Characterization of Aphid (Hemiptera: Aphididae) Species in Kenya using PCR-RFLP and DNA barcoding

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other university.

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DEDICATION

To my beloved mother, Naomi Wanjiku.

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ABBREVIATIONS AND ACRONYMS

Ac	*Aphis craccivora*
Af	*Aphis fabae*
Ag	*Aphis gossypii*
AIC	Akaike information criterion
AICc	Corrected Akaike information criterion
Ap	*Acyrthosiphon pisum*
BIC	Bayesian information criterion
BOLD	Barcode of Life Data Systems
BLAST	Basic local alignment search tool
BMCV	Bean common mosaic virus
Bb	*Brevicoryne brasssicae*
CaMV	Cauliflower mosaic virus
COI	Cytochrome *c* oxidase subunit I
COII	Cytochrome *c* oxidase subunit II
DNA	Deoxyribonucleic acid
dNTPs	Deoxynucleoside triphosphates
DT	Decision theory performance-based selection
EF1α	Elongation factor 1α
GPS	Global positioning system
GTR	General time reversible
icipe	International Centre of Insect Physiology and Ecology
IPM	Integrated pest management
ITS	Internal transcribed spacer
K2P	Kimura 2-parameter
Lp	*Lipaphis pseudobrassicae*
MEGA	Molecular Evolutionary Genetics Analysis
ML	Maximum likelihood
MtDNA	Mitochondrial DNA
Mp	*Myzus persicae*
NEB	New England Biolab
NCBI	National Centre of Biotechnology Information
NJ	Neighbour-joining
PCA	Principal Component Analysis
PCR	Polymerase chain reaction
RAPD	Random amplified polymorphic DNA
rDNA	Ribosomal DNA
RFLP	Restriction fragment length polymorphism
Taq	Thermus aquaticus
TuMV	Turnip mosaic virus

ABSTRACT

Aphids are among pests of economic importance throughout the world. Together with transmitting plant viruses, aphids are capable of inflicting severe crop production losses. They also excrete honeydew that favors the growth of sooty mold which reduces the quality of vegetables and fruits and hence their market values. Rapid and accurate identification of aphids to the species level is a critical component in effective pest management and plant quarantine systems. Even though morphological taxonomy has made a tremendous impact on species-level identifications, polymorphism, morphological plasticity and immature stages are among the many challenges to accurate identification. In addition, their microscopic size, presence of cryptic species and damaged specimens dictate the need for a strategy that will ensure timely and accurate identification. In this study, polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) based on mitochondrial COI gene and DNA barcoding were applied to characterize seven aphid species collected from 13 counties in Kenya. Three restriction enzymes *RsaI*, *AluI* and *Hinfl* produced banding patterns that allowed unambiguous discrimination of five species, namely, *Brevicoryne brassicae, Lipaphis pseudobrassicae, Acyrthosiphon pisum, Aphis gossypii* and *Myzus persicae*. However, PCR-RFLP could not distinguish *Aphis craccivora* from *A. fabae* by yielding fragments of equal sizes. DNA barcoding enabled characterization of the seven species, including the morphologically indistinguishable *A. craccivora* and *A. fabae* and separated two *subspecies* of *A. fabae.* Analyses of the barcode region indicated intraspecific and interspecific sequence divergences of 0.08% and 6.63% respectively. Phylogenetic analyses did not reveal any genetic variation among populations belonging to the same species, as they all clustered together despite being collected from different localities. Principal component analysis separated the species into seven distinct clusters and further confirmed the evolutionary relationships inferred by the phylogenetic tree. Network patterns detected eight distinct haplotypes among the seven aphid species, including two subspecies of *A. fabae*. Based on these results, both PCR-RFLP and DNA barcoding could provide quick and accurate tools for identification of aphid species within Aphididae subsequently aiding in effective pest management programmes and enhance plant quarantine systems in Kenya

CHAPTER ONE

INTRODUCTION

1.1 Background information

Globally, aphids (Hemiptera: Aphididae) are among the most economically important insect pests of crops (Blackman and Eastop, 2007). Aphids also rank high as invasive pests due to their ease of transport and parthenogenetic mode of reproduction (Foottit *et al.*, 2008). They are known to cause 70-80% of yield losses on different crops worldwide (Aslam *et al.*, 2007). These losses are due to direct feeding damage on plant sap that results in stunted growth, distortion, wilting, yellowing of plants consequently leading to severe crop production losses (Aslam *et al.*, 2007). Indirect damages results from transmission of plant viruses and their related diseases, plant deformation arising from toxic salivary secretions and excretion of honey dew that favours the growth of sooty mold fungus (Blackman and Eastop, 2000). Other than causing a reduction in photosynthetic activity, honey dew and sooty mold contaminate the quality of crops which in turn reduce both their aesthetic appeal and marketability (Worf *et al.*, 1995).

Considering their economic importance, timely and accurate identification of aphid species is crucial for effective pest management strategies and phytosanitary management (Miller and Foottit, 2009; Lee *et al.*, 2011). Traditionally, aphid species have been identified on the basis of their morphological characters (Blackman and Eastop, 2007). However, their microscopic size and reduction or loss of key morphological characteristics poses a serious problem in morphological identification (Miller and Foottit, 2009).

Aphids have complex lifecycles involving parthenogeneticity and high polymorphisms, and within a single species, there are different morphs with distinct morphological characters, which may colonize different host plants, further complicating species identification (Foottit *et al.*, 2008). Additionally, aphids are prone to morphological plasticity due to environmental and host plant effects making identification very difficult (Miller and Foottit, 2009). Moreover, identification of immature stages, cryptic species and damaged specimens by morphological means is problematic due to absence of key morphological characteristics (Armstrong and Ball, 2005; Lee *et al.*, 2011). Usually, closely related species with similar morphological characteristics have been identified on the basis of their host plants association (Coeur d'acier *et al.*, 2014), which is again complicated by the polyphagous nature of some species.

Recognition of these difficulties has signaled the need to explore alternative detection tools to supplement morphology including the use of genetic markers (Valenzuela *et al.*, 2007; Foottit *et al.*, 2008; Miller and Foottit, 2009; Helmi *et al.*, 2011; Lee *et al.*, 2011; Naaum *et al.*, 2012). This study seeks to avail molecular tools that will contribute to timely and accurate identification of aphid species collected from different counties in Kenya. These tools should in turn facilitate quicker and effective implementation of pest management strategies and strengthen plant quarantine diagnosis in Kenya and other countries affected by the target species.

1.2 Problem statement and justification

Aphids are a major economic menace to production of crops in many regions of the world and Kenya is no exception. In addition to transmission of plant viruses, aphids inflict direct crop damages to their host plants, which lead to major yield losses. 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, identification of aphid species using morphology is very difficult because they characteristically exhibit parthenogenetic reproduction associated with polymorphism, which leads to a significant intraspecific variation. In addition, aphids are subject to continuous morphological variation in response to environmental and host plant effects. Morphological characters have also proved insufficient for immature stages and closely related species with inseparable morphology. Deficiencies of morphological taxonomy approach necessitate the search for alternative tools to deliver accurate and timely identification of species in the family Aphididae. Several molecular techniques have been used to characterize aphid species in Australia, Europe, China, Korean Peninsula, Asia, North America, Egypt and Tunisia. Therefore the aim of the study was to identify a tool that could provide rapid and accurate identification of aphid species collected from different counties in Kenya. This study will provide baseline information, which is vital in the implementation of timely and appropriate crop protection measures as well as quarantine pest diagnostics.

1.3 Hypotheses

i. PCR-RFLP and DNA barcoding provide rapid and accurate tools for characterization of aphid species in Kenya.

ii. High genetic homogeneity exists between populations of aphid species collected from different counties in Kenya.

1.4 Objectives

1.4.1 General objective

To identify a rapid and accurate tool for characterization of aphid species collected from different counties in Kenya.

1.4.2 Specific objectives

i. To characterize aphid species using PCR-RFLP and DNA barcoding.

ii. To analyze genetic variation among Kenyan populations and generate a reference DNA barcode library for the target species.

CHAPTER TWO

LITERATURE REVIEW

2.1 General morphology of aphids

Aphids are small, soft-bodied and pear-shaped insects (Blackman and Eastop, 2000). They have two compound eyes, two long and thin antennae composed of two thick basal segments and a flagellum with as many as four segments, two ocular tubercles and a pair of cornicles at the posterior end of the abdomen (Capinera, 2008). They have piercing-sucking mouthparts called stylets and a proboscis that originates between and behind the forelegs. Depending on the species, aphids range from 1.5 to 2.5 mm in length (Blackman and Eastop, 2000). Their body colour also varies depending on the species, ranging from black, brown, grey, red, yellow, green to blue-green (Drees, 1993). Generally, adult aphids are wingless (Figure 2.1), but winged morphs (Figure 2.2) also occur, possessing two membranous pairs of wings, with the front pair larger than the hind pair. Development of wings is usually triggered by environmental conditions such as declining food quality and overcrowding (Drees, 1993).

Figure 2.1: Wingless adult of *Lipaphis pseudobrassicae* Davis © G. Kinyanjui, 2013

Figure 2.2: Winged adult of *Brevicoryne brassicae* (L.) © G. Kinyanjui, 2013

2.2 Lifecycle of aphids

Aphids have complex and varied life cycles involving polymorphism, alternation of asexual and sexual generations and host plant alternation (Foottit *et al.*, 2008). Typical aphid life cycle is divided into several stages; with each stage characterized by one or more morphs that differ in their external morphology (Dixon, 1985). Individuals of each morph are well adapted for reproduction, dispersal and surviving unfavourable climatic and nutritional conditions (Williams and Dixon, 2007). As a result, these pests have been reported to be among the most successful creatures in the world (Zand and Gavanji, 2012).

Aphid life cycles are majorly of two types depending on the patterns of host plant utilization, that is, autoecious and heteroecious (Williams and Dixon, 2007). Autoecious life cycles involve the host-specific aphids which remain on a single host plant or migrate between closely related plant species throughout the year (Dixon, 1985). Heteroecious life cycles involve the host alternating aphids which live on a primary host plant during winter, migrate to a secondary host plant in summer and back to the primary host in autumn (Williams and Dixon, 2007). About 10% of aphid species have heteroecious life cycles associated with host plant alternation (Minks and Harrewijn, 1987). These species exhibit holocyclic reproduction (Figure 2.3) in which asexual generations alternate with a single sexual generation (Dixon, 1985).

A typical life cycle involves fundatrix females hatching from overwintering eggs in spring. Usually, there are 4 nymphal instars in aphids. With successive moults and continuous growth, the parthenogenetic, viviparous and often wingless fundatrices becomes mature adults and in turn produce more parthenogenetic, viviparous females, both winged and wingless (Williams and Dixon, 2007). The winged females migrate to the secondary host plants where they reproduce parthenogenetically through summer. After several parthenogenetic generations, winged males and females are produced, and they migrate back to the primary host plant (Williams and Dixon, 2007). The last parthenogenetic generation then produces sexual oviparous females which then mate with the males and subsequently lay the overwintering eggs on the primary host (Ogawa and Miura, 2014).

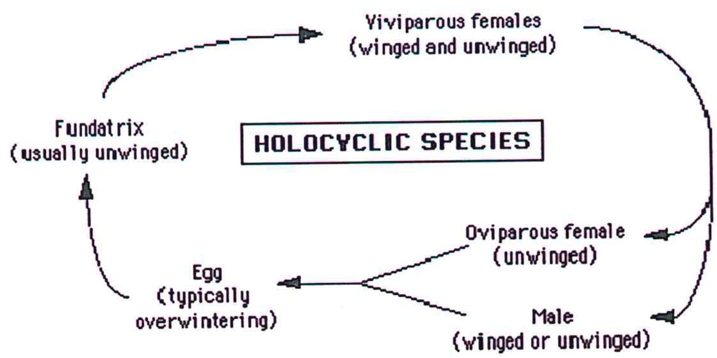


Figure 2.3: A holocyclic life cycle (Stern, 1995)

Autoecious aphids account for over 90% of all aphid species (Capinera, 2008). These species exhibit anholocyclic mode of reproduction (Figure 2.4). In an anholocyclic life cycle, there is complete absence of sexual reproduction and alternation of plant hosts is not practiced (Williams and Dixon, 2007). The males are rarely produced or totally absent so that only viviparous parthenogenetic females exist. Anholocyclic reproduction is common in the tropics with parthenogentic reproduction continuing throughout the year with all the offsprings being females (Capinera, 2008). Although many species are either holocyclic or anholocyclic, some aphid species have variable life cycles depending on the environmental conditions, with some possessing both holocyclic and anholocyclic lifecycles (Williams and Dixon, 2007).

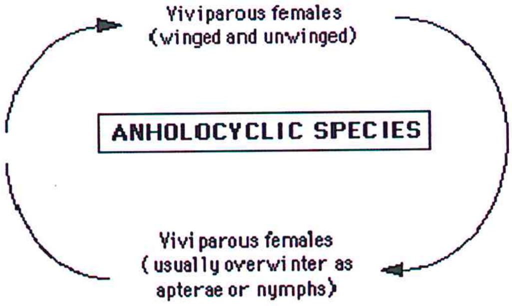


Figure 2.4: Anholocyclic life cycle (Stern, 1995)

2.3 Economic importance of aphids

There are approximately 4,700 species of Aphididae in the world (Remaudiere and Remaudiere, 1997). Of these, about 250 species have been recognized as important pests of agricultural and horticultural crops (Blackman and Eastop, 2000). For instance, *Brevicoryne brassicae* (L) and *Lipaphis pseudobrassicae* Davis are the species of most economic importance on crucifers with adverse effects on yield and quality of cabbage and kale (Nyambo and Löhr, 2005; Sæthre *et al.*, 2011). Other agriculturally important species included this study are *Acyrthosiphon pisum* Harris, *Aphis gossypii* Glover, *Aphis craccivora* Koch, *Myzus persicae* Sulzer and *Acyrthosiphon pisum* Harris which are equally damaging to their respective host range.

