ARYTAINA MOPANE'S ASSOCIATION WITH *COLOPHOSPERMUM MOPANE*

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DECLARATION

I declare that this dissertation hereby submitted to the University of Limpopo for the degree Masters of Science has not been previously submitted by me or for a degree at any other University, that it is my own work in design and execution, and that all material contained therein has been duly acknowledged.

Signature --------------------------------
C.K. Oppong

DEDICATION

This dissertation is dedicated to my wife, Mercy and to my children Vincent, Beatrice, Ronald and the late Bright Oppong

ABSTRACT

This dissertation reports on the results of field (Letsitele area) and laboratory investigations on the biology of *Arytaina mopane,* its ecological role as well as its physiological influences on the host plant *Colophospermum mopane.* The work is divided into three sections.

Section one describes the various aspects of the biology of *A. mopane,* which includes the morphology of the eggs, nymphs and adults including the behaviour of nymphs and adults. Damage caused to the host plant by infestation as well as predation of *A. mopane* is discussed.

Eggs are randomly laid on green and senescent *C. mopane* leaves, very often in clusters and along the veins. The eggs are black and conical in shape with a reticulate-sculptured membrane surrounding each. Each egg has a pedicel at the apical end and a filament at the basal end. An egg is not attached by a pedicel (contrary to the literature) but glued to the leaflet surface.

Arytaina mopane exhibits an incomplete metamorphosis with the life cycle consisting of an egg, 5 nymphal instar and an adult. The five nymphal stages differed only in size and minor morphological features except for development of wings. Wingpad development is prominent from the third instars onwards. Nymphs construct scutcheon-like encrustations, commonly known as lerps over their bodies, which partly protect them from enemies and desiccation. Lerps covered only about 0.2% of the adaxial leaflet surface, where they were more common. Nymphs feed by piercing through the epidermal cells into the vascular bundle tissue of the leaflet with their stylet to reach the phloem sap. Feeding damage by nymphs results in black and reddish-brown spots on the leaflet surface. Two forms of nymphs that varied in colour and abdominal markings were identified, that could either be two different female morphotypes of the species, gender variation or natural variation.

When not feeding, adults rest almost motionless on the leaflet or petiole with their stylet withdrawn and wings folded. Adults prefer walking or crawling to flying between

leaflets but sometimes jump when disturbed. When violently disturbed adults did fly short distances and returned to settle on a leaf of the same tree. The mean adult body length is 3.5 mm. In the laboratory, the life span of adults ranged between 5 and 8 days.

Predators include birds such as the Red winged starling (*Onychognathus morio*) and Tawnyflanked prinia (*Prinia subflava*), the Painted reed frog (*Hyperolius marmoratus taeniatus*), the larvae of the Brown lacewing (Neuroptera: Hemerobiidae), a suspected Coccinellid beetle, and ants belonging to the genus *Crematogaster*.

The second section reports on the physiological influences in terms of the chemical composition of lerps and the mineral content of both infested and uninfested *C. mopane* leaves. Lerps, infested and uninfested *C. mopane* leaves were tested for carbohydrate and mineral contents. The carbohydrate constituent of lerps and leaves (infested and uninfested) was sugar in the form of glucose, fructose and raffinose. Infested leaves contained significantly higher amounts of the macro elements calcium and magnesium than uninfested leaves. The uninfested leaves in contrast had significantly higher amounts of nitrogen, potassium, iron and copper.

The ecological role of the infestation on *C. mopane* is reported in section three. *Colophospermum mopane* leaves at certain times of the year are known to have high tannin levels, which presumably results in bitter tasting leaves. The sweet encrustation (lerp) of *A. mopane,* apart from possibly reducing this bitter taste of the senescent leaves, raises the energy content by adding to the glucose and fructose levels of the leaves. This could consequently increase *C. mopane*'s browsable potential to game and wild animals during autumn. This could have an important impact on the game industry of the Limpopo and Mpumalanga Provinces of South Africa.

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ABBREVIATIONS USED

ARC: Agricultural Research Council
CPD: Critical point dried
DM: Dry mass
EDS: Energy dispersive X-ray spectroscopy
FAA: Formalin acetate acid alcohol
FET: Further Education and Training
GMA: Glycol methacrylate
HPLC: High performance liquid chromatographic
ICP: Inductively-coupled plasma
MEF: Musina Experimental Farm
PEG: Polyethylene glycol
SD: Standard deviation
SEM: Scanning electron microscope
TCE: Trichloroethalene
U.D.: Undated
WMA: Water management area

CHAPTER 1

GENERAL INTRODUCTION

1 Introduction

Psyllids, commonly known as jumping plant lice, are plant–sucking homopterans belonging to the family Psyllidae. These insects are small to minute, less than 5 mm in length, with transparent wings, which are often patterned. They are powerful jumpers but weak fliers (Picker *et al*. 2002). Worldwide the family consists of either 12 or 16 genera depending on the source consulted and 1300 species (Sullivan U.D.). In South Africa there are 61 known species (Picker *et al*. 2002). Although related to aphids (Apidoidea), scale insects (Coccoidea) and whiteflies (Aleyrodoidea), (Urquhart & Stone 1995), they are generally less well known than these groups due to their comparably low occurrence as pests of cultivated crops and ornamental trees (Percy 2001). Psyllids are, however, known vectors of various plant diseases (McMullen & Jong 1971; Hodkinson 1974).

Adult psyllids generally live less than 10 days. Both nymphs and adults feed by sucking the phloem sap of the host plant (Urquhart & Stone 1995). Although psyllids feed on a wide variety of vascular plants they exhibit habitat and host specialization, which makes them ideal for investigating evolutionary patterns associated with habitat or host shifts and geographic isolation (Percy 2001).

Psyllids are cosmopolitan in their distribution. In North America, they are found in the USA and Canada. Among the Asia-Pacific countries, they occur in India, Sri Lanka, China, Japan, Korea and Australia. In Europe, they occur in many countries including Sweden and Britain. In Africa, psyllids are found in southern Africa, Kenya, Morocco, and the Canary Islands (Meyer 2001).

The nymphs feed on hard leaves, often causing pit-like galls or deformation of the leaves (Picker *et al*. 2002). Nymphs also cause blotching on leaves, leaf loss and dieback of branches (BHG Australia 2004). The nymphs of some free-living psyllids can produce excess sugary secretions called “honeydew”. These secretions attract ants and other insects that feed on the honeydew. Sooty mould may also develop on these secretions blackening the leaves and reducing the rate of photosynthesis (Urquhart & Stone 1995). Some nymphs build scale-like shelters or lerps while others are without coverings (BHG Australia 2004).

1.1 *Arytaina mopane* (Mopane psyllid)

Arytaina mopane (Pettey 1924) is one of the few endemic insects which utilize *Colophospermum mopane* (Benth.) J. Léonard as a host plant (Ernst & Sekhwela 1987). The nymphs of this insect live and feed exclusively on the leaf phloem sap of *C. mopane* (Ernst & Sekhwela 1987). They emerge when the leaves become senescent, which normally starts from June/July depending on climatic factors such as rainfall. Adults are attracted to light in great numbers (Picker *et al*. 2002). *Arytaina mopane*'s life cycle consists of an egg, five nymphal instars and an adult (Ernst & Sekhwela 1987). The feeding habits of the nymphs cause a local discolouration or malformation of the foliage (Urquhart & Stone 1995). Nymphs secrete protective waxy or sugary coverings called lerp on the leaf surface (Dobson 1851; Urquhart & Stone 1995). As nymphs grow they either enlarge the lerps or move to construct a new lerp.

1.2 Lerps

Dobson (1851) describes the term lerp as being derived from the aboriginal name for the sweet encrustations, sometimes produced in great abundance by psyllids on twigs and branches of malle *Eucalyptus* in Australia. The lerps provide protection for nymphs against desiccation and predation (White 1972; Gilby *et al.* 1976). David Livingstone (1857), perhaps, gives the earliest published account of this secretion in Africa in his "Travels and Researches South Africa (1857)". He states that on the leaves of *C. mopane* appear small larvae of winged insects, covered with sweet, gummy substances, which the people collect in great quantities and use as food.

