coordinate analysis, respectively. The lack of significant genetic diversity of aphids based on host crop and agro-ecological zones suggests that such factors may not infer the cause of a speciation event; rather they play an important role in the survival of the aphids. These results are in agreement with previous reports that showed near genetic homogeneity irrespective of the host crop or differences in geographical factors (Nibouche *et al.*, 2014; Cocuzzi *et al.*, 2015). This was also reported by Raboudi *et al.* (2011) who studied the genetic diversity of potato aphids in Tunisia using RAPD markers.

Molecular clock is a technique that uses substitution rates of DNA to calibrate a particular time in history when two or more life forms underwent speciation (Hasegawa *et al.*, 1985). It is used mainly to estimate divergence dates within and without species and populations of living organisms (Hasegawa *et al.*, 1985). Using the maximum likelihood model, molecular clock hypothesis rejected the null hypothesis at 5% level

of significance. The molecular clock assumes that all tips of the phylogenetic tree are equidistant from the root of the linear tree. The linear phylogenetic tree displayed some sequences that were not of the same distance with others from the root of the tree. This result is in agreement with those reported by Tamura *et al.* (2011), suggesting that the aphids under study may not have evolved at the same rate.

To further elucidate this relationship, the principle coordinate analysis (PCoA) plot bolstered the above theorems with the species spreading along in their coordinates in relation with their interspecies genetic distances.

Furthermore, mitochondrial cytochrome *c* oxidase I DNA sequences polymorphism was further subjected to haplotype analysis. The pattern of clustering as shown in Figure 8 was in agreement with that of the phylogenetic cladogram and the principal coordinate analysis where samples of the genus *Aphis* were closely related than those of *Macrosiphum* and *Myzus*.

5.2 Conclusion

Results in this study showed that *Aphis craccivora*, *Aphis fabae*, *Myzus persicae* Sulzer and the potato aphid, *Macrosiphum euphorbiae* were found attacking both amaranth and nightshades in Kenya and Tanzania. The ability of the barcode region to identify aphid species makes it an indispensable tool that can be used together with classical taxonomy in identification and diversity of aphid species that may be deemed invasive on the host crops. The sample species did not show host specificity, confirming previous results that aphids are generally polyphagous in nature. These aphids demonstrated low genetic diversity both among and between species, indicating that host crop or agro-ecological zone do not influence their diversity. This was supported further by aggregation of species into their distinct clades in the phylogenetic tree and clustering together of various aphid species into their haplotype and coordinates in haplotype network and principle coordinate analysis, respectively. An average

interspecies diversity of 8.6% was however substantive enough to delineate samples into their respective species. The process of detecting species attacking amaranth and nightshades in East Africa is important for quarantine practices can be exercised before further spread. Furthermore, it is an important tool in expediting the process of species discovery. Identification process is a critical element in pest control, understanding and management of potyviruses and downstream biological studies, especially of aphid groups that do have different subspecies. Besides, the COI sequence database created in this study for the aphids infesting amaranth and nightshade in the Kenya and Tanzania countries can be used in future as a reference point for determining mitochondrial DNA stability over time.

5.3 Recommendations

More sampling needs to be done to elaborate further the phylogenetic studies of the aphids of the species *A. fabae*, *M. persicae* and *M. euphorbiae*. Particularly, sampling of the population of *A. fabae* complex on their primary host (*Vicia faba*) and genotyping them with several other biological markers will help to reject or confirm the hypothesis that secondary host may actually be responsible for genetic adaptive changes. Moreover, the absence of green peach and potato aphids in Tanzanian samples needs to be investigated further. The latter species need to be particularly thoroughly sampled to confirm the results depicted in this study. Rainy season that was experienced throughout the sampling frame during the sampling period may have contributed to their wash-off. In addition, more sampling need to be done on the potato aphid since the zero genetic divergence may have been contributed by low samples that were collected in this study unlike other species represented. Furthermore, the number of regions as well as seasons needs to be increased to cover more countries in Africa that grow the two African indigenous vegetables. To confirm the results of the barcode region, other genomic regions need to be targeted to study the aphids infesting amaranth and nightshades in Kenya and Tanzania. Lastly, the use of the barcode region is therefore recommended for use in identifying animal species of interest.

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LIST OF APPENDICES

Appendix 1: Protocol for packaging samples for sequencing

1. Label sterile 1 ml eppendorf tubes according to the purified samples
2. Take sterile 20 μ l pipette tips and aliquot about 15 μ l of purified product onto the labeled tubes. The volumes of DNA depends on the sequencing company's requirements
3. Use a sterile parafilm to cover the lid of the tight to air-tight condition.
4. Package the samples in an order as per labeling.
5. Seal the samples and put them in a cool box ready for shipping

Appendix 2: Sequences of the aphids sampled in Kenya and Tanzania

>AcAs1

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