Aphids are phytophagous and feed directly on plant sap thereby reducing plant growth and consequent yield losses (Quisenberry and Ni, 2007). Heavy infestation causes curling and yellowing of leaves, wilting, deformation of plant tissues, stunted growth and may lead to plant death. In addition, aphids excrete honey dew onto the foliage, which favours the growth of sooty mold fungus, and together with waxy secretions, contaminate and give crops especially, vegetables and fruits, a dirty appearance. This significantly reduces their market value, often leading to rejection in local and international market and consequently, huge financial losses (Quisenberry and Ni, 2007; Miller and Foottit, 2009. Fouling of plants with sooty mold also reduces their photosynthetic efficacy leading to productivity losses (Worf *et al.*, 1995). Furthermore, honey dew has been observed to reduce the effectiveness of fungicides (Dik and van Pelt, 1992) and can contribute to the spread of fungi (Gillman, 2005). Most importantly, aphids transmit lots of plant viruses, which cause diseases of major economic importance in crops (Katis *et al.*, 2007).

2.3.1 *Brevicoryne brassicae* (L.)

Brevicoryne brassicae (L.), commonly known as the cabbage aphid (Figure 2.5) is a cosmopolitan pest restricted to crucifers including cabbages, broccoli, cauliflower and kale. It is widely distributed (22 countries in Africa) and mostly confined to mid- and high-altitude agroecologies. *Brevicoryne brassicae* is known to transmit over twenty plant viruses, of which *Cauliflower mosaic virus* (CaMV) and *Turnip mosaic virus* (TuMV) are known to occur in tropical Africa and can cause substantial reduction in cabbage production (Spence *et al.*, 2007; Capinera, 2008). It is usually found on lower and upper leaf surfaces and within the heads of cabbages. Winged females are green, with the head and ventral black and black transverse bars on the dorsal abdomen (Capinera, 2008). Wingless females are yellow-green or gray-green with a dark head and two rows of dark spots dorsally on the thorax and abdomen (Capinera, 2008). Typically the males are winged. Key morphological characteristics of *B. brassicae* include shorter cornicles than cauda, a cone-shaped or triangular cauda with seven to eight curved hairs and a white, waxy secretion covering the aphids and infested foliage (Liu and Sparks, 2001).

Figure 2.5: *Brevicoryne brassicae* (L.) female adult © G. Kinyanjui, 2013

2.3.2 *Lipaphis pseudobrassicae* Davis

Lipaphis pseudobrassicae Davis, commonly known as the turnip aphid (Figure 2.6) is a pest of cruciferous crops including cabbage, turnip, mustard, broccoli, kale and radish. The species is cosmopolitan and restricted to lowland agroecologies. It transmits about ten non-persistent plant viruses including cabbage ring spot, cabbage ring necrosis and mosaic viruses of cauliflower, radish and turnip (Blackman and Eastop, 2007). Wingless females are yellowish green to olive green in colour, with slightly darker spots on the dorsal surface of the abdominal segments in front of the cornicles (Liu and Sparks, 2001). The winged females have dusky green abdomens with dark lateral stripes and the antennae are also dark, except at the base (Liu and Sparks, 2001). Major characteristics of *L. pseudobrassicae* include tongue-shaped cauda, cornicles are not dark and longer than cauda and a thin layer of white, waxy secretion (Liu and Sparks, 2001).

Figure 2.6: *Lipaphis pseudobrassicae* Davis female adult © G. Kinyanjui, 2013

2.3.3 *Acyrthosiphon pisum* Harris

Acyrthosiphon pisum Harris, commonly known as the pea aphid (Figure 2.7) is a pest restricted to leguminous plants. It is a vector of over thirty plant viruses including pea and bean leaf roll viruses, potato virus Y, pea enation and pea mosaic viruses (Blackman and Eastop, 2007). *Acyrthosiphon pisum* is a large aphid with long, slender appendages, reddish eyes and range in colour from green, deep green or pink.

Figure 2.7: *Acyrthosiphon pisum* Harris female adult © G. Kinyanjui, 2013

2.3.4 *Aphis gossypii* Glover

Aphis gossypii Glover, commonly known as the melon and cotton aphid (Figure 2.8) is one of the most important pest of vegetables in tropical Africa. The species is very polyphagous on a range of crops including cabbages, kale, cauliflower, citrus plants, cocoa, melon, potato, apple trees, cotton, coffee, okra and many ornamentals (Capinera, 2008). *Aphis gossypii* has been reported from 40 countries in Africa. In Kenya, for example, yield losses due to insect pest problems on okra in Nguruman and Muhaka (for which *A. gossypii* is regarded as among the key pests) was estimated at 24-40% and 15-24%, respectively (Sithananthan *et al.*, 1998). *Aphis gossypii* can transmit more than fifty plant viruses causing symptoms that impair vegetable quality and yield but the true impact on crop losses have not been quantified. Some of these plant viruses include mosaic, crinkle, *cotton anthocyanosis virus,* lily rosette disease and Tristeza citrus fruit (Blackman and Eastop, 2007). *Aphis gossypii* vary greatly in colour ranging from pale yellow to green, dark gray or dark green to black (Blackman and Eastop, 2007). These aphids are not covered with waxy secretions. Key characteristics of *A. gossypii* include absence of frontal tubercles, black cornicles and cauda, shorter cauda than one-half the cornicles and slightly knobbed cauda with five to seven curved hairs (Liu and Sparks, 2001).

Figure 2.8: *Aphis gossypii* Glover female adult © G. Kinyanjui, 2013

2.3.5 *Aphis craccivora* Koch

Aphis craccivora Koch, variously known as the black legume or groundnut or cowpea aphid (Figure 2.9) is a cosmopolitan pest species with a worldwide distribution and particularly common in warmer climates. It is very polyphagous with a wide range of host plants including crucifers, groundnuts, mustard and a preference for crops in the family Fabaceae. Infestation by this aphid species can result in yield losses of up to 35% (Singh and Allen, 1980) and in extreme cases in complete crop failure (Ansari *et al.*, 1992). Apart from direct feeding damages, this cowpea specialist is an important vector of over thirty plant viruses including cowpea aphid-borne mosaic virus, groundnut rosette virus, peanut mottle virus, groundnut stunt virus and bean common mosaic virus (Blackman and Eastop, 2007; Bock and Conti, 1974). *Aphis craccivora* is dark brown to gray black in colour with a shiny dorsal shield and has white or pale yellow and black appendages.

Figure 2.9: *Aphis craccivora* Koch female adult
© http://www.nbair.res.in/Aphids/Aphis-craccivora.php

2.3.6 *Aphis fabae* Scopoli

Aphis fabae Scopoli (Figure 2.10) is commonly known as the black bean or bean aphid. It is a significant insect pest of common beans in tropical Africa and particularly in the higher altitude regions (Karel and Autrique, 1989). In addition, *A. fabae* is very polyphagous causing direct physical damages on a wide range of agricultural crops such as crucifers, cucurbits, sugar beet and tomato but mostly found on legumes. This bean specialist has a cosmopolitan distribution and transmits over thirty plant viruses including bean common mosaic virus (BMCV), plum pox virus and mosaic viruses of dahlia and cineraria (Blackman and Eastop, 2007). *Aphis fabae* represents a member of species complex with 6 subspecies, which are morphologically difficult to distinguish; hence, can only be identified on the basis of their host plants affiliation (Zhang *et al.*, 2010). *Aphis fabae* is a black or dark green, plump insect with an ovoid body, white appendages and black cornicles and cauda. Most often, the wingless adults and immature stages have discrete white waxy spots.

Figure 2.10: *Aphis fabae* Scopoli female adult © G. Kinyanjui, 2013

2.3.7 *Myzus persicae* Sulzer

Myzus persicae Sulzer, commonly known as the green peach or peach-potato aphid (Figure 2.11) is a highly polyphagous species with host plants ranging from crucifers, cucurbits, legumes, solanaceous crops, lettuce, peaches, sugar beet, tobacco and ornamental plants. It is cosmopolitan and a highly efficient vector of plant viral diseases, transmitting over one hundred plant viruses, including potato leaf roll virus, lettuce mosaic virus, pea enation mosaic virus and turnip and beet mild yellowing viruses (Blackman and Eastop, 2007). Usually adults are wingless and range in colour from pale greenish-yellow to various shades of green, pink and red. Winged female adults have yellowish- green abdomen with a shiny black dorsal patch. Key morphological characteristics include distinct frontal tubercles pointing inwards, cornicles longer than cauda and of the same colour as the body and three longitudinal dark green stripes on the pear-shaped body (Liu and Sparks, 2001).

Figure 2.11: *Myzus persicae* Sulzer female adult © G. Kinyanjui, 2013

2.4 Morphological identification of aphid species

Generally, aphids have been recognized by a number of key morphological characteristics that are shared within species. They have a five- or six- segmented antennae composed of two basal segments and a segmented flagellum with a terminal process (Blackman and Eastop, 2007). The length and segmentation of the antennae is a key characteristic used in species identification (Liu and Sparks, 2001). In addition, aphids 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). Other key characters include the length, shape, thickness and colour of the cornicles; and the size, shape and presence or absence of the frontal tubercles (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. Accurate morphology-based identification requires a lot of taxonomic expertise because of their small size and microscopic nature of some key diagnostic 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 (Foottit, 1997). As a matter of fact, morphological characters have proved unreliable in distinguishing closely related species, because of their remarkable morphology conservatism (Cocuzza and Cavalieri, 2014). Thus, such species are identified depending on their host plant association, which is complicated by the fact that most aphid species are polyphagous and several species could be found on a single host plant leading to misidentification. Further complications occur when closely related species form large cryptic species complex and also when there are damaged specimens (Stoeckle, 2003; Floyd *et al.*, 2009), often leading to erroneous identifications.

Accurate species identification 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, colour morphs, winged and wingless forms (Foottit *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). Specific environmental cues such as day length, temperature, and overcrowding may not only have profound effects on their morphology, including body size and colouration, but may also trigger the production of different morphs with discrete morphological differences within a single species, which pose significant problems in species identifications (Agarwala, 2007; Miller and Foottit, 2009). 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 species identifications (Mehrparvar *et al.*, 2012). Moreover, identification is restricted to adult specimens since immature life stages lack the key morphological characters. Rearing of immature stages to adults limits quick diagnostics with delays for appropriate crop protection measures and consequent crop yield and financial losses. Nevertheless, huge economic impact of aphids coupled with high demand for pest free produce in the market puts increasing pressure for prompt detection and eradication interventions. Accordingly, implementation of effective management programmes and phytosanitary systems for these pests dictate the need for timely and accurate identification of target species (Lee *et al.*, 2011).

2.5 Molecular identification of aphid species

Molecular tools are useful in many areas of research and are becoming increasingly important in resolving the problems inherent to morphological-based identifications. Besides accurate species-level identifications, these tools provide a more rapid and reliable approach towards detection of pests of quarantine concern (Armstrong and Ball, 2005), identification of cryptic species, immature life stages, and pests with ambiguous morphological characteristics (Choe *et al.*, 2006; Valenzuela *et al.*, 2007). Furthermore, molecular tools are applicable in discovery of new species, delimitation of species boundaries and also provide good evidence for phylogenetic reconstruction among taxa (Sperling and Roe, 2009; Kim *et al.*, 2010).

In recent years, a number of molecular tools have been widely used for identification of aphid species. These include polymerase chain reaction (PCR) (Miller and Foottit, 2009), polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) (Valenzuela *et al.*, 2007), deoxyribonucleic acid (DNA) barcoding (Foottit *et al.*, 2008; Lee *et al.*, 2011), real-time PCR (Naaum *et al.*, 2012), random amplified polymorphic DNA (RAPD) and microsatellite markers (Helmi *et al.*, 2011). Among these techniques, DNA barcoding offer a considerable advantage by employing a standardized approach towards species-level identifications in different animal groups (Hajibabaei *et al.*, 2007).

2.5.1 Mitochondrial DNA markers

Molecular markers that have been exploited as species-specific markers for identification of aphid species include mitochondrial cytochrome *c* oxidase subunit I (COI), subunit II (COII), nuclear elongation factor 1α (EF1α) and internal transcribed spacer (ITS) gene regions (Raboudi *et al.*, 2002; Kim *et al.*, 2010). However, mitochondrial DNA (mtDNA) has several specific biological properties that make it a better molecular marker compared to nuclear markers. It has a higher rate of mutation, which results in significant variation in DNA sequences to differentiate even closely related species (Leite, 2012). In addition, mitochondrial genes are shared across diverse taxa in animals and are strongly conserved to allow use of universal primers (Galtier *et al.*, 2009). MtDNA is also highly abundant in the cells and thus, facilitates amplification during PCR and its haploid nature as well as lack of introns makes sequence alignments of the amplified genes easier. Among mtDNA markers, COI has a high application rate because it possesses a greater range of phylogenetic signal and has a high success rate in distinguishing species (Hebert *et al.*, 2003a; Hebert *et al.*, 2004).

2.5.2 PCR-RFLP

PCR-RFLP involves discrimination of species based on restriction profiles. It is based on digestion of PCR amplicons with specific restriction enzymes to produce smaller and distinct polymorphic fragments, often visualized as markers for identification of species. The enzymes cleave DNA sequences at specific recognition sites which are highly conserved to generate fragments of variable sizes amongst species (Jenkins *et al.*, 2012). Several studies have utilized PCR-RFLP to differentiate between species and haplotypes in the family Aphididae as well as other agriculturally important pests (Armstrong *et al.*, 1997; Brunner *et al.*, 2002; Raboudi *et al.*, 2002; Shufran, 2003; Valenzuela *et al.*, 2007; Masahiro *et al.*, 2008). For instance, Valenzuela *et al.* (2007) used PCR-RFLP of COI based on five restriction enzymes to characterize twenty five aphid species including immature life stages from southern Australia. This technique has also been used to distinguish between *Rhopalosiphum* species and enabled identification of a new species within the studied genus (Yeh *et al.*, 2005; Valenzuela *et al.*, 2009). In addition, PCR-RFLP of ITS gene of ribosomal DNA based on three restriction enzymes revealed the coexistence of two different haplotypes within *Myzus persicae* (Raboudi *et al.*, 2002).