The local people in the northern region of South Africa call it *mapodêla* in Sepedi (Malatji, personal communication) and use it to supplement their food, especially among the cattle tenders. Baboons (*Papio ursinus*) and monkeys (*Cercopithecus aethiopicus*) pick the *C. mopane* leaves to remove and consume these sweet tasting scales, presumably to supplement their nutritional needs (Pettey 1925). There is consequently large-scale defoliation of heavily infested *C. mopane* trees as a result of such feeding activities. A wide variety of birds including Burchell's Starlings (*Lamprotornis australis*) and Cape Turtle Doves (*Streptopelia capicola*) also feed on the lerps (Herremans-Tonnoeyr & Herremans 1995).

Sometimes the infestation is so excessive that the lerp of neighbouring nymphs overlap, resulting in the construction of lerps on the petioles of leaves. According to Van Wyk (1972), large-scale infestations can result in lerps covering large areas of the leaflet surface thereby reducing the penetration of light and hence reducing photosynthesis in the leaflet. Ernst and Sekhwela (1987) speculate that the lerps can increase the leaflet mass by a factor of ten.

1.3 Palatability

Badenhorst (2003), citing research done by Du Hoven, shows that plants have the ability to defend themselves from browsing pressure. By producing more condensed tannins, leaves lose their taste after a while, which “signals” to the animals the necessity for moving on to other trees. In this regard *A. mopane* might play a vital role possibly in improving the taste of the leaves with the sugary lerps even after the production of condensed tannins in *C. mopane* leaves. This might result in an improved condition to the animal as it needs not move as much between trees during a browsing session as might be the case in the absence of *A. mopane.*

1.4 *Colophospermum mopane*

Indigenous forests, woodlands, savannah and grasslands cover 65 percent of southern Africa (SADC Region) (CFAN 2003). The forests and woodlands cover an area of approximately 440 million hectares of southern Africa (Prior 1996). Mopane woodland is one of the ten types of woodlands occurring in southern Africa and is dominated by *C. mopane* (CFAN 2003).

Colphospermum mopane, commonly known as mopane tree, is one of the best-known and valuable tree species indigenous to southern Africa (Fig. 1). Where it occurs, it is often dominant and forms a species-poor woodland or shrubland. The tree is especially adapted to the drier regions of southern Africa, which stresses its importance as a source of browse during periods of the year when other trees are leafless (Palmer & Pitman 1972). De la Hunt (1954) stated that browsing on *C. mopane* increases from June through the winter period, especially on dry leaves, which are still attached to the tree and fallen ones.

Fig. 1. *Colophospermum mopane* trees at study site.

1.4.1 Description

Colophospermum mopane is a small to medium–sized slow growing winter deciduous tree, 5–18 m in height, belonging to the family Fabaceae, sub-family Caesalpinioideae, tribe Detarieae (Lock 1989). It has a tall, narrow crown, with the bole often forked (Ross 1977). The tree bears compound leaves with two, stiff sessile leaflets joined at their base by a pulvinus. The leaflets are distinctly butterfly-shaped with rounded (Fig.2) or tapering tip (Fig. 20). Crushed leaves have a strong turpentine odour. The tree is generally leafless from August to October (Timberlake 1995) but can carry its old leaves up to November, depending on rainfall and temperature patterns.

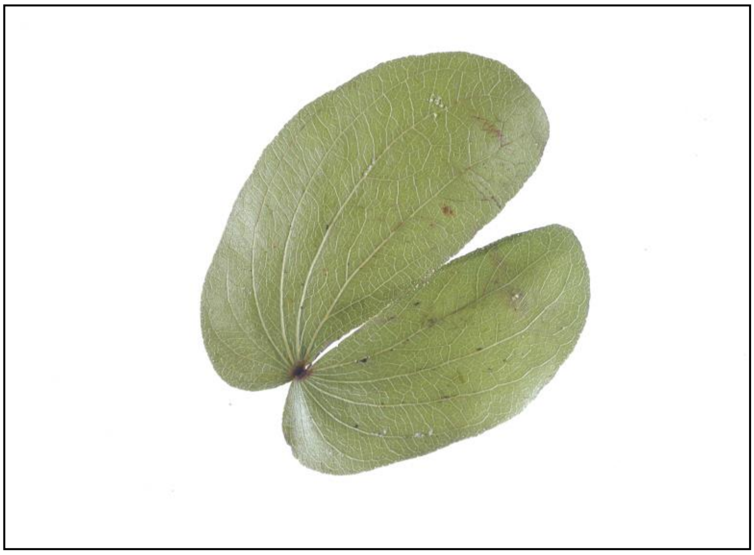


Fig. 2. Compound leaf of *C. mopane*.

1.4.2 Distribution

The distribution of *C. mopane* is mainly determined by rainfall (400-800 mm) and the 5ºC isotherm of mean daily minimum temperature for the coldest month (Werger 1978). It grows in alkaline soils, which are not well drained and in alluvial soils (Timberlake 1995; Aubrey 2004).

The tree occurs in the arid regions of southern Africa, which include Angola, Botswana, Zambia, Malawi, Zimbabwe, Mozambique and South Africa, covering an area of approximately 550 000 km² (Mapaure 1994). Mopane woodland is primarily associated with the wide flat valley bottoms of the Kunene, Shire, Luanga, Zambezi, Okavango, and Limpopo rivers (Mapaure 1994). The northern parts of Limpopo and Mpumalanga Provinces of South Africa are covered by approximately 2 000 km² of mopani veld (Styles 1994).

1.4.3 Nutritional value

Crude protein content is known to be high in *C. mopane* leaves ranging from 8-16% (Bonsma 1942; DHV 1979). Calcium and phosphorous levels in the leaves are also relatively high (Bonsma 1942; Timberlake 1995). The leaves of *C. mopane* have varying concentrations of secondary compounds (tannins) depending on age. Senescent *C. mopane* leaves have few condensed tannins and low fibre content (Styles & Skinner 1996). Game animals, particularly elephants (*Loxodonta africana*) and domestic animals such as goats (*Capra hircus*) readily consume the protein-rich leaf and pod (Aubrey 2004). The leaves are nutritious even when dry, being eaten by animals during the dry winter months (Kelly & Walker 1976). Van Wyk (1972) reported on the ease with which browsers could utilize *C. mopane* due to its relatively large leaves and absence of spines. The long dry season in southern Africa is a period of severe nutritive stress for game and livestock leading to loss of weight. But in areas where *C. mopane* is common, particularly in shrub or low tree form, game and livestock avidly feed on the leaves and this can markedly reduce weight loss (Timberlake 1995).

There appears to be no estimates of the economic value of mopane browse in the form of reduce weight loss in browsers during the long dry season as well as in the making of otherwise, marginal land productive. The old leaves undergo microbiological decomposition and help in the build-up of organic matter and humus. However, it is likely to be tens of millions of US$ per year, principally in northern South Africa (Limpopo and Mpumalanga Provinces), southern Zimbabwe and eastern Botswana (Timberlake 1995).

1.4.4 Host

The biology of *C. mopane* and its relationship with the fauna that utilize it are indeed intricate, suggesting a long history of co-evolution of this tree species with its mammalian and insect fauna (Styles 1994). *Colophospermum mopane* is the host plant for a few endemic insect species such as the well-known mopane worm, which is the caterpillar of the emperor moth *Imbrasia belina*, the caterpillar of the foxy charaxes butterfly *Charaxes jasius saturnus*, ants of the genus *Crematogaster* and the psyllid, *Arytaina mopane* (Timberlake 1995). Mopane woodlands also offer many nesting sites to various animals, such as the hole-nesting birds, hornbills. The tiny mopane bee (*Plebina denoita*) populary known for its attempts at hovering into ones eyes, ears, and nose, which produces a small amount of edible honey, also make their nests in hollow trunks with a small wax tube as an opening to the outside (Aubrey 2004).

1.5 Previous research

Dobson (1851), Basden (1970), White (1972), and Hodkinson (1974) have done extensive studies in Australia on psyllids occurring on eucalypts. They described the biology of various eucalypt psyllids, construction of lerps and the economic importance of psyllids. In the northern hemisphere, Watmough (1968a, 1968b) and Oloya (1964) undertook research on *Arytaina* species. They reported on the biology of two species of Psyllidae, *A. spartiophila* and *A. genista* occurring together on Broom, *Sarothamnus scoparius.*

Our knowledge on *A. mopane* is, however, limited to the works of Pettey (1925) and Ernst and Sekhwela (1987). Pettey (1925) taxonomically described six males and six females collected on *C. mopane* trees in the Musina area of the Limpopo Province of South Africa. Ernst and Sekhwela (1987) studied the life cycle of *A. mopane* as well as the chemical composition of the lerp in Botswana.