PCR-RFLP provides a simple, rapid and cost effective diagnostic tool for identification of aphid species. It is a relatively sound technique that could be beneficial in low budget situations. It is also applicable in situations where there may be no access to sequence analysis software and skills to analyze sequence data. However, PCR-RFLP relies on few informative DNA sequence positions and only a fraction of sequence variations is detected (Brunner *et al.*, 2002). Moreover, the possible existence of intra-specific polymorphism at the restriction sites may lead to gain or loss of restriction fragments making it difficult to accurately interpret observed polymorphism as either species or population level variation and consequent false results (Armstrong and Ball, 2005; Pereira *et al.*, 2008).

Production of unscorable and unexpected fragments as well as overlapping patterns leads to ambiguous results and misidentifications; thus, making PCR-RFLP less suitable for a robust identification approach. This technique is not amenable for automation and standardization, since it requires significant amounts of high quality DNA (Pereira *et al.*, 2008). In addition, studies involving many samples require combination of several restriction enzymes and generate highly complex restriction profiles with so many bandings which are time-consuming, cumbersome and difficult to interpret. Also, the banding pattern only provides qualitative data rendering PCR-RFLP undesirable for high throughput analysis.

2.5.3 DNA barcoding

Increasingly, DNA barcoding is being widely employed due to its accuracy in species identification and delineation (Hebert *et al.*, 2003a). It is based on the principle that a short standardized DNA sequence can characterize species in a myriad of taxonomic groups in the animal kingdom (Hebert and Gregory, 2005). A 658 base pair fragment near the 5' end of COI gene has been adopted as the global barcoding marker in identification of individuals in the same species (Hebert *et al.*, 2003a; Hebert *et al.*, 2003b). Basically, DNA barcoding involves sequencing target gene regions and comparing the results with orthologous reference sequences in public databases.

Recent studies have shown that over 95% of species possess unique COI barcode sequences, with a considerable barcode gap between the mean interspecific and mean intraspecific divergences, which enable species-level identifications in diverse groups of organisms in the animal kingdom (Hajibabaei *et al.*, 2007). These include birds (Hebert *et al.*, 2004), fishes (Ward *et al.*, 2005), crustaceans (Costa *et al.*, 2007) and most insect pests of economic importance (Armstrong and Ball, 2005; Ball and Armstrong, 2006; Hajibabaei *et al.*, 2006; Smith *et al.*, 2008; Floyd *et al.*, 2009; Nagoshi *et al.*, 2011; Park *et al.*, 2011; Khamis *et al.*, 2012).

In the family Aphididae, DNA barcoding has facilitated identification of diverse aphid species including closely related species with similar morphology in Europe (Coeur d'acier *et al.*, 2014), China (Wang *et al.*, 2011), Korean Peninsula (Lee *et al.*, 2011), Asia (Kim *et al.*, 2010) and North America (Foottit *et al.*, 2008). Importantly, DNA barcoding is not limited by life stages and makes it possible to identify aphid samples at all developmental stages, including distinct lifecycle forms and immature stages within a species (Foottit *et al.*, 2009). Also, by associating different morphological forms (Foottit *et al.*, 2009), DNA barcoding could enable identification of various morphs within a species including colour morphs, winged and wingless morphs (Rebijith *et al.*, 2013).

It has also enabled identification of cryptic aphid species in *Brevicoryne brassicae* (L), *Hyperomyzus carduellinus* (Theobald) and *Brachycaudus helichrysi* (Kaltenbach) (Foottit *et al.*, 2009; Rebijith *et al.*, 2013) and discovery of new species in the genus *Rhopalosiphum* (Bulman *et al.*, 2005; Valenzuela *et al.*, 2009). Morever, DNA barcoding has provided a good basis for constructing phylogenetic relationships among aphid species (Foottit *et al.*, 2008; Foottit *et al.*, 2009; Kim *et al.*, 2010; Lee *et al.*, 2011).

2.6 Aphids management

Naturally, aphids are often controlled by their natural enemies. However, due to their pest status, invasive potential and negative impact on their host crops productivity and quality, aphids have attracted substantial use of pesticides (Dewar, 2007). Synthetic pesticides often disrupt the action of natural enemies, threaten the stability of an ecosystem and have negative effects on human health and environment (Foster *et al.*, 2009). Pesticides may also persist on harvested products, leading to crop contamination and most notably food safety concerns. In addition, most aphid species often develop resistance to pesticides and thus limit their use (Foster *et al.*, 2009).

Development and implementation of alternative aphid control strategies is therefore necessary for optimum suppression of aphid populations and avoidance of insecticide tolerant strains. In particular, integrated pest management (IPM) programs will help reduce producer and consumer risks to synthetic pesticides as well as enhance incomes and livelihoods (Lim *et al.*, 1996). IPM involves integration of several techniques such as monitoring and forecasting, host-plant resistance, biological, cultural and selective chemical control (Emden and

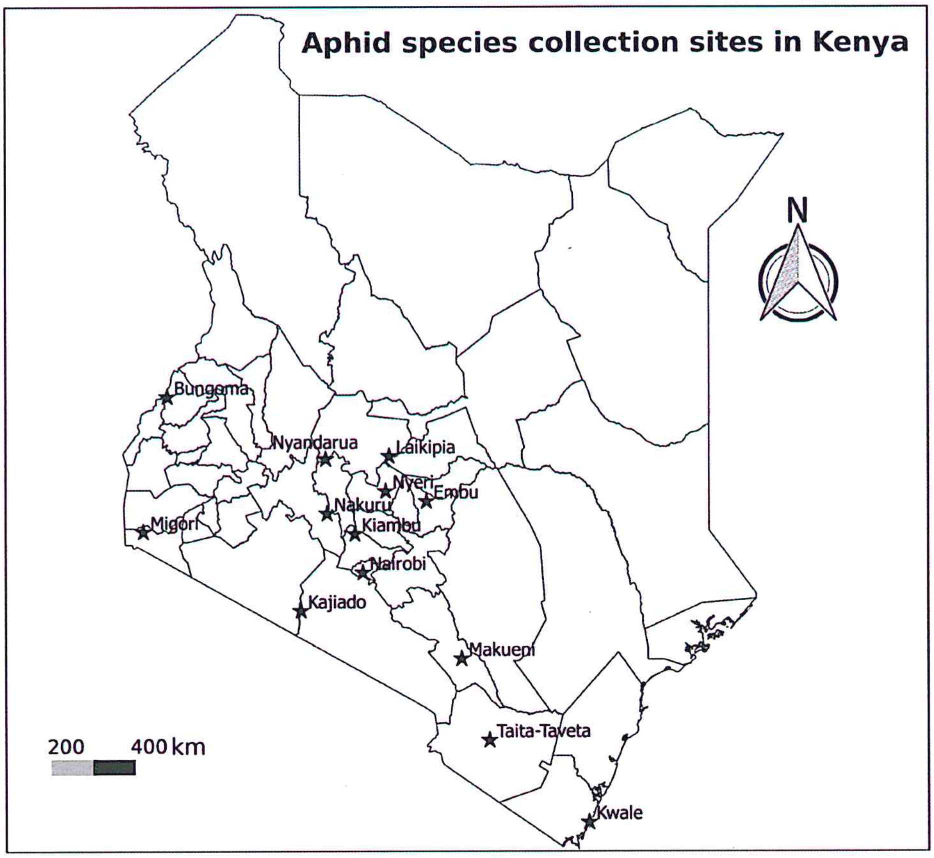
Harrington, 2007). The first critical step towards successful IPM strategies and use of species-specific biological control agents is timely and accurate diagnosis of the target aphid species, the main objective of this study.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Samples collection and processing

Adults and late instar nymphs belonging to seven aphid species were collected from twenty one sites representing thirteen counties in Kenya (Figure 3.1). Fifty individuals were collected from each population, preserved in 95% ethanol (Kim *et al.*, 2010; Lee *et al.*, 2011) and taken to the laboratory for processing. Aphids were collected from the leaves of their host plants using a soft camel brush. Twenty samples from each site were randomly selected, identified and photographed dorsally, laterally and ventrally at x25 with a Leica LAS EZ4D stereo microscope with an integral digital camera (Leica Microsystems Limited, Switzerland) before DNA extraction. Voucher specimens from each collection were deposited at the arthropod pathology unit molecular laboratory in the International Centre of Insect Physiology and Ecology (*icipe*).



Legend

County	Species Code
★ Bungoma	Bb
★ Embu	Bb, Lp
★ Kajiado	Ag, Bb, Lp
★ Kiambu	Bb, Lp
★ Kwale	Ag
★ Laikipia	Bb
★ Makueni	Ag, Bb, Lp
★ Migori	Bb
★ Nairobi	Ac, Ag, Af, Bb, Lp, Mp
★ Nakuru	Bb, Lp
★ Nyandarua	Bb
★ Nyeri	Af, Ap, Bb
★ Taita-Taveta	Ac, Bb

Ac - *Aphis craccivora*
Af - *Aphis fabae*
Ag - *Aphis gossypii*
Ap - *Acyrthosiphon pisum*
Bb - *Brevicoryne brassicae*
Lp - *Lipaphis pseudobrassicae*
Mp - *Myzus persicae*

Figure 3.1: Map of Kenya showing the sampling sites for seven aphid species between February 2013 and September 2013 © G. Kinyanjui, 2013

3.2 DNA extraction and quality check

Each individual photographed sample was surface-sterilized using 3% bleach and rinsed three times with distilled water. Genomic DNA was extracted using proteinase K buffer. Each aphid sample was put into a sterile 1.5 ml Eppendorf tube and 100 μl 1x proteinase K buffer (10x proteinase K buffer composed of 25 mM KCl, 10 mM Tris-HCl at pH 9.0 at 25°C and 10 mM Triton X-100) (Appendix I) and 0.5 μl of 20 mg/ml proteinase K (Thermo Scientific, USA) were added. Each sample was homogenized using a sterile pestle and incubated overnight at 37°C in a water bath. The homogenate was then heated at 95°C in a water bath for 5 min to inactivate Proteinase K. The samples were each centrifuged at 15,000 xg for 5 min and 40 μl of supernatant was aliquoted into a sterile Eppendorf tube. Extracted DNA was then stored at -20°C for downstream processes. The purity and concentration of extracted DNA was determined using Nanodrop 2000/2000c Spectrophotometer. Two microlitres of each sample were loaded onto the pedestal and concentration measured. A ratio of absorbance A260/A280 was determined to assess the purity of the samples.

3.3 PCR-RFLP

A primer pair; A-pissum Fwd TCAACTAATCATAAAGATATTGGAA and A-pissum Rv TATAAATGAATTTTAAGTTC was designed to amplify a 1540 bp fragment of mitochondrial COI gene. The primers were manually generated from a sequence that was retrieved from a complete genome of mitochondrion of

Acyrthosiphon pisum Harris in the NCBI database (FJ411411.1). The PCR suitability tests such as melting temperature of each primer, percentage GC content, hairpin formation and self annealing properties were conducted using sequence manipulation suite software (http://www.bioinformatics.org/sms2/pcr_primer_ stats.html). The primers were also tested *in silico* for their ability to amplify the seven aphid species under study. PCR was carried out in a total reaction volume of 20 µl containing 5x My *Taq* Reaction Buffer (Bioline, London, UK) composed of 5 mM dNTPs, 15 mM $MgCl_2$, stabilizers and enhancers, 10 µmole of each primer, 1.25 mM $MgCl_2$, 6.25 units My *Taq* DNA polymerase (Bioline, London, UK) and 15 ng/µl of DNA template. This reaction was set up in an Arktik thermal cycler (Thermo Fisher Scientific Inc., USA) using the following cycling conditions: initial denaturation for 1 min at 95°C, followed by 35 cycles of 15 sec at 95°C, 1 min at annealing temperature of 49.1°C and 1 min at 72°C, then a final elongation step of 10 min at 72°C. Amplified products were analyzed by electrophoresis in 1% agarose gel stained with ethidium bromide. The program NEB cutter V2.0 (New England BioLabs Inc., MA, USA) (http://tools.neb.com/NEBcutter2/index.php) was used to predict the potential restriction sites. Three restriction enzymes; *RsaI, AluI* and *HinfI* were selected based on the size of the resulting fragments and the ability to distinguish the species studied. Restriction digest was done in 18 µl reaction volumes that comprised of 10 µl nuclease-free water, 2 µl fast digest buffer (Thermo Fisher Scientific Inc., USA), 1 µl of restriction enzyme and 5 µl PCR product. PCR products were digested separately and incubation conditions of 37°C for 14 hours, enzyme inactivation at 65°C for 5 min and a hold temperature of 10°C were used. Restriction products were resolved through a 2% agarose gel. Electrophoresis was set at 70V for 90 min, followed by visualization of DNA under ultraviolet (UV) transilluminator in a KETA gel documentation imaging system (Wealtec Corp., Nevada, USA).