1.6 Aim and objectives

1.6.1 Aim

The aim of this study was to investigate the biology of *A. mopane* as well as its ecological role in mopani veld and physiological influences on *C. mopane.*

1.6.2 Objectives

The following objectives pertain to the biological section of the aim.

1.6.2.1 Eggs

- Determine the morphology, mean number per leaflet, places of distribution on the leaflet and petiole and calculate the number of eggs per tree.
- Assay mean percentage hatched, and possible predation.
- Describe how eggs are attached to leaflet and how they dehisce.

1.6.2.2 Nymphs

- Identify different stages of nymphs and possible colour variation of instars.
- Ascertain the distribution pattern of nymphs on the leaflet and determine possible predators.
- Investigate feeding mechanisms.

1.6.2.3 Lerps

- Describe morphology of lerps and their distribution on a leaflet.
- Elucidate the number of lerps per leaflet surface and calculate the lerps per tree.
- Describe the construction of lerps and test for starch in lerps.
- Determine if two or more nymphs co-inhabit a lerp.
- Assay what happens to various nymph instars when lerps are removed.
- Measure the mean mass of lerps and the size of lerps corresponding to the different instar stages.
- In view of Ernst & Sekhwela's findings (1987) that although lerps are composed mostly of sugars they are insoluble in water it was decided to solve this contradiction by confirming the lerps insolubility in water.

1.6.2.4 Adult

- Determine the morphological differences between males and females.
- Describe adult behaviour when disturbed and identify possible predators.

The following objectives refer to the physiological and ecological sections of the aim.

1.6.2.5 Mineral and carbohydrate content

- Elucidate mineral content of senescent and green *C. mopane* leaves.
- Determine the carbohydrate and other organic content of lerps and hence possible effect(s) on the tree and browsers.

CHAPTER 2

LITERATURE REVIEW

SECTION 1

2.1 What are psyllids (Homoptera)?

2.1.1 Classification

According to Hodkinson (1974), Meyer (2001) and Dahlsten *et al.* (2004), *Arytaina* belongs to the family Psyllidae in the order Homoptera. The family Psyllidae comprises different genera, ranging between 12 and 16 according to the source cited; yet they all include *Arytaina* and *Psylla*. There are approximately 1300 species described under the family (Sullivan U.D.). Psyllids are classified as follows:

Phylum: Arthropoda
Class: Insecta
Subclass: Pterygotha
Division: Exopterygotha
Order: Homoptera
Superfamily: Psylloidea
Family: Psyllidae
Subfamily: Arytaininae
(Hodkinson 1974; Meyer 2001 and Dahlsten *et al.* 2004).

Nearctica (1998) have the following genera: *Acizzia, Amorphicola, Arytaina, Arytainilla, Cacopsylla, Ceanothia, Euglyptoneura, Euphalerus, Heteropsylla, Nyctiphalerus, Paachypsylla, Pexopsylla, Psylla, Purshivora, Spanioneura and Tetragonocephala*. The Psyllidae Type Collection Holdings (1997) cite the following: *Aphalara, Arytaina, Calophya, Choricymoza, Craspedolepta, Euphalerus, Euphyllua, Frysuila, Katacephala, Kuwayama, Leuronta, Nyctiphalerus, Psylla, Synoza, Trioza* and *Vailakiella.* Fabio Stoch (2003) lists the following genera: *Acizzia, Arytaina, Arytainilla, Asphagidella, Baeopelma, Cacopsylla, Chamaepsyylla, Cyamophila, Livilla, Psylla, Psyllopsis, and Spanioneura.*

The subfamily Arytaininae comprises 13 genera, of which 9 feed on host plants in the Leguminosae, two feed on host plants in the Rosaceae and the remaining two feed on host plants in the Rhamnaceae. Arytaininae genera that feed on legumes include: *Arytaina, Arytainilla, Cyamophila, Livilla* and *Pseudacanthopsylla* (Percy 2002).

2.1.2 Morphological traits

Psyllids are small insects with a 3-segmented labrum and 5 to 10 (usually 10)-segmented antennae (Meyer 2001). Although related to aphids, scale insects and whiteflies (Urquhart & Stone 1995), they differ by having strong jumping legs and short antennae. Mature adults commonly jump when disturbed using their strong hind-legs (hence the name Psyllidae) (Hodkinson 1974).

Adults are slender, pale green or brown in colour with areas of orange and yellow (Garrison 1998). At maturity, their body length ranges between 2.5 and 4.0 mm (Dreistadt *et al.* 1999). Adults have two pairs of wings with the fore-wings often thicker and larger than the hind-wings. Their wings are held roof-like over their bodies. Psyllid mouthparts are modified in the form of a piercing and sucking tube (stylet) (Hodkinson 1974; Meyer 2001), which is used to withdraw phloem sap from vascular plants (White 1971). The tarsi are two-segmented with two claws.

2.1.3 Host specificity

Psyllids are generally narrowly host specific (Gegechkori 1968; Hodkinson 1974), with most species living and feeding only on a group of closely related plants or a single plant species. For instance, *Arytaina mopane* closely follows the distribution of *C. mopane* (Ernst & Sekhwela 1987), while *Cardiaspina* species feed exclusively on *Eucalyptus* species (Hodkinson 1974). *Livilla monospermae* is an example of a legume (Genisteae)-feeding psyllid in the subfamily Arytaininae (Psyllidae) (Percy 2001). The Fig psyllid, *Mycopsylla fici* feeds exclusively on *Ficus macrophylla* (BGT-Fig Psyllids 1998). On the other hand, some species especially of the genus *Trioza* are to a certain extent polyphagous (Heslop-Harrison 1937).

2.1.4 Psyllids as vectors and pests

Psyllids are known vectors of viral and bacterial diseases of plants, which include citrus leaf-mottle yellows disease (Martinez & Wallace 1967), greening disease of citrus (McClean & Oberholzer 1965; Schwartz *et al.* 1970) and fireblight of pears (Wilde *et al.* 1971). According to McMullen and Jong (1971) and Hodkinson (1974) psyllids are pests of cultivated crops and ornamental trees and are even developing resistance to insecticides. Many native Californian trees and shrubs such as the lemonade berry and sugar bush (*Rhus* species), manzanita (*Arctostaphylos* species) and willow (*Salix* species) that are planted as ornamentals are examples of plants that act as hosts for native psyllid species (Dreistadt *et al.* 2004). Several gall-making *Pachypsylla* species infesting hackberry (*Celtis occidentalis*) and the boxwood psyllid (*Psylla buxi*) are pests with the latter causing the terminal leaves of *Buxus* (boxwood) to become cupped (Dreistadt *et al.* 2004). *Pachypsylla celtidis-mamma* infests hackberry (*Celtis occidentalis*) and causes the plant to produce gall-like structures (McDermott *et al*. 1996). Both adults and nymphs of the carrot psyllid *Trioza apicalis* are pests that especially attack carrots in the northern parts of Europe (Laska 1964; Hodkinson 1974; Markkula *et al.* 1976). The Asian citrus psyllid, *Diaphorina citri* is the primary vector of citrus greening disease caused by the bacteria *Liberobacter asiaticum* (Shivankar *et al.* 2000; Michaud 2003). Tomato psyllids on members of the Solanaceae produce "psyllid yellows", a disease condition first described by Richards (1928). Symptoms of psyllid yellows are caused by a chlorosis-inducing toxemia that is produced mainly by nymphal feeding (Carter 1950). In tomato severe symptoms of this disease lead to the production of small, poor quality fruit, a disrupted fruit set and consequently yield loss (Daniels 1954; Abernathy 1991).

2.2 Parasites and predators of the Psylloidea

2.2.1 Parasites

Hodkinson (1974) reports on the following psyllid parasites: *Diptera* of the family Cecidomydae, and Hymenoptera of the families Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Pteromalidae, Thysanidae, Torymidae, Cynipidae, Braconidae, Ceraphronidae, and Platygasteridae. Cecidomyiid midges of the genus *Endopsylla* are parasitic on adult psyllids (Lal 1934), whereas the Hymenoptera are nymphal parasites with the exception of *Sectiliclava cleone*, which is parasitic on adults. Some parasites such as the females of the *Psyllaephagus bliteus* wasp lay an egg in a psyllid nymph. The egg hatches and the wasp larva consume the psyllid nymph (Dahlsten & Rowney 2000).

2.2.2 Predators

Many birds including honeyeaters, hornbills, pardalotes and rosellas are predators of psyllids. Birds such as Longtailed Starlings (*Lamprotornis mevesii*), Burchell's Starlings (*L. australis*), and Cape Turtle Dove (*Streptopelia capicola*) feed on the lerps (Herremans-Tonnoeyr & Herremans 1995). Spiders cover the lerps with webs and trap the adult psyllids as they emerge (Dahlsten & Rowney 2000). Insects such as assassins, ladybirds, lacewings and wasps are among their natural predators (BHG Australia 2004; Urquhart & Stone 1995).

The recorded predators include some members of the following families: Miridae, Anthocoridae, Lygaeidae, Nabidae, Syrphidae, Coccinellidae, Formicidae, and the Neuroptera larvae (Dempster 1968; Catling 1970) as well as members of Aracnida, Acarina, Phalangida and Araneida (Dempster 1968; Catling 1970; Hodkinson & Flint 1971).

Predators in general are not specific and feed opportunistically on psyllids (Catling 1970; Hodkinson 1974) with the possible exception of *Anthocoris sarothamni*, a predator of *Arytaina* species in Britain, which feeds exclusively on psyllids. In *Arytaina* species the number of eggs laid per female appears to be related to the amount of predation the eggs of the species suffer (Watmough 1968a).

2.3 Damage to host plant

According to White (1970b) adult feeding causes little damage to the host. This may be due to the degeneration of the mycetome in adults (Richards & Brooks 1958). Feeding damage is mostly caused by the nymphal stages to the host plants' leaves (Annecke & Cilliers 1963; Clark 1963). Feeding damage and gall formation can be traced to a systemic toxaemia caused by salivary injection (Laska 1964; Williams & Benson 1966). Visible damage to the leaf ranges from localized necrosis to severe galling and malformation of the meristematic tissue. Nymphs can cause blotching on the leaves, leaf loss and dieback of branches (BHG Australia 2004). Additional damage includes reduction of nitrogen in the leaf and pigment concentration resulting from death of leaf tissues. Heavy infestations cause severe leaf drop, which in turn can weaken trees and increase tree susceptibility to damage from other insects and diseases (Dahlsten *et al.* 2004). Furthermore, it lowers the visual appeal of ornamental and garden trees on which it occurs (Eyer 1937; Plant Talk 2003; Dreistadt *et al.* 2004).

2.3.1 Salivary injection

In *Cardiaspina*, nymphs settle down after hatching on leaf surfaces and insert their stylets through the stomata in order to reach their food supply (Clark 1962). *Cardiaspina* nymphs appear to inject small amounts of a salivary secretion into the phloem, which diffuses into the surrounding tissue according to Crawford and Wilkens (1996). Nymphs of the Asian citrus psyllid (*Diaphorina citri*), inject a feeding substance that causes considerable leaf distortion on citrus, often leading to abatement of terminal elongation and the abscission of leaves and whole shoots (Mead 1976). The saliva injected by *Trioza apicalis* adults during feeding causes curling of the green parts while nymphal feeding causes reduction of root growth in carrots (Valterová *et al.* 1997). The chemical structure of the active salivary substance is still unknown (Laurema 1989).

2.3.2 Inducing nitrogen release

The salivary secretion induces a breakdown of the mesophyll tissue, resulting in the liberation of copious amounts of soluble nitrogen at the feeding site (White 1970a). Psyllids ameliorate their food source by this mechanism according to White (1970a). The increased availability of soluble nitrogen, particularly amino acids, in the phloem tissue is vital as this determines the rate of growth and survival of the nymphs (Hodkinson 1974).

2.3.3 Necrosis and leaf defoliation

The feeding of the nymphs results firstly in a yellow, and later in a purple discolouration and finally necrosis of the leaf tissue. When nymphs complete their development the necrotic tissue remains as a characteristic dry, brown patch on an otherwise healthy green leaf. When insect numbers are high, whole leaves may be shed in response to intense feeding by psyllids and entire trees are almost defoliated. According to Crawford and Wilkens (1996) this effect has also been reported for a number of other species of *Cardiaspina* on their host eucalypts (Clark & Dallwitz 1975; Morgan 1984). White (1970a), Morgan (1984) and Crawford and Wilkens (1996), suggest that nymphs of *Cardiaspina* species induce a condition that resembles advanced senescence in leaf tissues.

2.3.4 Gardeners' nightmare

Psyllids are devastating insects for gardeners growing tomatoes or potatoes. *Paratrioza cockerelli* causes tomato fruit to stop forming when infested during the vegetative stage or ripening. In tomato, psyllids cause the mid-vein and margin of the leaves at the apex to turn yellow or purple, new leaves remain small, narrow and stand upright in a feathery appearance. Severe infestation by *Paratrioza cockerelli* on potato can result in the upward curling and yellowing of older leaves, the purpling of the margin of the younger leaves, enlargement of the nodes and petioles, rosetting and production of auxiliary shoots and tubers. It also induces many small potato tubers to develop and sprout prematurely before harvesting (Plant Talk 2003). The Fig psyllid (*Mycopsylla fici*), is responsible for the periodic defoliation of Moreton Bay fig trees (*Ficus macrophylla*) (BGT-Fig Psyllids 1998). Markkula and Laurema (1971), Laurema (1989) and Valterová *et al.* (1997) state that feeding by the adults of *Trioza apicalis* is usually considered to be most serious and that very young seedlings of carrots are more badly damaged than older ones.

2.4 Biological control

Natural enemies including lady beetles (Coccinellidae), lacewing larvae (Hemerobiidae) and parasitic wasps provide partial control of psyllids (Dreistadt *et al*. 2004). Introduced species of natural enemies now occur naturally throughout California in the U.S.A. For instance, a tiny parasitic wasp (*Psyllaephagus pilosus*) effectively controls the bluegum psyllid, while the *Eugenia* psyllid is partially controlled by parasitic wasp (*Tamarixia* species). In San Francisco (California) *Acacia* psyllid populations have been greatly reduced by the black lady beetle (*Diomus pumilo*) introduced from Europe and *Psyllaephagus bliteus*, a psyllid-specific parasitic wasp has been introduced from Australia to control psyllids (Dalhstein *et al* 2004; Dreistadt *et al.* 2004). There is no record on biological control of *Arytaina mopane.*

2.5 Honeydew

While some psyllids secrete a white wax, all produce honeydew, sometimes in palletized or crystallized form, on which blackish sooty moulds can grow (Dreistadt *et al*. 2004). A selected number of animals use honeydew as a source of food. The honeydew attracts many species of ants, which provide care and protection for the psyllids in exchange for the honeydew (Meyer 2001). The major component of psyllid honeydew is carbohydrate, with amylose being the major constituent in many species of nymphal Spondyliaspidae (Catling 1971; White 1972).

2.6 Elimination and source of heavy metals for predators

Iron, zinc, copper, manganese, aluminium, nickel, cadmium and mercury were found in 14 species of psyllids and in leaves of their host plants (Glowacka *et al*. 1997). They (Glowacka *et al*. 1997) report that, generally, psyllids accumulate low amounts of metals, but their accumulation generally increased with age. They further report that exuvia were important in the discharge of Al, Ni, and Mn and larval wax for Al, Cu and Ni. *Psyllopsis fraxini* discharges large amounts of Al, Fe, Cu, Mn and Cd with honeydew. Adults of *Cacopsylla mali, C. sorbi, Psyllopsis fraxini,* and *P. betulae* fall prey to ants leading to the transfer of Zn, Fe, Cu, and Ni to the ants (Glowacka *et al*. 1997).

2.7 Life cycle features

All psyllids pass through a life cycle consisting of an egg and five nymphal instars before emerging as an adult (Hodkinson 1973; Ernst & Sekhwela 1987). According to Hodkinson (1974) citing Lauterer (1963) and Linnavouri (1951), psyllids are strictly bisexual with the possible exception of *Psylla myrtilli*, which is claimed to be parthenogenetic. The male is the heterogametic sex (Walton 1960; Bhattacharya 1972). Male and female nymphs are morphologically distinct by the fifth instar (Ball &

Jensen 1966; Hodkinson 1974), with the females being larger than the males. Development of eggs is speculated to occur quickly in females and oviposition can begin within five days of emergence (Burts & Fischer 1967). Under tropical conditions, generations are continuous throughout the year but with growth rates governed by prevailing climatic factors and host-plant condition (Atwal *et al*. 1970; Pande 1972; Hodkinson 1974). There may be two to six generations per year depending on the species (Urquhart & Stone 1995), but most temperate psyllids have only one generation per year and seldom reach high population levels (Hodkinson 1974). The number of generations of *A. mopane* is still unknown.