3.4 DNA barcode region amplification and sequencing

PCR was done to amplify the barcode region using universal primers; LCO 1490 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO 2198 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer *et al.*, 1994). PCR was carried out in a total reaction volume of 20 µl containing 5x My *Taq* Reaction Buffer ((Bioline, London, UK) composed of 5 mM dNTPs, 15 mM $MgCl_2$, stabilizers and enhancers, 10 µmole of each primer, 1.25 mM $MgCl_2$, 6.25 units My *Taq* DNA polymerase (Bioline, London, UK) and 15ng/µl of DNA template. This reaction was set up in Arktik thermal cycler (Thermo Fisher Scientific Inc., USA) using the following cycling conditions: initial denaturation for 1 min at 95°C, followed by 35 cycles of 15 sec at 95°C, 1 min at annealing temperature of 48.3°C and 1 min at 72°C, then a final elongation step of 10 min at 72°C. The target gene region was approximately 700 bp. Amplified PCR products were resolved through a 1% agarose gel. Electrophoresis was set at 100 volts for 1 hour, followed by visualization of DNA under ultraviolet (UV)-illumination. PCR products were purified using Isolate II PCR and Gel Kit (Bioline, London, UK) according to the manufacturer's instructions. Five purified DNA samples from each population were bi-directionally sequenced using ABI 3730xl DNA sequencer (Applied Biosystems, Foster City, California) at a commercial sequencing facility (Macrogen Inc., Europe).

3.5 Data analysis

Sequences from 175 aphid samples were assembled and edited using Chromas version 2.1.1 (Technelysium Pty Ltd, Queensland, Australia). For conclusive identifications, sequences were queried via basic local alignment search tool (BLAST) at the GenBank database hosted by National Center for Biotechnology Information (NCBI) (http://www.ncbi.nlm.nih.gov/) (Altschul *et al.*, 1990). Megablast (for highly similar sequences) program was used for all the sequences. Alignment was done using MUSCLE v3.8.31 (Edgar, 2004). Unaligned sequence ends were trimmed and gaps removed in Jalview v2.8.2 (Waterhouse *et al.*, 2009). The program jModeltest v2.1.7 (Darriba *et al.*, 2012) was used to determine the appropriate substitution model for phylogenetic analyses. Transition model TIM1+G was selected as the best-fit model by the 4 different criteria (Akaike information criterion (AIC), corrected Akaike information criterion (AICc), Bayesian information criterion (BIC) and decision theory performance-based selection (DT)). Maximum likelihood (ML) estimates were obtained using the TIM1+G model under a general time reversible GTRGAMMA substitution model with 1000 bootstrap replicates in RAxML v8.2.0 (Stamatakis, 2014). Generated trees were viewed and edited in Fig Tree v1.4.2 (http://tree.bio.ed.ac.uk/software/figtree). Genetic divergences were determined at the species, genus and family levels using pairwise distance model as generated by the distance summary tool available in BOLD (http://www.boldsystems.org/). Evolutionary divergence over sequence pairs between groups were estimated using the p-distance model in MEGA 6.0 (Tamura *et al.*, 2013). Molecular clock test was performed by comparing the maximum likelihood (ML) value for the given topology with and without the molecular clock constraints under GTR model (Nei and Kumar, 2000). To further infer relationships among the aphid species, principal component analysis (PCA) was conducted. A table of genetic distances generated by MEGA 6.0 (Tamura *et al.*, 2013) was used to create principal component plots using GenAlEx 6.41 (Peakall and Smouse, 2006). The program DnaSP 5.0 (Librado and Rozas, 2009) was used to analyze DNA polymorphism in the nucleotide sequences within and between populations. In this program, DNA sequence variation generated a haplotype file which was used to construct a phylogenetic network using the haplotype median-joining algorithm in Network 4.6.1.1 (Fluxus Technology Ltd, Suffolk, England). Finally, COI sequences were submitted to the Barcode of Life Data systems (BOLD) database and deposited in GenBank.

CHAPTER FOUR

RESULTS

4.1 Samples collection and DNA extraction

Seven aphid species were collected during the study. These included *Brevicoryne brassicae* (Bb), *Lipaphis pseudobrassicae* (Lp), *Acyrthosiphon pisum*, (Ap), *Aphis gossypii* (Ag), *Aphis craccivora* (Ac), *Aphis fabae* (Af) and *Myzus persicae* (Mp). Genomic DNA was successfully extracted from individual insects belonging to different populations and species. The concentration and purity of DNA at 260/280 wavelengths was on average 15ng/µl and 1.5 respectively.

4.2 PCR-RFLP

In silico restrictions predicted a specific profile for each species except *craccivora* and *A. fabae*. A 1540 bp fragment of COI was amplified from genomic DNA of seven aphid species (Figure 4.1). *In silico* predictions were then confirmed by subjecting the amplicons to restriction digests using three restriction enzymes; *RsaI*, *AluI* and *HinfI*. Restriction products ranged from 1000 to less than 75 bp and fragments less than 100 bp were not considered as diagnostic.

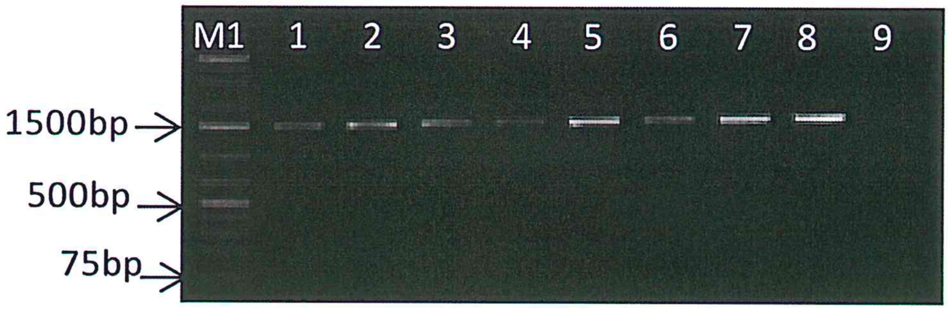


Figure 4.1: Gel showing PCR products of 1540 bp fragment amplified from genomic DNA of seven aphid species

Legend
1% agarose gel, voltage set at 100V for 1 hr
M1: O' Gene Ruler 1 kb Plus DNA ladder
Lane 1: *Aphis gossypii*
Lane 2: *Myzus persicae*
Lane 3: *Lipaphis pseudobrassicae*
Lane 4: *Brevicoryne brassicae*
Lane 5: *Acyrthosiphon pisum*
Lane 6: *Aphis craccivora*
Lane 7: *Aphis fabae* subspecies
Lane 8: *Aphis fabae* subspecies
Lane 9: Negative control

RsaI yielded fragments of ~500 and ~1000 bp for *A. gossypii, M. persicae, B. brassicae* and *A. pisum* (Figure 4.2). However, *RsaI* ruled out *L. pseudobrassicae, A. craccivora* and *A. fabae* (Figure 4.2, lanes 3, 6, 7 and 8).

Figure 4.2: Gel showing PCR-RFLP banding profile of seven aphid species digested using restriction enzyme *RsaI*

Legend
2% agarose gel, voltage set at 70V for 1 hr 30 min
M1: O' Gene Ruler 1 kb Plus DNA ladder

Lane 1: *Aphis gossypii*
Lane 2: *Myzus persicae*
Lane 3: *Lipaphis pseudobrassicae*
Lane 4: *Brevicoryne brassicae*
Lane 5: *Acyrthosiphon pisum*
Lane 6: *Aphis craccivora*
Lane 7: *Aphis fabae* subspecies
Lane 8: *Aphis fabae* subspecies
M2: O' Gene Ruler 100 bp DNA ladder

AluI yielded fragments of ~150, ~250, ~450 and ~550 bp for *A. gossypii* whereas, fragments for *A. pisum* were ~150, ~350, ~400 and ~500 bp (Figure 4.3, lanes 1 and 5). This enzyme also produced fragments of equal sizes for both *L. pseudobrassicae* and *B. brassicae* which were ~150, ~250, ~500 and ~600 bp. For *M. persicae*, *AluI* yielded fragments of ~150, ~300, ~500 and ~600 bp. Finally, *AluI* digestion yielded fragments of ~250, ~500 and ~700 bp for *A. craccivora* and *A. fabae* and could not therefore discriminate between the two species (Figure 4.3, lanes 6, 7 and 8).

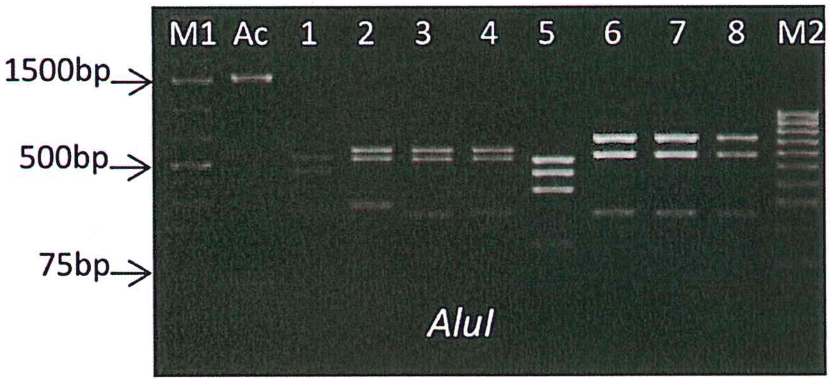


Figure 4.3: Gel showing PCR-RFLP banding profile of seven aphid species digested using restriction enzyme *AluI*

Legend
2% agarose gel, voltage set at 70V for 1 hr 30 min
M1: O' Gene Ruler 1 kb Plus DNA ladder
Lane 1: *Aphis gossypii*
Lane 2: *Myzus persicae*
Lane 3: *Lipaphis pseudobrassicae*
Lane 4: *Brevicoryne brassicae*
Lane 5: *Acyrthosiphon pisum*
Lane 6: *Aphis craccivora*
Lane 7: *Aphis fabae* subspecies
Lane 8: *Aphis fabae* subspecies
M2: O' Gene Ruler 100 bp DNA ladder

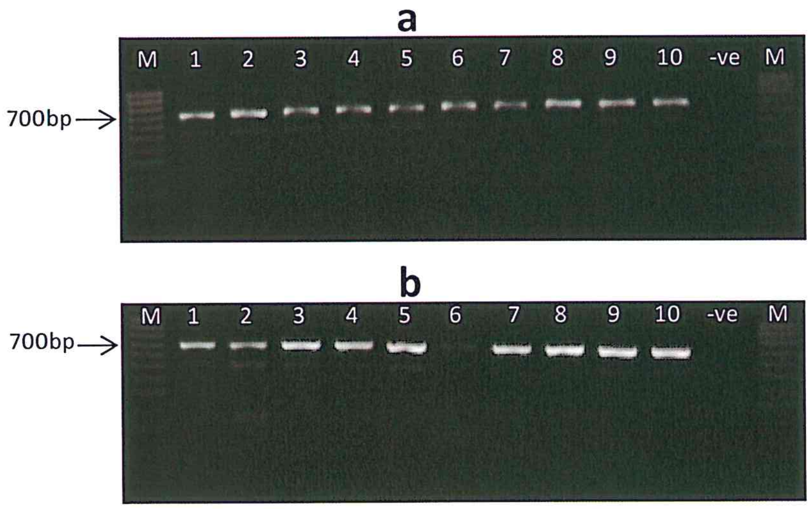
Digestion of *A. gossypii* using *HinfI* resulted in fragments of ~300, ~450 and ~600 bp, while those of *M. persicae* were ~100, ~200, ~300 and ~1000 bp (Figure 4.4, lanes 1 and 2). *HinfI* produced fragments of ~250, ~400 and ~500 bp for *L. pseudobrassicae* whereas those of *B. brassicae* were ~300, ~400 and ~1250 bp (Figure 4.4, lanes 3and 4). Finally, *HinfI* digestion of *A. pisum* yielded fragments of ~200, ~500 and ~700 bp. However, it was quite a challenge to distinguish between *A. craccivora* and *A. fabae* because they yielded fragments of equal sizes (250, 400 and 1000 bp) upon digestion with *HinfI* enzyme (Figure 4.4, lanes 6, 7 and 8).

Figure 4.4: Gel showing PCR-RFLP banding profile of seven aphid species digested using restriction enzyme *HinfI*

Legend
2% agarose gel, voltage set at 70V for 1 hr 30 min
M1: O' Gene Ruler 1 kb Plus DNA ladder
Lane 1: *Aphis gossypii*
Lane 2: *Myzus persicae*
Lane 3: *Lipaphis pseudobrassicae*
Lane 4: *Brevicoryne brassicae*
Lane 5: *Acyrthosiphon pisum*
Lane 6: *Aphis craccivora*
Lane 7: *Aphis fabae* subspecies
Lane 8: *Aphis fabae* subspecies
M2: O' Gene Ruler 100 bp DNA ladder

4.3 PCR amplification of the DNA barcode region

The COI gene region (~700 bp) was amplified between species and across regions (Figure 4.5). Species such as *Lipaphis pseudobrassicae*, *Aphis gossypii* and *Aphis craccivora* consistently yielded good amplicons while others like *Myzus persicae, Aphis fabae* and *Acyrthosiphon pisum* yielded faint bands. PCR amplification of *Brevicoryne brassicae* samples yielded good results for many regions with few exceptions for samples collected from Nairobi and Kajiado.