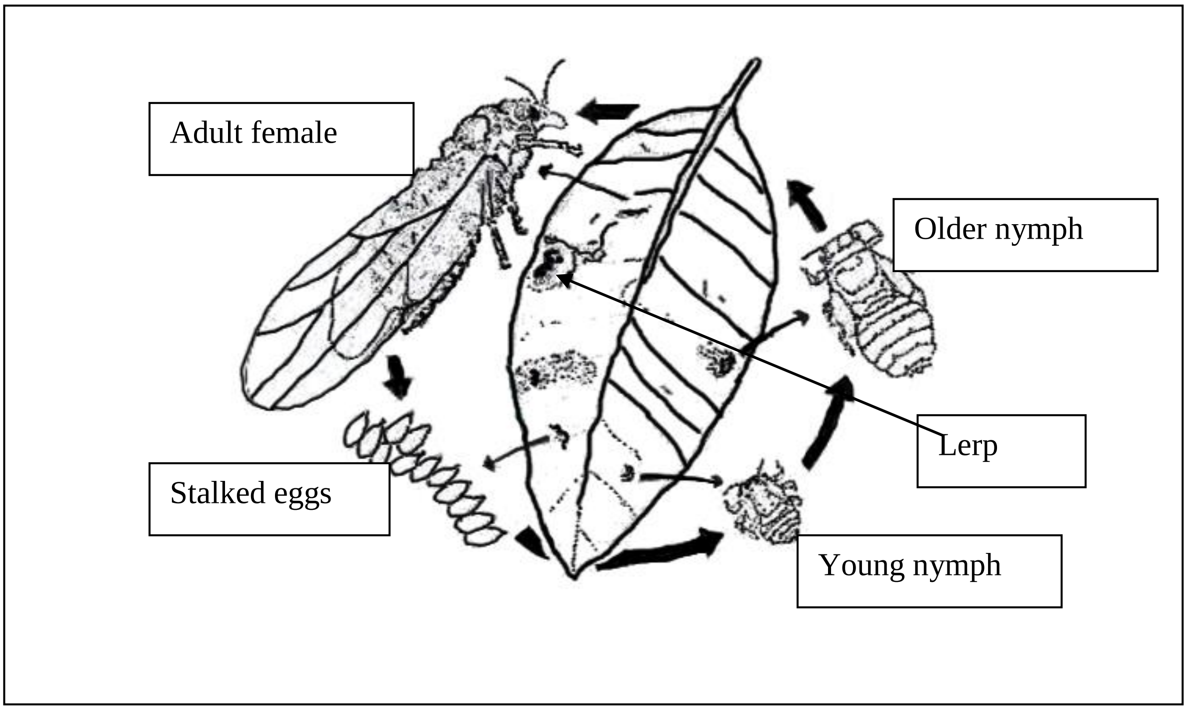


Fig. 3. A typical psyllid life cycle (Urquhart & Stone 1995).

2.7.1 Courtship and mating

Courtship behaviour precedes mating. The aggressive male approaches the passive female from the side, rotates his abdomen and grasps the female's valves with his parameters before inserting the aedagus (Cook 1963; Hodkinson 1971). In *Cardiaspina densitexta*, the males will repeatedly attempt to copulate, but the female will repel them (White 1970b), still others stridulate (Ossiannilsson 1950; Heslop-Harrison 1960; Campbell 1964) in an attempt to bring the sexes together especially in low densities (White 1970b).

Mating is a rather uncomplicated act in many psyllid species (Hodkinson 1974). Although copulation usually lasts no longer than about 30 minutes in most species (White 1970b; Hodkinson 1971; Pande

1971), it can last up to four hours in some species (Burts & Fischer 1967). In *Psylla pyricola*, a female must mate repeatedly to produce eggs to her full capacity (Hodkinson 1974). Each male of this species is capable of fully inseminating four females (Hodkinson 1974). An extensive and exhaustive search of the literature revealed no information pertaining to the courtship and mating behaviour of *A. mopane*.

2.7.2 Eggs

2.7.2.1 Morphology

According to Urquhart and Stone (1995), psyllids generally lay yellow, brown or black-stalked eggs. Clark (1962) describes the eggs of *Cardiaspina albitextra* as reddish-brown with a smooth, fairly thick chorion attached to leaves by stalks driven through the leaf cuticle during ovipositing.

Capener (1973) describes the eggs of the following psyllids: *Rhinocola crotalariae* sharply pointed at the apex, *Pseudophacopteron electum* elongate, pointed anteriorly and rounded posteriorly, with a very short stalk which rests in close contact with the leaf surface. Dreistadt *et al.* (1999) describe the eggs of the following psyllids; *Acacia* psyllids have tiny, golden-coloured eggs, Bluegum psyllids lay pale yellow to cream-coloured eggs, *Eugenia* psyllids have tiny, golden-coloured eggs, Pepper tree psyllids lay tiny, translucent white ovoid eggs (Dreistadt *et al*. 2004). The eggs of potato and tomato psyllids are very small and ovoid-shaped (Anonymous 2004). Fig psyllids have orange brown eggs, which are very small (0.5 mm in diameter) and often not visible to the naked eye (BGT-Fig psyllids 1998).

2.7.2.2 Laying areas, distribution and protection

Studies have shown that eggs are laid on various parts of the shoot system of the host plant. Clark (1962) and Urquhart and Stone (1995) state that stalked eggs can be laid on leaves, buds or in leaf axils. Eggs can be laid superficially or embedded. *Paratrioza cockerelli* lays its eggs superficially on a leaf or bud surface while *Arytaina spartii* deeply embeds its eggs in the plant tissue. In contrast, *Strophingia ericae* deposits its eggs in leaf axils (Hodkinson 1974). Bluegum psyllids lay eggs in crevices between buds and young leaf petioles or openly on young leaves, while *Eugenia* psyllids deposit their eggs primarily along the edges of young *Eugenia* leaves (Dreistadt *et al*. 2004). Fig psyllids' eggs are placed on the margin of the leaf but occasionally near the mid-vein or the centre of the leaf blade (BGT-Fig psyllids 1998). *Rhinocola crotalariae* eggs are oviposited on the flowers and young leaves of *Rhus* species while *Pseudophacopteron electum* eggs with their short stalks rest in close contact with the leaf surface and *Euphalerus marginalis* deposits its eggs between the folds of young *Burkea africana* leaves (Capener 1973).

Eggs are distributed either solitary or in clusters, rows, in circles or scattered, as in pepper tree psyllids (Dreistadt *et al.* 1999). Fig psyllids' eggs are placed in tightly packed clusters of up to 50 eggs per cluster (BGT-Fig psyllids 1998).

According to Watmough (1968a), eggs laid in protected areas such as leaf axils suffer less predation than those laid superficially on leaf surfaces. All psyllid eggs posses a basal pedicel, which is inserted into the host-plant tissue. Water is absorbed from the plant through the pedicel and the eggs quickly desiccate if the water source is removed (White 1968a; Hodkinson 1974).

2.7.2.3 Number laid and hatching

A mature psyllid female can lay over 500 eggs (Anonymous 2004). When females are numerous, hundreds and occasionally thousands of eggs may be placed on the same leaf (Clark 1962). Hatching of eggs is positively influenced by higher temperatures and retarded in shady areas (Watmough 1968b). Depending on climatic conditions it usually takes between 7 and 10 days for the eggs to hatch (Erbilgin *et al*. 2004).

2.7.3 Nymphs

The bodies of psyllid nymphs are flattened (Dreistadt *et al.* 1999) and have waxen threads projecting from the extremity of the abdomen (Urquhart & Stone 1995). Nymphs are yellow or yellow and brown (Garrison 1998). There are five instars that are largely similar in their morphological features (Compere 1916). The main structural changes occurring in their development are: increase in body size and mass, appearance of wings and an added number of marginal wax glands (Rowe & Knowlton 1935). Wing pad development is first noted in the third instar and becomes marked in the fourth and fifth instars (Pletsch 1947). The mean nymphal development period varies between 12 and 21 days (Knowlton & Janes 1931).

Nymphs are less active than adults. After hatching, they find suitable feeding sites where they remain to feed and develop through the five nymphal stages before emerging as adults unless some catastrophe (such as the death of the leaf) overtakes them (White 1971; Urquhart & Stone 1995). Most psyllids feed on leaves but some feed on fruits, flowers, stems or trunks (White 1971). Increases in soluble nitrogen sources in plant tissues, associated with water stress of the host plant (Catling 1969;

White 1969) and formation of new growth (Catling 1971; Pande 1972), enhance nymphal survival and growth rates.

Psyllid nymphs are highly susceptible to desiccation, particularly at high temperatures, which is an important factor contributing to population control (Catling & Annecke 1968; Atwal *et al.* 1970; Green & Catling 1971). The dorsoventral flattening of nymphs gives them a high surface area to volume ratio and hence a high potential for water loss (Hodkinson 1974). Consequently, they have evolved various mechanisms to reduce water loss. For instance, in *Cardiaspina densitexta,* nymphs emerge just after dawn and thus have time to settle and begin feeding before being exposed to the effects of high temperature and low humidity (White 1968b). Nymphs may also form an enveloping protective lerp or nest from the honeydew which they produce, as evident in some Australian species of the family Spondyliaspidae and A*rytaina mopane* in southern Africa (Russell 1971; White 1972; Ernst & Sekhwela 1987). Some species such as *Trioza fletcheri* live in the mesophyll tissue of the host plant (Bindra & Varma 1969). Others, according to Hodkinson (1974) and McDermott *et al.* (1996), live in the humidity-buffered environment of nipple galls on the foliage. Nymphs of *Pseudophacopteron electum* on emergence wander away from the eggshells and migrate to the abaxial surface of the leaf, where they establish themselves and sink below the surface as a pit-gall forms around them (Capener 1973).

Those species living in protected areas such as leaf axils, for example, *Aphalara* species produce small amounts of wax; temperate species living on stems such as *Psylla floccosa* produce copious amounts of flocculent wax threads (Patch 1909; Hodkinson 1974). In some tropical free-living forms such as *Swezeyana* species, the nymph is completely covered in a characteristic meshwork of wax filaments (Tuthill 1966).

In the lerp building psyllids like *Arytaina mopane* and C*ardiaspina densitexta,* ecdysis in the first four nymphal instars occurs beneath the lerp, the cast exoskeleton being pushed out from under the lerp by the nymph (White 1970a, 1972). Before the final moult to adulthood, the fifth instar nymph abandons its lerp and sits nearby until the skin ruptures and the adult skin emerges (White 1970a).

2.7.4 Dispersal of adult psyllids

Adult psyllids are restricted in their ability to fly long distances under their own power (Clark 1962). Air currents, however, assist in long distance dispersal. Glick (1939) reports *Paratrioza cockerelli* as a significant component of aerial plankton. Long-range dispersal (up to 13 km) by wind is most apparent in northern temperate species, which disperse in the autumn to seek shelter plants on which to overwinter (Hodkinson 1972). Some adults move between neighbouring leaves and shoots either by crawling (Clark 1962) or jumping with their strong hind-legs (White 1971). When disturbed some adults fly away for several metres and then turn around and land on another part of the same tree (Evans 1931).

2.8 Lerps

2.8.1 Structure

Lerps consist of a solid white structure, insoluble in water and polar and non-polar solvents and covered by a yellow-brownish layer (Ernst & Sekhwela 1987). Gilby *et al.* (1976) studied the structure of lerps of *Lasiopsyll rotundipennis* and *Cardiaspina albitextura* and found that the lerps of *C. albitextura* were open, lace-structured whereas that of *Lasiopsyll rotundipennis* were a solid shell with a surface structure of repeated parallel arcs.

2.8.2 Construction

It was initially thought that lerp construction was a specialization found only in some Australian genera of the Psyllidae (White 1972), but later research showed that *Arytaina mopane*, a southern African psyllid, also constructs lerps on mopane leaves (Ernst & Sekhwela 1987). As the nymph moult the new lerps are built on top of each other resulting in the lerp of the fifth instar nymph being conical (Ernst & Sekhwela 1987).

Wooster (1880) describes how three psyllid species (no species names reported) construct their lerp. The first makes its lerp almost exactly like a minute oyster shell, slightly convex, the rings of enlargement being added to the edge in such a way as to leave the starting point of the scale still at one edge, just as the hinge of an oyster shell. This species leaves its lerp plain; nothing is added on the outside for ornamentation or defence.

The second species constructs its lerp by adding around the edge equally, thus keeping the starting point in the centre. This kind of lerp is covered with curved silky hairs or loops, which are so numerous that they almost hide the dome. The third builds lerps that are conical when full-sized, and when 20 or 40 are together on one leaf, it looks like a miniature veritable soldiers’ camp. These tent-like structures have the starting point at the apex; the additions being made evenly all round the edge. When full-sized, they are plain, with the appearance of a series of flounces round the lower half; but when first formed and very small, they have a few or many glassy loops or threads round the edge, often longer than the diameter of the tent-like structure.

White (1972) describes how *Cardiaspina densitexta* builds its lerp. The nymph uses the tip of its abdomen to construct the lerp. Once it has started feeding the first instar larva builds a narrow arch over its body. One end of the arch is fixed to the leaf and the other end is left free. The larva then settles with its head pressed against the fixed end (White 1972). It is then able, by simply pivoting its body in a semi-circle around the point of insertion of its stylet, to build onto the arch to form a cover over its entire body. This is added to as the insect grows.

2.8.3 Chemical composition

The first recorded chemical analysis of lerp material was Anderson (1849) on the lerps of *Cardiaspina pervagata* (White 1972). He found starch as one of its constituents. Chemical analyses of the lerps of *C. densitexta* and a number of other species by various tests point to starch identical to that of the host plant, being the major constituent of the lerps (White 1972). The tests include spot testing with iodine, potentiometric iodine titration, precipitation with butanol, the production of spherocrystals of amylose, hydrolysis with sulphuric acid and paper electrophoresis of the hydrolysis products of lerps (White 1972). This observation is of interest as the occurrence of starch is not common in the animal kingdom (White 1972). In insects, Villneuve and Lemonde (1965) and Gilby *et al*. (1976) identified amylose and amylopectin in the pupae of a beetle. Starch has also been reported in certain Protozoa (Archibald *et al.* 1960) and from human granulating wounds (Nikuni *et al.* 1962).

Ernst and Sekhwela (1987) provide the chemical composition of *Arytaina mopane'*s lerps and compared it to that of Australian psyllids feeding on leaves of *Eucalyptus* species (Table 1). The most obvious difference is the lack of starch and the high amounts of monosaccharides and water insoluble carbohydrates, mainly uronic acid, in the lerp of *A. mopane*. In the Australian species, the stability of the lerp is provided by starch, while in the mopane psyllid it may be based on uronic acid (Ernst & Sekhwela 1987).

Table 1. Chemical composition of *A. mopane* lerps in Botswana (Ernst & Sekhwela 1987).

Chemical component	% Lerp (by weight)
Water	13.70 ± 0.50
Lipid	0.01
Ash	1.06 ± 0.05
Protein	1.44 ± 0.24
Phenolic acids	0.10 ± 0.01
Water-soluble sugars	46.90 ± 8.34
Starch	<1.00
Water-insoluble carbohydrates	36.77 ± 8.31

2.9 Psyllid hibernation

In northern temperate and arctic regions, adult psyllids have evolved mechanisms to survive the winter period when the host-plant is dormant (Hodkinson 1974, citing Vondráček 1957). Shrubs, grass and similar low herbage often serve as shelter plants for hibernation. For instance, *Psylla melanoneura* utilizes thick clumps of grass as shelter plants, which grow among its host species. *Trioza alacris*, the Bay psyllid, passes the winter months in a comatose condition in curled-up leaves and debris lying among its true food-plant. *Arytaina genistae* hibernates on broom and Deyer's Greenweed (*Genista tinctoria*), and lay eggs whenever temperatures are high enough (Watmough 1968b). *Trioza apicalis,* one of the 93 psyllids found in Sweden hibernates as an adult on a shelter plant and migrates to its host, *Daucus carota,* in early summer shortly after the carrot seedlings have emerged (Valterová *et al.* 1997). The hackberry nipple gall maker, *Pachypsylla*, usually has one generation per year, with the adults emerging from crevices in the rough bark of the hackberry where they overwinter (Johnson & Lyon 1988; McDermott *et al*. 1996).

Hibernation may also take place in the egg stage as with *Arytaina spartiophila* in Britain. Larval hibernation has been recorded only in species belonging to the subfamilies Aphalrinae, Psyllinae and Triozinae (Heslop-Harrison 1937).