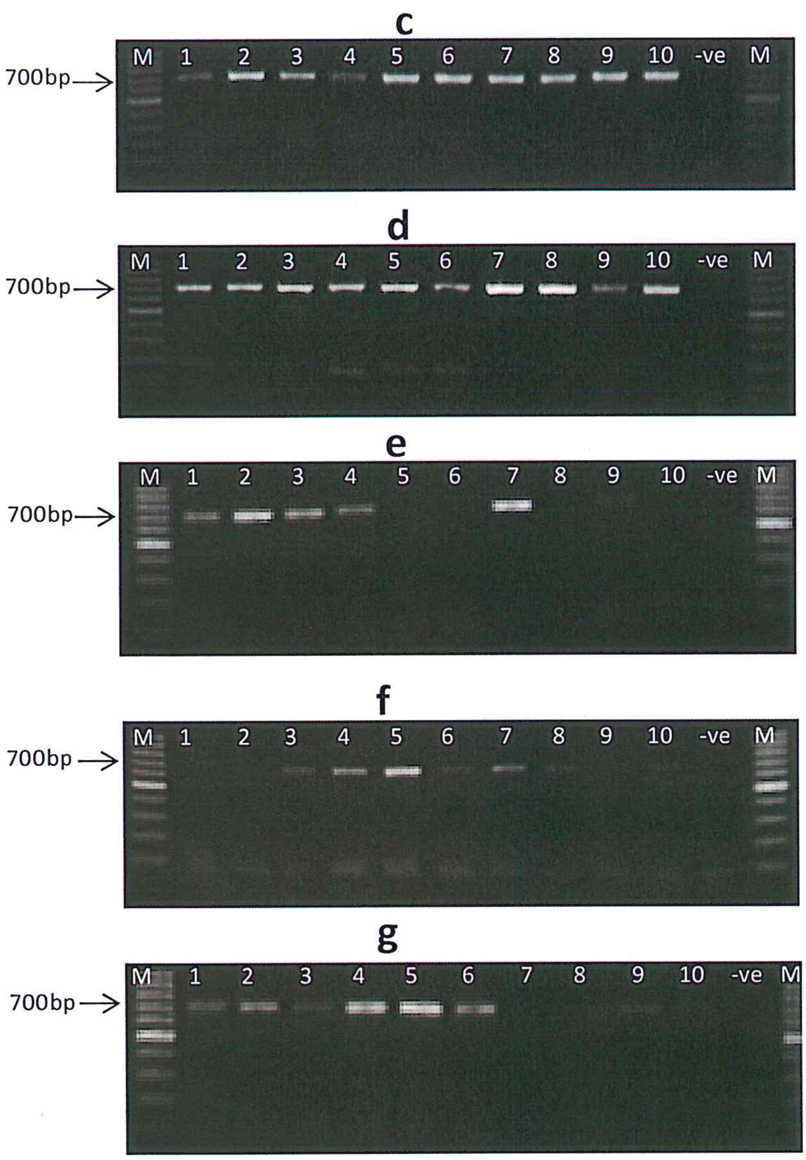


Figure 4.5: Representative gels of PCR products of mitochondrial COI gene region of seven aphid species amplified using LCO 1490 and HCO 2198 primers

Legend
1% agarose gel electrophoresis, voltage set at 100 volts for 1 hour
Gel a: *Aphis gossypii* from Kajiado
Gel b: *Lipaphis pseudobrassicae* from Kajiado
Gel c: *Brevicoryne brassicae* from Taita-Taveta
Gel d: *Aphis craccivora* from Taita-Taveta
Gel e: *Aphis fabae* from Nyeri
Gel f: *Acyrthosiphon pisum* from Nyeri
Gel g: *Myzus persicae* from Nairobi
M: 100 bp O'GeneRuler DNA ladder (Thermo Scientific)
Lanes 1-10 are samples analyzed
–ve: Negative control

4.4 BLAST analysis

A total of 175 consensus sequences (Appendix II) obtained by amplification of the COI gene region were analyzed. BLAST hits between sequence dataset and those from the NCBI Genbank database displayed a high percentage identity ranging from 99 to 100% as well as an E-value of 0.00, thus, revealing a high degree of sequence homology (Appendix III). In addition, sequences deposited in GenBank were given accession numbers KR084990- KR085164 (Table 4.1).

Table 4.1: Collection data of aphid samples used in this study with species name, host plant, global positioning system (GPS) coordinates of the sampling locations and GenBank accession numbers

Species name	Sample name	Host plant	Coordinates	GenBank Accession numbers
Aphis gossypii	Ag1-Ag5	Okra	S4°22'32.94" E39°31'57.29"	KR085019, KR085018, KR085017, KR085016, KR085015
Aphis gossypii	Ag6-Ag10	Okra	S2°23'33.1" E37°59'49.1"	KR085020, KR085021, KR085022, KR085023, KR085024
Aphis gossypii	Ag11-Ag15	Okra	S1°48'22.1" E36°03'41.2"	KR085025, KR085026, KR085027, KR085028, KR085029
Aphis gossypii	Ag16-Ag19	Okra	S1°13'14.59" E36°53'43.73"	KR085030, KR085031, KR085032, KR085033
Brevicoryne brassicae	Bb1-Bb5	Kale	N0°02'15.98" E36°21'40.59"	KR085076, KR085075, KR085034, KR085074, KR085073
Brevicoryne brassicae	Bb6-Bb10	Kale	S0°30'42.09" E36°19'21.30"	KR085072, KR085071, KR085070, KR085069, KR085068
Brevicoryne brassicae	Bb11-Bb15	Cabbage	S0°37'27.19" E36°22'42.60"	KR085067, KR085066, KR085065, KR085064, KR085063
Brevicoryne brassicae	Bb16-Bb20	Kale	S0°17'06.11" E36°04'52.08"	KR085062, KR085061, KR085060, KR085059, KR085058
Brevicoryne brassicae	Bb21-Bb25	Kale	N0°00'01.78" E36°13'51.88"	KR085057, KR085056, KR085055, KR085054, KR085053
Brevicoryne brassicae	Bb26-Bb30	Kale	S0°50'46.05" E34°09'20.29"	KR085052, KR085051, KR085050, KR085049, KR085048
Brevicoryne brassicae	Bb31-Bb35	Kale	S1°09'03.16" E36°57'33.75"	KR085047, KR085046, KR085045, KR085044, KR085043
Brevicoryne brassicae	Bb36-Bb40	Cabbage	S1°04'37.98" E36°37'12.39"	KR085042, KR085041, KR085040, KR085039, KR085038
Brevicoryne brassicae	Bb41-Bb45	Cabbage	S3°22'41.20" E38°20'14.86"	KR085037, KR085036, KR085035, KR085122, KR085121
Brevicoryne brassicae	Bb46-Bb49	Kale	S1°48'22.1" E36°03'41.2"	KR085120, KR085119, KR085118, KR085117
Brevicoryne brassicae	Bb50, Bb80, Bb81, Bb86, Bb87	Kale	S1°26'13.30" E36°41'06.06"	KR085116, KR085086, KR085085, KR085080, KR085079
Brevicoryne brassicae	Bb51-Bb54, Bb66	Kale	S0°04'20.29" E37°07'42.99"	KR085115, KR085114, KR085113, KR085112, KR085100
Brevicoryne brassicae	Bb61-Bb65	Kale	N0°47'30.91" E34°26'40.42"	KR085105, KR085104, KR085103, KR085102, KR085101
Brevicoryne brassicae	Bb67-Bb71	Kale	S0°28'36.10" E37°34'59.84"	KR085099, KR085098, KR085097, KR085096, KR085095
Brevicoryne	Bb55, Bb82,	Kale	S1°13'14.59"	KR085111, KR085094, KR085093,

Species name	Sample name	Host plant	Coordinates	GenBank Accession numbers
brassicae	Bb72-Bb74		E36°53'43.73"	KR085092, KR085084
Brevicoryne brassicae	Bb56, Bb57, Bb75- Bb77	Kale	S2°23'11.20" E38°00'14.20"	KR085110, KR085109, KR085091, KR085090, KR085089
Brevicoryne brassicae	Bb58-Bb60, Bb78, Bb79	Kale	S0°21'10.69" E37°5'14.35"	KR085108, KR085107, KR085106, KR085088, KR085087
Brevicoryne brassicae	Bb83-Bb85, Bb88, Bb89	Kale	S1°12'56.82" E36°53'47.73"	KR085083, KR085082, KR085081, KR085078, KR085077
Lipaphis pseudobrassicae	Lp1-Lp5	Kale	S1°10'12.85" E36°54'09.88"	KR085144, KR085143, KR085142, KR085141, KR085140
Lipaphis pseudobrassicae	Lp6-Lp10	Kale	S1°39'41.32" E37°26'56.78"	KR085139, KR085138, KR085137, KR085136, KR085135
Lipaphis pseudobrassicae	Lp11-Lp15	Kale	S0°37'27.19" E36°22'42.60"	KR085134, KR085133, KR085132, KR085131, KR085130
Lipaphis pseudobrassicae	Lp16-Lp18	Kale	S1°09'03.16" E36°57'33.75"	KR085129, KR085128, KR085127
Lipaphis pseudobrassicae	Lp19-Lp23	Kale	S0°28'27.95" E37°34'49.23"	KR085126, KR085125, KR085124, KR085152, KR085153
Lipaphis pseudobrassicae	Lp24-Lp28	Kale	S1°13'14.59" E36°53'43.73"	KR085154, KR085155, KR085156, KR085157, KR085158
Lipaphis pseudobrassicae	Lp29-Lp33	Kale	S1°12'56.82" E36°53'47.73"	KR085159, KR085148, KR085149, KR085150, KR085151
Lipaphis pseudobrassicae	Lp34-Lp37	Kale	S1°48'22.1" E36°03'41.2"	KR085123, KR085145, KR085146, KR085147
Aphis craccivora	Ac1-Ac5	Cowpeas	S3°16'8.3" E37°44'17.7"	KR084997, KR085001, KR085002, KR085003, KR085004
Aphis craccivora	Ac6-Ac10	Cowpeas	S1°13'25.5" E36°53'50.5"	KR084999, KR084998, KR085000, KR084996, KR084995
Aphis fabae	Af1-Af5	Rose coco beans	S0°21'10.69" E37°5'14.35"	KR085014, KR085013, KR085012, KR085011, KR085010
Aphis fabae	Af6-Af10	Black nightshade	S1°13'14.59" E36°53'43.73"	KR085009, KR085008, KR085007, KR085006, KR085005
Myzus persicae	Mp1-Mp5	Cabbage	S1°13'14.59" E36°53'43.73"	KR085160, KR085161, KR085162, KR085164, KR085163
Acyrthosiphon pisum	Ap1-Ap5	Garden peas	S0°21'11.30" E37°5'20.18"	KR084994, KR084993, KR084992, KR084991, KR084990

4.5 Sequence analysis of DNA barcodes

Genetic sequence divergences were analyzed at the species, genus and family level, and as expected genetic divergences increased with higher taxonomic levels.

Sequence divergence within species ranged from 0% to 1.04% with an average of 0.08% (Table 4.2) and all species displayed intra specific genetic distances of less than 2%. Mean sequence divergence between species of the same genus was 6.63%, with a range of 5.67% to 7.91% and comparison of all species pair revealed that all species showed genetic distances greater than 2%. The sequence divergence between different genera of the same family ranged from 5.01% to 9.89% with a mean of 6.90%. Therefore, there was a significant barcode gap which clearly separated species from each other.

Table 4.2: Genetic sequence divergence of mitochondrial COI gene region between different taxonomic levels of Aphididae as determined using pairwise distance model

	n	Taxa	Comparisons	Min Dist (%)	Mean Dist (%)	Max Dist (%)	SE Dist (%)
Within Species	175	7	4863	0	0.08	1.04	0
Within Genus	39	1	480	5.67	6.63	7.91	0
Within Family	175	1	9882	5.01	6.90	9.89	0

Less interspecific divergences were found between *L. pseudobrassicae* and *B. brassicae* (0.052) whereas *M. persicae* and *A. craccivora* were the most genetically divergent species (0.098) as determined using p-distance model in Mega 6.0 (Tamura *et al*., 2013) (Table 4.3). Also noted was the close distance between *A. pisum* and *B. brassicae* with a value of 0.060. In addition, *A. fabae* was shown to be genetically close to *A. gossypii* and *A. craccivora* with distances of 0.061 and 0.062, respectively.

Table 4.3: Estimates of evolutionary divergence of mitochondrial COI gene region over sequence pairs between groups

	Ag	Ac	Af	Bb	Lp	Ap	Mp
Ag	0						
Ac	0.077	0					
Af	0.061	0.062	0				
Bb	0.075	0.086	0.077	0			
Lp	0.074	0.088	0.085	**0.052**	0		
Ap	0.089	0.078	0.085	0.060	0.071	0	
Mp	0.089	**0.098**	0.088	0.083	0.085	0.089	0

Ag - *Aphis gossypii*, Ac - *Aphis craccivora*, Af - *Aphis fabae*, Bb - *Brevicoryne brassicae*, Lp - *Lipaphis pseudobrassicae*, Ap - *Acyrthosiphon pisum* and Mp - *Myzus persicae.* Numbers in bold indicate the lowest (Lp and Bb) and the highest (Mp and Ac) values between the species.

Mean nucleotide frequencies were T=0.4377, A=0.3440, C=0.1149 and G=0.1035, with a bias towards thymine and adenine composition and no stop codons were observed within the sequences.

4.6 Phylogenetic analyses

Evolutionary analyses generated by Mega 6 program (Tamura *et al.*, 2013) showed that all sequences fulfilled the molecular clock hypothesis. Two log-likelihood values were calculated and displayed, one with (-1751.249) and one without (-

1747.630) the clock hypothesis as shown in table 4.4. The value without the clock hypothesis will always be larger than the value with the null hypothesis. The molecular clock null hypothesis of equal evolutionary rate throughout the tree was not rejected at a 5% significance level (P= 1).

Table 4.4: Results from a test of molecular clocks using the Maximum Likelihood method of COI sequences of aphids

	In*L*	**Parameters**	**(+*G*))**	**(+*I*)**
With Clock	-1751.249	182	n/a	n/a
Without Clock	-1747.630	355	n/a	n/a

A phylogenetic tree was generated from 175 samples belonging to different populations and different species. The tree separated into two major groups that were supported by high bootstrap values of 92% (Figure 4.6). The first group had the clustering of *Aphis* species, in which *A. gossypii* formed a sister group with strong support of 92% bootstrap value with the cluster containing the 2 clades of *A. craccivora* and *A. fabae*. The second group had the clustering of 4 species with robust support of 100% bootstrap values. *L. pseudobrassicae* and *B. brassicae* branched from the same node whereas; *M. persicae* formed a clade with *A. pisum*. Negative log likelihood (-InL) was 1751.1144 and ML estimate of the gamma shape parameter was 0.0820. The tree was drawn to scale, and the branch lengths were denoted by the rate of substitution per nucleotide position. Aphid samples of *B. brassicae* were collected from 18 different regions in twelve counties namely, Bungoma, Embu, Kajiado, Kiambu, Laikipia, Makueni, Migori, Nairobi, Nakuru, Nyandarua, Nyeri and Taita-Taveta (Table 4.1). Some samples were collected from cabbage and others from kale (Brassicaceae). It was noted that these populations clustered together in a single group irrespective of their host plants and geographic locations. Also, there was no clustering associated with sampling localities for populations of *L. pseudobrassicae, A. gossypii* and *A. craccivora* collected from kale, okra and cowpea respectively. For instance, sequences of *L. pseudobrassicae* samples collected from Embu, Kiambu, Makueni, Nairobi, Nakuru and Kajiado formed a single cluster. Similarly, sequences of *A. gossypii* samples collected from Kajiado, Kwale, Makueni and Nairobi were clustered together while *A. craccivora* samples from Nairobi and Taita-Taveta formed a single group. This clustering could suggest existence of a single genetically uniform population within these species. There were two populations of *A. fabae* collected from rose coco beans in Nyeri and black night shade in Nairobi. These populations clustered into two clades based on their host plant affiliations. A population of *M. persicae* was collected from cabbage in Nairobi while *A. pisum* was collected from garden peas in Nyeri.

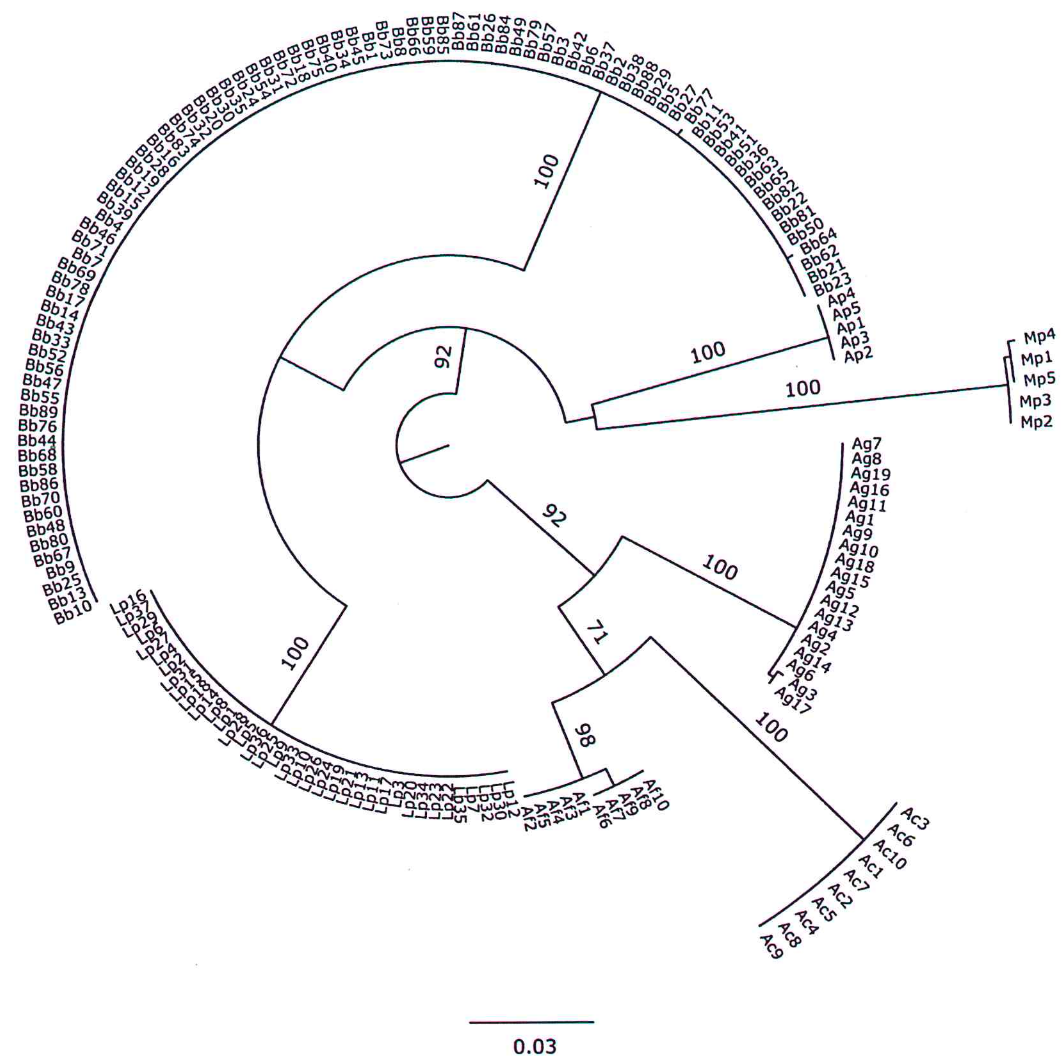


Figure 4.6: Maximum likelihood tree inferred from COI sequences of 175 samples using TIM1+G model of molecular evolution under GTRGAMMA model for 7 aphid species. Support values designated at the nodes (next to the branches) represent percentage bootstrap values after 1000 replications. Bootstrap values less than 50% are not indicated

PCA plot separated the species into 7 distinct clusters (Figure 4.7). The first and second principal coordinates contributed to 47.19% of the total variance (coordinate 1=25.91 and coordinate 2=21.28). The cluster belonging to *B.*

brassicae was shown to be much closer to the cluster consisting of *L. pseudobrassicae* than it was to the cluster consisting of *A. pisum*. *M. persicae* formed a cluster that was distantly related from the other species. Consistently, the PCA results revealed a close relationship between *A. fabae, A. craccivora* and *A. gossypii*.

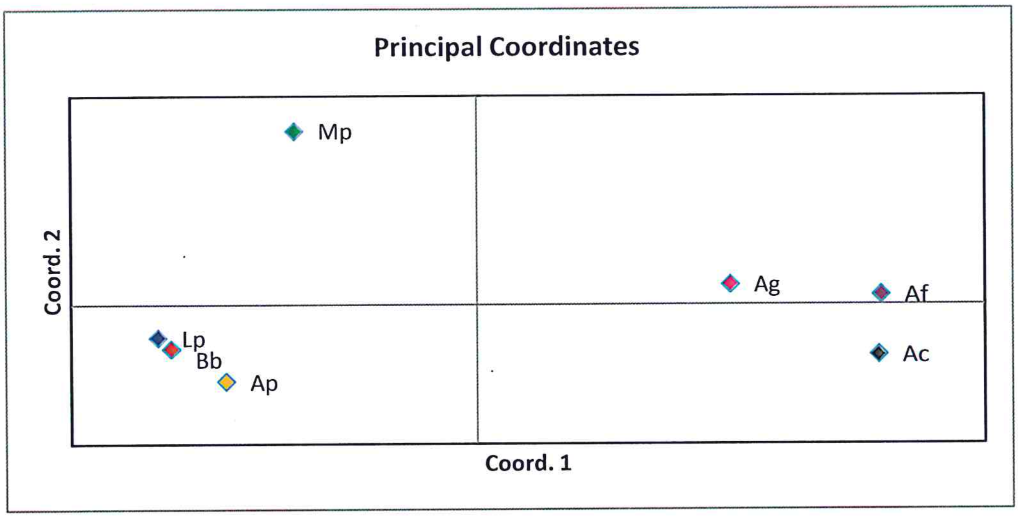


Figure 4.7: Plots of principal component analysis (PCA) for seven aphid species as calculated using GenAlEx

Eight distinct haplotypes were detected among the 7 aphid species with a haplotype diversity, Hd =0.6822 (Figure 4.8). All sites containing gaps and missing data were excluded. There were a total of 650 sites in the final dataset and the number of variable sites was 122. The size of the branch in the network was proportional to the number of mutations that occurred. *Aphis craccivora* and *A. fabae* diverged from the same median vector, suggesting a close relationship between these species. Moreover, *A. craccivora, A. fabae* and *A. gossypii* were found to be related as they all split from a common median vector. The two sub groups of *A. fabae* were distinctly clustered, confirming the results obtained from the phylogenetic tree. Also, a close relationship was confirmed between *B. brassicae* and *L. pseudobrassicae*, whose median vectors split from a common median vector. Finally, it was observed that *A. pisum* and *M. persicae* formed separate clusters which were derived from the central median vectors independently.

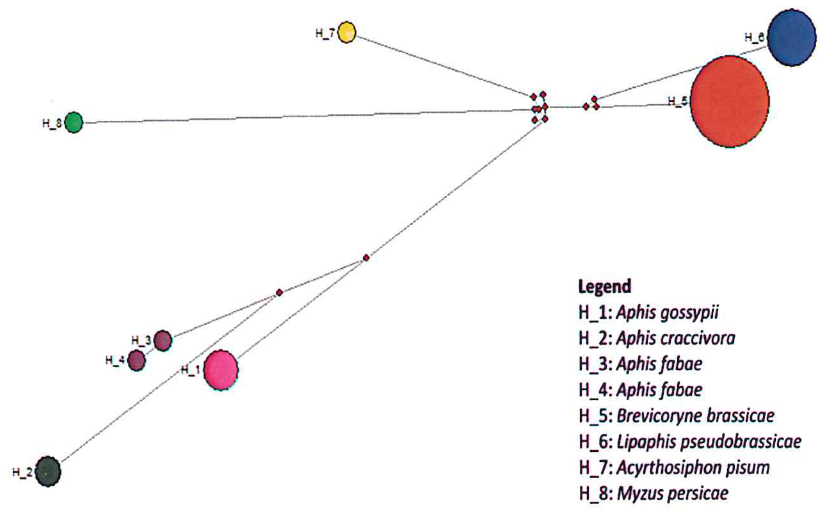


Figure 4.8: Phylogenetic network showing evolutionary relationships among 7 aphid species. The coloured full nodes represent the sampled sequences and the size of each node is proportional to the corresponding haplotype (sequence) frequency. The small empty nodes represent the median vectors

CHAPTER FIVE

GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

5.1 GENERAL DISCUSSION

Molecular markers have been successfully employed as reliable tools for identification of species within the family Aphididae (Valenzuela *et al.*, 2007; Foottit *et al.*, 2008; Helmi *et al.*, 2011; Lee *et al.*, 2011; Naaum *et al.*, 2012). In this study, RFLP markers were first developed from the COI region to detect sequence variation among seven aphid species found in Kenya. DNA barcoding was also used to discriminate the species and analyze the genetic variation within and between species.

Restriction enzymes *RsaI, AluI* and *HinfI* exhibited varying banding patterns that gave informative results for all the species and corresponded to their respective *in silico* predictions. For instance, the results clearly indicated that restriction sites of *RsaI* did not exist in the COI region of *L. pseudobrassicae, A. craccivora* and *A. fabae.* In addition, *AluI* profile allowed accurate discrimination of three species, namely *A. gossypii*, *M. persicae* and *A. pisum* while *HinfI* differentiated all the species except *A. craccivora* and *A. fabae*. Considering that several restriction enzymes are required for accurate species identifications (Pereira *et al.*, 2008), this study combined three restriction enzymes to produce a profile that could serve as a molecular diagnostic key for the target species. Analysis of PCR-RFLP also revealed a close relationship between *A. craccivora* and *A. fabae* which were indistinguishable based on the size of the scorable fragments.

For DNA barcoding, COI sequences retrieved from 175 aphid samples gave a high resolution of the species and two subspecies of *A. fabae*. These results agree with previous studies carried out in Europe, North America, Korea and India that demonstrated DNA barcoding based on COI gene as a potentially useful tool for identification of species within Aphididae (Foottit *et al.*, 2008; Lee *et al.*, 2011; Rebijith *et al.*, 2013; Coeur d'acier *et al.*, 2014). Also, by providing quantitative data with sequence divergence and bootstrap values as a measure of reliability (Armstrong and Ball, 2005), DNA barcoding presented a more accurate and robust approach towards separation of the aphid species and defining their identity as compared to PCR-RFLP. Also noted was that DNA barcode-based analyses were quick, easier to perform and interpret, allow all sequence data to be observed at a glance and applicable to large samples as compared to RFLP.

Virgilio *et al.* (2010) reported that intraspecific sequence divergences of DNA barcodes belonging to 1,995 insect species ranged from 0.0% to 7.64% and aphids were reported to lie at the lower ranges. In this study, the mean intraspecific sequence divergence obtained was as low as 0.08% and is therefore within the ranges reported by previous authors. COI sequence divergences among species can vary among different groups of animals ranging from of 0.0% to 53.7% among 13,320 species pairs (Hebert *et al.*, 2003b). The mean interspecific sequence divergence observed in the study was 6.63%, and significantly greater than the mean intraspecific divergence. This created a substantial barcode gap that enabled accurate discrimination of all the species. These results are within the expected limits and fall within the range of variation exhibited in previous studies within Aphididae (Foottit *et al.*, 2008; Foottit *et al.*, 2009; Lee *et al.*, 2011; Wang *et al.*, 2011) and demonstrate that COI DNA barcode region is a reliable marker for separating aphid species. Clustering of species on the phylogenetic tree was in accordance with the results obtained from the PCA plot and phylogenetic network. Moreover, the close relationship between *B. brassicae* and *L. pseudobrassicae* and between *A. gossypii*, *A. craccivora* and *A. fabae* was confirmed.