SECTION 2

2.10 *Arytaina*

Arytaina is one of the five Arytaininae psyllid genera that feed on legumes. The four other genera are: *Arytainilla, Livilla, Pseudacanthopsylls* and *Cyamophila*. The genus *Arytaina* consists of 16 species (Watmough 1968a; Capener 1970; Sullivan U.D.; Foreign Exploration Objective 1 2002; Percy 2002) (Table 2).

Table 2. *Arytaina* species, occurrence and host plants.

Species	Occurrence	Host plant
A. adenocarpi	Africa	*Adenocarpus* species
A. Africana	Africa	*Cytisus* species
A. bicolor	Europe	*Cytisus villosus*
A. boharti	Europe	*Cytisus* species
A. capensis	No data	*Rhus* species
A. devia	Canary Islands	*Chamaecytisus proliferus*
A. genistae	Canary Islands, Europe	*Cytisus scoparius, Sarothamnus scoparius*
A. karrooensis	Africa	*Acacia karroo*
A. maculate	Canary Islands	*Cytisus* species
A. Montana	No data	*Spartocytisus* species
A. mopane	Southern Africa	*Colophospermum mopane*
A. nubivaga	Canary Islands	*Spartocytisus supranubius*
A. spartii	Europe	*Cytisus scoparius*
A. spartiophila	Europe	*Sarothamnus scoparius*
A. torrifrons	Asia	*Spartocytisus* species
A. vittata	Asia	*Spartocytisus filipes*

Arytaina devia and *A. nubivaga* are endemic to the Canary Islands. *Arytaina* is suggested to be the only unambiguously monophyletic genus in the Genistae feeding Arytaininae. Members of *Arytaina* predominantly feed on host plants in or allied to the genus *Cytisus* (Percy 2001). The distribution of *Arytaina* is very cosmopolitan (Percy 2001).

2.11 *Arytaina mopane*

Our knowledge on *A. mopane* is severely limited, consisting only of the works of Pettey (1925) and Ernst and Sekwhela (1987). In the report of Pettey (1925), morphological descriptions of males and females are provided. Ernst and Sekwhela (1987) analysed the chemical composition of lerps and nutrients in *C. mopane* leaves.

2.11.1 Morphology

Pettey (1925) describes *A. mopane* from six male and six females collected by Claude Fuller on *Colophospermum mopane* from Musina, Limpopo Province as follows:

Head: Is somewhat deflexed, not quite as broad as the thorax, including the eyes. Vertex about twice as wide as long; slightly rugose, not pubescent; emarginate (curved towards genae) at posterior margin; flat; each half somewhat elevated at its anterior inner angle bordering the median ocellus; a distinct broad fovea in the center of each half, deepest in the middle of each half, on the same plane as genae. Genae slightly depressed, rather short, broadly rounded at apex, concave near base of antennae, divergent near apex, coarsely pubescent, each with one or two longer hairs at the apex just outside the middle of each genae and somewhat central, but directed forward. Frons not visible. Middle ocellus depressed a little below vertex; posterior ocelli in outer posterior angles of vertex and slightly raised above plane of vertex. Ocelli yellowish-brown. Compound eyes are of normal size and slightly recessive and reddish brown. Antennae slender and longer than head and thorax combined; sparsely pubescent; third segment longest; segments four to seven inclusive sub-equal; segments nine and ten, combined, shorter than eight, which is shorter than seven; ten terminated by two rather short, sub-equal spines. Antennae pale yellow, segments four to eight inclusive, brown at tips; nine and ten dark brown. Terminal segments of labrum dark brown.

Thorax: Of medium depth; broad; somewhat arched; very finely punctate, not pubescent. Pronotum flat; not extending laterally farther down than the middle of the eye; with two foveae on each side, the innermost of which is behind each posterior ocellus; praescutum with two rather large semicircular depressions, one on each of the middle line and on the anterior margin; middle line of scutum indistinct. Thorax pale yellow with a narrow, brown lateral line extending dorsoventrally, dividing the mesothorax from the metathorax.

Wings: Hyaline. Fore-wings are rather long; slender; rounded at apex; widest some distance before apex; all veins with a double row of small hairs; margin of wing with minute hairs except inner margin at base (anal area). Pterostigma opaque, long, narrow and covered with minute scattered hairs; both marginal cells of about equal length.

Legs: Fairly stout; long; pubescent; hind-tibia without basal spur, with about six small black spines at apex, arranged on the anterior margin; metacoxal spurs well developed, slender, conical, at least twice as long as wide at base; tarsal segments sub-equal. Legs are pale yellow with black claws. The apex of tibia and the first tarsal segments of the hind-legs bear spines.

Female genitalia: Genitalia segments of medium size; not very long; stout; minutely pubescent except several very long hairs before the apex on the dorsal valve; dorsal valve longer than the ventral and blunter at tip; ventral valve swollen ventrally, the hairs more scattered at the acute apex.

Male genitalia: Genitalia segment of medium size; minutely pubescent except a cluster of long hairs on the anterior margin of the ventral valve; forceps slender, cone-shaped, narrowly rounded at apex shorter than anal valve; basal half of anal valve wider than the apical half which is abruptly narrower posteriorly at the middle of the valve.

Measurements: Female: length of body 3.7 mm, length of fore-wing 3.16 mm, width 1.36 mm. Male; length of body 3.6 mm, fore-wing 2.6 mm, width 1.05 mm. Female: width of head plus eyes 0.95 mm, male 0.88 mm.

Two female types described as follows: one has numerous, scattered, very small dark brown spots on the vertex, genae, thorax, and wings; four broad reddish-brown longitudinal stripes on the scutum; a brownish transverse stripe on each segment of the abdomen, more distinct and darker brown above; dorsal valve of genitalia brown, and the ventral valve yellow, except the apical third which is black; the fore-wings with numerous small brown maculae, much more numerous in the apical fourth and along the inner margin; the first marginal cell, cell M, the second marginal cell, and cell R with more or less semi-circular hyaline area bordering the outer margin of the wing. The other female similar to the one just described except that the wings have only a few scattered, very small, brown maculae.

2.11.2 Life cycle and mineral content of lerp

The life cycle consists of an egg, five instar nymphs and the adult (Ernst & Sekhwela 1987). Composition of the lerp of *A. mopane* consists predominantly of monosaccharides, fructose and glucose and contains high potassium but low nitrogen concentrations (Tables 3 and 4). Ernst and

Sekhwela (1987) in comparing the mineral nutrients of lerps and leaves of *C. mopane*, found that the concentration of mineral nutrients in the lerps were high for potassium and nitrogen and low for manganese and zinc. Furthermore, these values were twice (potassium) and 16 times (manganese) lower than in the leaves.

Table 3. Concentration and amount of mineral nutrients of the lerps of *A. mopane* and leaves of *C. mopane* in Botswana.

Mineral nutrient							
	N	P	K	Ca	Mg	Mn	Zn
Concentration (µ mol/g dry mass) Lerps of psyllid	124±21.0	14.1±0.5	247±2.0	1.4±0.1	1.5±0.0	0.1±0.0	0.1±0.0
Concentration (µ mol/g dry mass) Leaves of *C. mopane*	1470±45.0	46±3.0	450±18.0	17.0±0.4	7.5±0.1	1.6±0.1	0.7±0.0
Amount (µ mol per leaf with two leaflets) Lerps of psyllid	377.6±44.1	32.7±4.3	568.1±78.0	3.11±0.3	3.45±0.4	0.35±0.0	0.23±0.0
Leaf	311.6±57.0	9.84±1.4	95.9±10.5	3.52±0.8	1.60±0.3	0.33±0.1	0.15±0.0
Mean ratio lerp/leaf	1.21±0.2	3.34±0.9	5.92±0.2	0.86±0.1	2.16±0.2	1.05±0.1	1.53±0.3

(n = 15, mean ± SE) (Ernst & Sekhwela 1987).

Table 4. Concentration of water–soluble sugars in the lerps of *A. mopane,* feeding on leaves of *C. mopane* in comparison to the concentration of water-extractable sugars from uninfested *C. mopane* leaves in Botswana.

	Lerp (mg/g DM)	Leaf (mg/g DM)
Sucrose	9.7±1.20	0.03±0.00
Raffinose	4.1±0.10	0.10±0.02
Glucose	42.1±4.40	3.34±0.05
Galactose	>0.001	>0.01
Fructose	102.7±15.60	1.67±0.08
Anthron-sugar (after hydrolysis)	469.0±83.40	No data

(n = 5) (Ernst & Sekhwela 1987).