Molecular clock null hypothesis asserts that the rate of evolutionary change of any specified DNA or protein sequence is constant over time and over different evolutionary lineages (Bromham and Penny, 2003). Thus, all taxa sharing a common ancestor should have accumulated same number of base substitutions since they diverged (Perez-Brocal *et al.*, 2011). All sequences used in the study did not reject the molecular clock null hypothesis. In this case, they were used to reveal the phylogenetic relationships between the species and all tips of the phylogenetic tree were equidistant from the root of the tree. Clades belonging to *B. brassicae*, *L. pseudobrassicae, A. craccivora* and *A. gossypii* consisted of populations collected from different localities in Kenya. COI barcodes revealed that no genetic variation existed between populations belonging to the same species, despite different geographical locations as they were all grouped together within a cluster. Genetic uniformity was also observed among populations of *B. brassicae* collected from kale and cabbage. These results concur with previous studies on aphid species in the family Lamiaceae and *Brachycaudus helichrysi* Kaltenbach, where the clustering of populations was not related to their geographic locations (Piffaretti *et al.*, 2012; Cocuzza and Cavalieri 2014). Genetic uniformity has also been observed in the genus *Hyalopterus* Koch, where populations of each species clustered together irrespective of widespread geographical sampling (Lozier *et al.*, 2008). Similarly, COI sequences belonging to *A. gossypii* and *M. persicae* which are both cosmopolitan and highly polyphagous species revealed that there was no significant genetic variation among populations collected from different geographical locations and different host plants (Rebijith *et al.*, 2012).

The great morphological similarity between *Aphis craccivora* and *A. fabae* makes it very difficult to separate them based on morphological characters. However, previous studies have presented DNA barcoding as a very useful tool in separation of these species (Coeur d'acier *et al.*, 2007; Lee *et al.*, 2011). In this study, not only were the species identified, but DNA barcoding was able to reveal that both aphids are sister species in a clade that also formed a sister group relationship with *A. gossypii*. This relationship is also evident in the PCA plot and the median joining haplotype network, where the three species formed neighbouring clusters. DNA barcoding also distinctly separated two subgroups of *A. fabae* collected from black nightshade (*Solanum nigrum* L.) and rose coco beans (*Phaseolus vulgaris* L.). All sequences of *A. fabae* displayed very high BLAST hits between 99 to

100% with a Genbank sequence assigned to the same species. However, these results could not separate the two subgroups and only tended to be diagnostic at the species level. It has been reported that *A. fabae* species constitutes a complex of six morphologically inseparable subspecies, whose identification is based on host plants affiliations (Zhang *et al.*, 2010). Clustering of study sequences of *A. fabae* into 2 subspecies agrees with a previous study that distinctly clustered the species into four highly supported subspecies (Coeur d'acier *et al.*, 2007). These results were further confirmed by the phylogenetic network, which positioned the two subspecies as distinct haplotypes with a very close relationship.

Complex life cycles of aphids associated with parthenogeneticity and polymorphism including colour morphs, winged, unwinged, sexual and asexual morphs is a common trait among aphids (Foottit *et al.*, 2008). In the study, no genetic variation was observed in the DNA barcodes obtained from samples with morphological variations including the yellow and black morphs of *A. gossypii.* Based on these results, it can be concluded that morphological variations that occur among species populations in response to environmental factors and host plant effects are not reflected in their genetic makeup. The immature stages of the various aphid species must be reared to adult stages to allow for morphological identification – a process that is laborious and time consuming. The current study has shown that both PCR-RFLP and DNA barcoding could be used reliably for the identification of immature stages, different morphs and various life stages within a species (Valenzuela *et al.*, 2007; Foottit *et al.*, 2009; Shufran and Puterka, 2011).

5.2 CONCLUSION

In this study, RFLP markers were developed for the identification of five aphid species, which are among the most damaging pests of vegetables in Kenya. These include *Aphis gossypii*, *Myzus persicae*, *Acyrthosiphon pisum*, *Lipaphis pseudobrassicae* and *Brevicoryne brassicae*. However, restriction enzymes *RsaI*, *AluI* and *HinfI* could not separate *Aphis craccivora* and *A. fabae* and this revealed that these two species were closely related. Also, PCR-RFLP analysis could not detect any intrapopulation variation in *A. fabae*.

DNA barcoding enabled characterization of the seven species including two subspecies of *A. fabae*. Phylogenetic tree clustered the species on separate clades and showed that *Aphis craccivora* was closely related to *A. fabae*. DNA sequences generated in this study will contribute to the growing database of reference barcodes for future identifications of the target species. In a principal component analysis, the first and second principal coordinates accounted for 47.19% of the total variation and separated the seven species into seven distinct clusters. Phylogenetic network also separated the seven aphid species into distinct haplotypes and confirmed the presence of two subspecies of *A. fabae*.

Sequence analyses of COI gene revealed high degree of genetic uniformity among populations belonging to the same species, despite being collected from different geographical locations in Kenya.

5.3 RECOMMENDATIONS

1. Both PCR-RFLP and DNA barcoding provide quick and accurate tools for identification of aphid species and could therefore be adapted for quick pest diagnostics in the Kenyan phytosanitary systems.
2. Extensive sampling is needed in future studies in order to generate a more comprehensive and resourceful barcode database for aphid species in Kenya. This should include increasing both sample species and geographical coverage.
3. Additional work is also necessary to investigate the occurrence of different subspecies of *A. fabae* on different host plants.
4. Although analyses of COI sequences revealed no genetic variation among Kenyan populations, other genetic markers such as microsatellites should be used to study the population genetic variability within and between aphid species.

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APPENDICES

Appendix I: Proteinase K buffer's contents

Proteinase K buffer (10x), 50 ml

To 48.2 ml of distilled water, the following reagents were added:

i. 1250 µl 1M KCl
ii. 500 µl 1M Tris - HCl (pH 9.0, at 25°C)
iii. 50 µl Triton - X - 100

For 1x Proteinase K buffer, 1 part of the 10x buffer was added to 9 parts of distilled water and stored at - 20°C.

Appendix II: Consensus sequences obtained by amplification of the mtCOI gene region

>Ag1
ATAAAGATATTGGAACTTTATATTTTTATTTGGTATTTGATCAGGTAT
AATTGGTTCTTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATT
AATTCAATTATTAATAATAATCAATTATATAATGTAATTGTTACAATTC
ATGCTTTTATTATAATTTTTTTATAACTATACCAATCGTTATTGGAGGT
TTTGGAAATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTT
TTCCACGACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAAT
AATAATAATTTGCAGATTTATAATTAATAACGGAACAGGAACAGGATG
AACTATTTATCCACCTTTATCAAATAATATTGCTCATAATAATATTTCA
GTAGACTTAACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTT
AGGAGCAATTAATTTCATCTGTACTATCTTAAATATAATACCTAATAAT
ATAAAATTAAATCAAATTCCTCTATTTCCATGATCAATTTTAATTACAG
CTATATTATTAATTTTATCCTTACCTGTATTAGCTGGTGCTATTACTATA
TTATTAACAGATCGAAATTTAAATACATCATTTTTTGATCCAGCAGGTG
GGGGAGACCGCTATTCTTTATCAACATTTATTTT
>Ag2
ATTGGAACTTTATATTTTTATTTGGTATTTGATCAGGTATAATTGGTTC
TTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATTAATTCAATT
ATTAATAATAATCAATTATATAATGTAATTGTTACAATTCATGCTTTTA
TTATAATTTTTTTATAACTATACCAATCGTTATTGGAGGTTTTGGAAAT
TGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTTTCCACGAC
TAAATAATATTAGATTCTGATTATTACCACCCTCATTAATAATAATAAT
TTGCAGATTTATAATTAATAACGGAACAGGAACAGGATGAACTATTTA
TCCACCTTTATCAAATAATATTGCTCATAATAATATTTCAGTAGACTTA
ACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTTAGGAGCAA
TTAATTTCATCTGTACTATCTTAAATATAATACCTAATAATATAAAATT
AAATCAAATTCCTCTATTTCCATGATCAATTTTAATTACAGCTATATTAT
TAATTTTATCCTTACCTGTATTAGCTGGTGCTATTACTATATTATTAACA
GATCGAAATTTAAATACATCATTTTTTGATCCAGCAGGTGGGGGAGAC
CGCTATTCTTTATCAACATTTATTT
>Ag3
AATATTGGAACTTTATATTTTTATTTGGTATTTGATCAGGTATAATTGG
TTCTTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATTAATTCA
ATTATTAATAATAATCAATTATATAATGTAATTGTTACAATTCATGCTT
TTATTATAATTTTTTTATAACTATACCAATCGTTATTGGAGGTTTTGGA
AATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTTTCCAC
GACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAATAATAAT
AATTTGCAGATTTATAATTAATAACGGAACAGGAACAGGATGAACTAT
TTATCCACCTTTATCAAATAATATTGCTCATAATAATATTTCAGTAGAC

TTAACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTTAGGAGC
AATTAATTTCATCTGTACTATCTTAAATATAATACCTAATAATATAAAA
TTAAATCAAATTCCTCTATTTCCATGATCAATTTTAATTACAGCTATATT
ATTAATTTTATCCTTACCTGTATTAGCTGGTGCTATTACTATATTATTAA
CAGATCGAAATTTAAATACATCATTTTTTGATCCAGCAGGTGGGGGAG
ACCCGTATTCTTTATCAAACATTTATTT
>Ag4
TATTGGAACTTTATATTTTTTATTTGGTATTTGATCAGGTATAATTGGTT
CTTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATTAATTCAAT
TATTAATAATAATCAATTATATAATGTAATTGTTACAATTCATGCTTTT
ATTATAATTTTTTTTATAACTATACCAATCGTTATTGGAGGTTTTGGAA
ATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTTTCCACG
ACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAATAATAATA
ATTTGCAGATTTATAATTAATAACGGAACAGGAACAGGATGAACTATT
TATCCACCTTTATCAAATAATATTGCTCATAATAATATTTCAGTAGACT
TAACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTTAGGAGC
AATTAATTTCATCTGTACTATCTTAAATATAATACCTAATAATATAAAA
TTAAATCAAATTCCTCTATTTCCATGATCAATTTTAATTACAGCTATATT
ATTAATTTTATCCTTACCTGTATTAGCTGGTGCTATTACTATATTATTAA
CAGATCGAAATTTAAATACATCATTTTTTGATCCAGCAGGTGGGGGAG
ACCGCTATTCTTTATCAACATTTATTT
>Ag5
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GGTTCTTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATTAATT
CAATTATTAATAATAATCAATTATATAATGTAATTGTTACAATTCATGC
TTTTATTATAATTTTTTTTATAACTATACCAATCGTTATTGGAGGTTTTG
GAAATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTTTCC
ACGACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAATAATA
ATAATTTGCAGATTTATAATTAATAACGGAACAGGAACAGGATGAACT
ATTTATCCACCTTTATCAAATAATATTGCTCATAATAATATTTCAGTAG
ACTTAACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTTAGGA
GCAATTAATTTCATCTGTACTATCTTAAATATAATACCTAATAATATAA
AATTAAATCAAATTCCTCTATTTCCATGATCAATTTTAATTACAGCTAT
ATTATTAATTTTATCCTTACCTGTATTAGCTGGTGCTATTACTATATTAT
TAACAGATCGAAATTTAAATACATCATTTTTTGATCCAGCAGGTGGGG
GAGACCCTATTCTTTATCAACATTT
>Ag6
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TTAGAATTTTAATCCGATTAGAATTAAGTCAAATTAATTCAATTATTAA
TAATAATCAATTATATAATGTAATTGTTACAATTCATGCTTTTATTATA
ATTTTTTTTATAACTATACCAATCGTTATTGGAGGTTTTGGAAATTGATT
AATTCCTATAATAATAGGATGTCCAGATATATCTTTTCCACGACTAAAT
AATATTAGATTCTGATTATTACCACCCTCATTAATAATAATAATTTGCA
GATTTATAATTAATAACGGAACAGGAACAGGATGAACTATTTATCCAC

CTTTATCAAATAATATTGCTCATAATAATATTTCAGTAGACTTAACTAT
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AATTCCTCTATTTCCATGATCAATTTTAATTACAGCTATATTATTAATTT
TATCCTTACCTGTATTAGCTGGTGCTATTACTATATTATTAACAGATCG
AAATTTAAATACATCATTTTTTGATCCAGCAGGTGGGGGAGACCCTATT
CTTTATCAACATTTATTGTT
>Ag7
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AATTGGTTCTTCTCTTAGAATTTTAATCCGATTAGAATTAAGTCAAATT
AATTCAATTATTAATAATAATCAATTATATAATGTAATTGTTACAATTC
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TTTGGAAATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTT
TTCCACGACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAAT
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>Ag8
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GCTTTTATTATAATTTTTTTTATAACTATACCAATCGTTATTGGAGGTTT
TGGAAATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTTT
CCACGACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAATAA
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CTATTTATCCACCTTTATCAAATAATATTGCTCATAATAATATTTCAGTA
GACTTAACTATTTTTTCCCTACATTTAGCAGGTATCTCATCAATTTTAGG
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>Ag9
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GGAGACCCTATTCTTTATCAACATTTATTTT
>Ag10
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TGCTTTTATTATAATTTTTTTTATAACTATACCAATCGTTATTGGAGGTT
TTGGAAATTGATTAATTCCTATAATAATAGGATGTCCAGATATATCTTT
TCCACGACTAAATAATATTAGATTCTGATTATTACCACCCTCATTAATA
ATAATAATTTGCAGATTTATAATTAATAACGGAACAGGAACAGGATGA
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Appendix III: BLAST hits results showing similarity percentages between study sequences and those from the NCBI GenBank database

No.	Sample name	Length (bp)	Corresponding taxon (GenBank)	Accession No.	Percentage similarity
1	Ag1	658	*Aphis gossypii*	KF446154.1	99
2	Ag2	682	*Aphis gossypii*	EU930156.1	99
3	Ag3	1563	*Aphis gossypii*	AB506726.1	99
4	Ag4	658	*Aphis gossypii*	DQ499026.1	99
5	Ag5	680	*Aphis gossypii*	EU930160.1	100
6	Ag6	679	*Aphis gossypii*	EU930153.1	100
7	Ag7	679	*Aphis gossypii*	EU930153.1	100
8	Ag8	678	*Aphis gossypii*	EU930157.1	100
9	Ag9	1563	*Aphis gossypii*	AB506727.1	100
10	Ag10	681	*Aphis gossypii*	EU930151.1	100
11	Ag11	1563	*Aphis gossypii*	AB506727.1	100
12	Ag12	676	*Aphis gossypii*	EU930155.1	100
13	Ag13	658	*Aphis gossypii*	DQ499026.1	99
14	Ag14	1563	*Aphis gossypii*	AB506730.1	99
15	Ag15	658	*Aphis gossypii*	EU701339.1	100
16	Ag16	677	*Aphis gossypii*	EU930163.1	100
17	Ag17	658	*Aphis gossypii*	KF446144.1	99
18	Ag18	676	*Aphis gossypii*	EU930155.1	100
19	Ag19	676	*Aphis gossypii*	EU930151.1	99
20	Bb1	666	*Brevicoryne brassicae*	JQ920915.1	100
21	Bb2	597	*Brevicoryne brassicae*	GU457798.1	100
22	Bb3	665	*Brevicoryne brassicae*	JQ240191.1	100
23	Bb4	658	*Brevicoryne brassicae*	EU701547.1	100
24	Bb5	666	*Brevicoryne brassicae*	JQ920915.1	100
25	Bb6	666	*Brevicoryne brassicae*	JQ240190.1	100
26	Bb7	658	*Brevicoryne brassicae*	JX051386.1	99
27	Bb8	665	*Brevicoryne brassicae*	JQ240191.1	100
28	Bb9	666	*Brevicoryne brassicae*	JQ920915.1	100
29	Bb10	665	*Brevicoryne brassicae*	JQ240191.1	100
30	Bb11	666	*Brevicoryne brassicae*	JQ920915.1	100
31	Bb12	597	*Brevicoryne brassicae*	GU457798.1	100
32	Bb13	666	*Brevicoryne brassicae*	JQ920915.1	100

No.	Sample name	Length (bp)	Corresponding taxon (GenBank)	Accession No.	Percentage similarity
33	Bb14	597	*Brevicoryne brassicae*	GU457798.1	100
34	Bb15	597	*Brevicoryne brassicae*	GU457798.1	100
35	Bb16	665	*Brevicoryne brassicae*	JQ240191.1	100
36	Bb17	665	*Brevicoryne brassicae*	JQ240191.1	100
37	Bb18	597	*Brevicoryne brassicae*	GU457798.1	100
38	Bb19	597	*Brevicoryne brassicae*	GU457798.1	100
39	Bb20	658	*Brevicoryne brassicae*	DQ499033.1	99
40	Bb21	666	*Brevicoryne brassicae*	JQ920915.1	100
41	Bb22	597	*Brevicoryne brassicae*	GU457798.1	100
42	Bb23	597	*Brevicoryne brassicae*	GU457798.1	100
43	Bb24	665	*Brevicoryne brassicae*	JQ240191.1	100
44	Bb25	665	*Brevicoryne brassicae*	JQ240191.1	100
45	Bb26	658	*Brevicoryne brassicae*	EU701547.1	100
46	Bb27	665	*Brevicoryne brassicae*	JQ240191.1	100
47	Bb28	597	*Brevicoryne brassicae*	GU457798.1	100
48	Bb29	597	*Brevicoryne brassicae*	GU457798.1	100
49	Bb30	666	*Brevicoryne brassicae*	JQ240190.1	100
50	Bb31	665	*Brevicoryne brassicae*	JQ240191.1	100
51	Bb32	597	*Brevicoryne brassicae*	GU457798.1	100
52	Bb33	665	*Brevicoryne brassicae*	JQ240191.1	100
53	Bb34	665	*Brevicoryne brassicae*	JQ240191.1	100
54	Bb35	597	*Brevicoryne brassicae*	GU457798.1	100
55	Bb36	597	*Brevicoryne brassicae*	GU457798.1	100
56	Bb37	665	*Brevicoryne brassicae*	JQ240191.1	100
57	Bb38	666	*Brevicoryne brassicae*	JQ920915.1	100
58	Bb39	658	*Brevicoryne brassicae*	EU701547.1	100
59	Bb40	658	*Brevicoryne brassicae*	EU701547.1	100
60	Bb41	666	*Brevicoryne brassicae*	JQ920915.1	100
61	Bb42	597	*Brevicoryne brassicae*	GU457798.1	100
62	Bb43	597	*Brevicoryne brassicae*	GU457798.1	100
63	Bb44	658	*Brevicoryne brassicae*	EU701547.1	100
64	Bb45	665	*Brevicoryne brassicae*	JQ240191.1	100
65	Bb46	597	*Brevicoryne brassicae*	GU457798.1	100
66	Bb47	597	*Brevicoryne brassicae*	GU457798.1	100
67	Bb48	665	*Brevicoryne brassicae*	JQ240191.1	100
68	Bb49	665	*Brevicoryne brassicae*	JQ240191.1	100

No.	Sample name	Length (bp)	Corresponding taxon (GenBank)	Accession No.	Percentage similarity
69	Bb50	597	*Brevicoryne brassicae*	GU457798.1	100
70	Bb51	597	*Brevicoryne brassicae*	GU457798.1	100
71	Bb52	665	*Brevicoryne brassicae*	JQ240191.1	100
72	Bb53	665	*Brevicoryne brassicae*	JQ240191.1	100
73	Bb54	666	*Brevicoryne brassicae*	JQ240190.1	100
74	Bb55	666	*Brevicoryne brassicae*	JQ240190.1	100
75	Bb56	665	*Brevicoryne brassicae*	JQ240191.1	100
76	Bb57	665	*Brevicoryne brassicae*	JQ240191.1	100
77	Bb58	597	*Brevicoryne brassicae*	GU457798.1	100
78	Bb59	597	*Brevicoryne brassicae*	GU457798.1	100
79	Bb60	666	*Brevicoryne brassicae*	JQ920915.1	100
80	Bb61	666	*Brevicoryne brassicae*	JQ920915.1	100
81	Bb62	597	*Brevicoryne brassicae*	GU457798.1	100
82	Bb63	597	*Brevicoryne brassicae*	GU457798.1	100
83	Bb64	665	*Brevicoryne brassicae*	JQ240191.1	100
84	Bb65	665	*Brevicoryne brassicae*	JQ240191.1	100
85	Bb66	658	*Brevicoryne brassicae*	EU701547.1	100
86	Bb67	658	*Brevicoryne brassicae*	EU701547.1	100
87	Bb68	597	*Brevicoryne brassicae*	GU457798.1	100
88	Bb69	597	*Brevicoryne brassicae*	GU457798.1	100
89	Bb70	665	*Brevicoryne brassicae*	JQ240191.1	100
90	Bb71	665	*Brevicoryne brassicae*	JQ240191.1	100
91	Bb72	658	*Brevicoryne brassicae*	EU701547.1	100
92	Bb73	658	*Brevicoryne brassicae*	EU701547.1	100
93	Bb74	665	*Brevicoryne brassicae*	JQ240191.1	100
94	Bb75	665	*Brevicoryne brassicae*	JQ240191.1	100
95	Bb76	597	*Brevicoryne brassicae*	GU457798.1	100
96	Bb77	666	*Brevicoryne brassicae*	JQ920915.1	99
97	Bb78	666	*Brevicoryne brassicae*	JQ920915.1	100
98	Bb79	666	*Brevicoryne brassicae*	JQ920915.1	99
99	Bb80	666	*Brevicoryne brassicae*	JQ240190.1	100
100	Bb81	597	*Brevicoryne brassicae*	GU457798.1	100
101	Bb82	666	*Brevicoryne brassicae*	JQ920915.1	100
102	Bb83	597	*Brevicoryne brassicae*	GU457798.1	100
103	Bb84	597	*Brevicoryne brassicae*	GU457798.1	100
104	Bb85	665	*Brevicoryne brassicae*	JQ240191.1	100

No.	Sample name	Length (bp)	Corresponding taxon (GenBank)	Accession No.	Percentage similarity
105	Bb86	658	*Brevicoryne brassicae*	EU701547.1	100
106	Bb87	597	*Brevicoryne brassicae*	GU457798.1	100
107	Bb88	666	*Brevicoryne brassicae*	JQ920915.1	100
108	Bb89	665	*Brevicoryne brassicae*	JQ240191.1	100
109	Lp1	658	*Lipaphis pseudobrassicae*	EU701712.1	99
110	Lp2	658	*Lipaphis pseudobrassicae*	EU701711.1	100
111	Lp3	658	*Lipaphis pseudobrassicae*	EU701713.1	99
112	Lp4	657	*Lipaphis pseudobrassicae*	EU701710.1	99
113	Lp5	658	*Lipaphis pseudobrassicae*	EU701711.1	100
114	Lp6	658	*Lipaphis pseudobrassicae*	EU701711.1	100
115	Lp7	658	*Lipaphis pseudobrassicae*	EU701711.1	100
116	Lp8	658	*Lipaphis pseudobrassicae*	EU701711.1	100
117	Lp9	658	*Lipaphis pseudobrassicae*	EU701711.1	100
118	Lp10	658	*Lipaphis pseudobrassicae*	EU701711.1	100
119	Lp11	658	*Lipaphis pseudobrassicae*	EU701711.1	100
120	Lp12	658	*Lipaphis pseudobrassicae*	EU701711.1	100
121	Lp13	658	*Lipaphis pseudobrassicae*	EU701711.1	100
122	Lp14	658	*Lipaphis pseudobrassicae*	EU701711.1	100
123	Lp15	658	*Lipaphis pseudobrassicae*	EU701711.1	100
124	Lp16	658	*Lipaphis pseudobrassicae*	EU701711.1	100
125	Lp17	658	*Lipaphis pseudobrassicae*	EU701711.1	100
126	Lp18	658	*Lipaphis pseudobrassicae*	EU701711.1	100
127	Lp19	658	*Lipaphis pseudobrassicae*	EU701711.1	100
128	Lp20	658	*Lipaphis pseudobrassicae*	EU701711.1	100
129	Lp21	658	*Lipaphis pseudobrassicae*	EU701711.1	100
130	Lp22	658	*Lipaphis pseudobrassicae*	EU701711.1	100
131	Lp23	658	*Lipaphis pseudobrassicae*	EU701711.1	100
132	Lp24	658	*Lipaphis pseudobrassicae*	EU701711.1	100
133	Lp25	658	*Lipaphis pseudobrassicae*	EU701711.1	100
134	Lp26	658	*Lipaphis pseudobrassicae*	EU701711.1	100
135	Lp27	658	*Lipaphis pseudobrassicae*	EU701711.1	100
136	Lp28	658	*Lipaphis pseudobrassicae*	EU701711.1	100
137	Lp29	658	*Lipaphis pseudobrassicae*	EU701711.1	100
138	Lp30	658	*Lipaphis pseudobrassicae*	EU701711.1	100
139	Lp31	658	*Lipaphis pseudobrassicae*	EU701711.1	100
140	Lp32	658	*Lipaphis pseudobrassicae*	EU701711.1	100

No.	Sample name	Length (bp)	Corresponding taxon (GenBank)	Accession No.	Percentage similarity
141	Lp33	658	*Lipaphis pseudobrassicae*	EU701711.1	100
142	Lp34	658	*Lipaphis pseudobrassicae*	EU701711.1	100
143	Lp35	658	*Lipaphis pseudobrassicae*	EU701711.1	100
144	Lp36	658	*Lipaphis pseudobrassicae*	EU701711.1	100
145	Lp37	658	*Lipaphis pseudobrassicae*	EU701711.1	100
146	Ac1	658	*Aphis craccivora*	GQ904082.1	100
147	Ac2	658	*Aphis craccivora*	GQ904082.1	100
148	Ac3	658	*Aphis craccivora*	GQ904082.1	100
149	Ac4	1563	*Aphis craccivora*	AB506712.1	99
150	Ac5	651	*Aphis craccivora*	HM062926.1	100
151	Ac6	651	*Aphis craccivora*	HM062926.1	100
152	Ac7	658	*Aphis craccivora*	GQ904082.1	100
153	Ac8	658	*Aphis craccivora*	GQ904082.1	100
154	Ac9	658	*Aphis craccivora*	GQ904082.1	100
155	Ac10	658	*Aphis craccivora*	GQ904082.1	100
156	Af1	671	*Aphis fabae solanella*	AB506722.1	99
157	Af2	670	*Aphis fabae fabae*	KF638817.1	100
158	Af3	629	*Aphis fabae*	EU294096.1	100
159	Af4	670	*Aphis fabae*	EU701325.1	99
160	Af5	667	*Aphis fabae*	EU930137.1	99
161	Af6	672	*Aphis fabae*	JQ916136.1	99
162	Af7	1563	*Aphis fabae solanella*	AB506722.1	99
163	Af8	679	*Aphis fabae*	EU930137.1	99
164	Af9	1563	*Aphis fabae solanella*	AB506722.1	99
165	Af10	679	*Aphis fabae*	EU930137.1	99
166	Ap1	665	*Acyrthosiphon pisum*	AB506720.1	100
167	Ap2	666	*Acyrthosiphon pisum*	EU701277.1	100
168	Ap3	665	*Acyrthosiphon pisum*	GU978852.1	100
169	Ap4	662	*Acyrthosiphon pisum*	GU978912.1	100
170	Ap5	656	*Acyrthosiphon pisum*	EU071328.1	100
171	Mp1	659	*Myzus persicae*	KC008069.1	99
172	Mp2	672	*Myzus persicae*	AB506739.1	99
173	Mp3	674	*Myzus persicae*	KC286666.1	100
174	Mp4	665	*Myzus persicae*	EU701802.1	100
175	Mp5	667	*Myzus persicae*	JX844420.1	99