SECTION 3

According to Newberry (1980) and Becerra and Venable (1989), considerable reductions in leaf production, leaf size and even seed production are known to occur in plants infested with homopterans. Vranjic and Gullan (1990) and Styles (1993) state that infestation of sap-sucking insects' results in a decrease in both the value and palatability of browse in such plants. The presence of *Arytaina mopane* on *C. mopane* consequently may effect changes on the browsability of *C. mopane*, which in turn will impact either positively (e.g. the sugary lerps on leaves may be a source of additional energy) or negatively (e.g. reduction in seed production or leaf size in line with homopterans) on game farming.

2.12 Game farming in the Limpopo Province

Game farms provide a valuable source of income to the Limpopo Province and its inhabitants through its four levels of operation. The first level is the sale of hunts and venison; the second level is the sale of live game at auctions and the translocation of these animals; the third level being the processing of animal products and the fourth level is the game lodge, conference facilities, and related services. Job opportunities open up at all four levels and the value-added production on the land rises dramatically.

From 1983 to 1998 foreign trophy hunters contributed gross revenue of 48 million South African Rand per year to the economy of the Limpopo Province. Wildlife sales earned a total income of *ca*. R56 million per year to the game farmers of the Limpopo Province. Venison generated an income of R7 million per year and local hunting R82 million. In addition, the game farms in the Limpopo Province during this period created employment for at least 20 000 people. It turns out that wildlife in the Limpopo Province plays an important role in the income and employment of the area (Bothma 2002).

2.13 Factors influencing browsing by animals

Palatability depends upon a number of interacting factors linked to animals as well as the environment. Feeding behaviour is controlled by factors of animal and plant interaction. The animal factors include species type, physiological status and previous experience with a specific vegetation type, and habitat exploration. The plant variables relate, among other things, to availability and the physical and qualitative characteristics of plant biomass: environmental variables comprise botanical composition, plant structure, forage quality and grazing pressure (Dicko & Sikena 2005). The forage intake environment is influenced by a number of important factors, including:

- Herbivore species and size.
- Forage quality.
- Plant characteristics (leaf size or shape, spines or thorns and tree height).

The quality of leaves as food for herbivores involves a complex combination of characteristics, which often change in the course of a season (Schroeder & Malmer 1980; Cooper *et al*. 1988). As forage quality increases the amount of forage necessary to meet nutrient requirements decreases (Cooper *et al*. 1988). Although nutrient requirements are useful guidelines, animals do not stop foraging once requirements for a certain performance level are met. Therefore, in general, as forage quality increases, intake also increases. Studies involving all-forage diets have consistently shown that intake increases as forage digestibility increases from 40 to 80 percent (Lyons *et al*. U.D.). In southern Africa browse is more important to mixed feeding herbivores in the dry season than grass (Anderson & Walker 1974), the nutritional value of browse generally being higher than that of grass, especially when grass lignifies (Bonsma 1942; Dietz 1965).

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

The study area (Fig. 4), located between Tzaneen and Letsitele, is about 0.6 hectares of abandoned farmland dominated by *C. mopane* trees and positioned approximately 500 metres from the main road in the Ritavi District. It lies approximately 24 km east of Tzaneen on the Tzaneen-Phalaborwa road (R71). According to the S.A.Weather Service (2005) stations classification, the area falls under Station [0679106A8] Grenshoek, Tzaneen and lies between S 23˚ 50' 30. 9", E 30˚ 21' 56. 7" and S 23˚ 50' 28.7", E 30˚ 21' 58.6". The area lies 508.4 m above sea level. The two main urban concentrations are Tzaneen and Nkowankowa and the smaller urban center of Letsitele. A large number of smaller villages are scattered around the area (DWAF 2003).

3.1.1 Vegetation

The vegetation is typically a short, fairly dense stand of woody *C. mopane* associated with a number of *Acacia* species with an extensive grass layer underneath (Fig. 5). The grass layer includes *Anthephora pubescens, Brachiaria ngropedata, Heteropogon contortus, Stippagrotis uniplumis, Eragrostis nindensis, Panicum maximum* (patches) and *Chloris roxburghiana* (Acocks 1988).

3.1.2 Climate

Climatic conditions in Tzaneen offers a markedly different climate, with subtropical conditions of the escarpment providing weather more suited to dense forests (high summer rainfall) than the thorny bushveld above the escarpment (Tzaneeninfo 2004).

The mean maximum and minimum winter temperatures (June 2002 to September 2004) were 22.8˚C and 11.4˚C respectively (Table 5) (S.A. Weather Service 2005). The mean total rainfall for the same period was 12.6 mm (Table 6). The percentage humidity for the same period at 8:00, 14:00 and 20:00 were 64.2, 41.7 and 57.9 respectively (Table 7) (S.A.Weather Service 2005).

Although Tzaneen experiences a moderate all-year climate, a high summer rainfall can be expected between December and February (Table 6). Rainfall can be well over 1 000 mm per year along the western escarpment while in the Lowveld region in the eastern parts, rainfall decreases to less than

300 mm per year. The Letaba area has a mean annual precipitation of 612 mm with a mean annual evaporation of 1 669 mm (DWAF 2003).

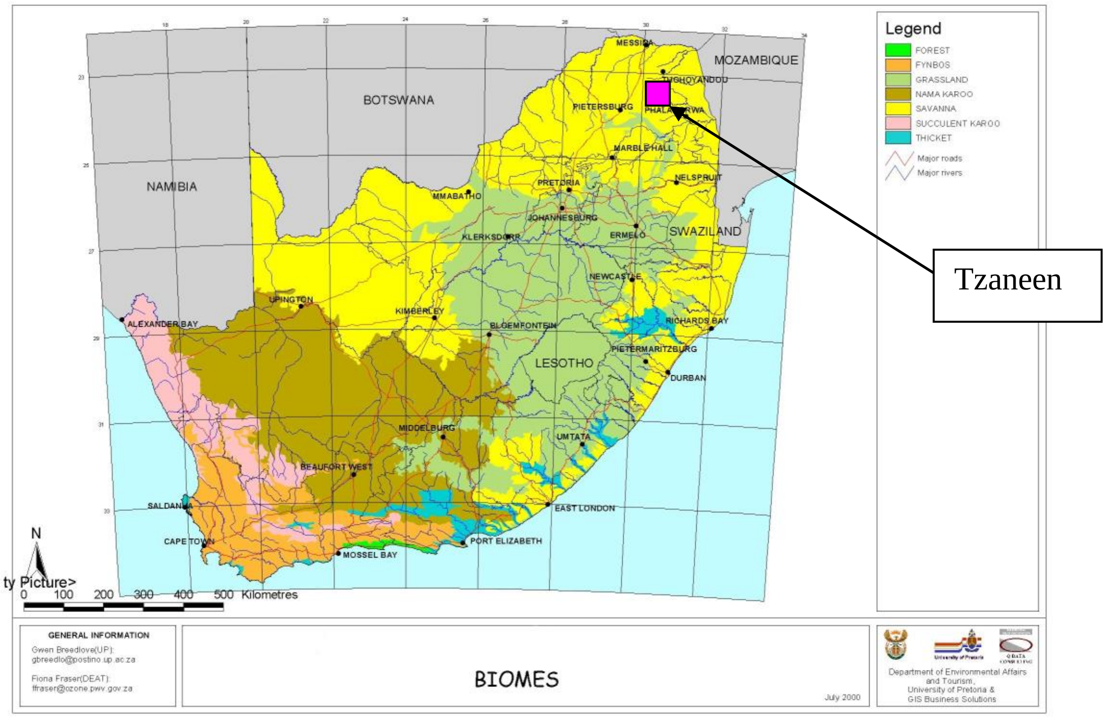


Fig. 4. Map of South Africa showing the study area (DWAF 2000).

Fig. 5. Vegetation of the study area.

Table 5. Monthly mean maximum and minimum temperature (˚C) data for Station [0679106A8] Grenshoek, Tzaneen.

Maximum												
Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2002	28.4	26.8=	27.3	25.6	24.3	20.6	22.5	22.9	24.5	25.6	26.2	27.9
2003	29.5	29.0	27.8	26.3	23.6	20.3=	22.0=	23.5	25.2	26.6	26.8	29.3
2004	27.7	26.7	24.2	24.5	23.1	20.5	20.7	24.9	25.4	27.1	30.3	29
2005	29.0	30.1	27.6	25.4	25.4=	24.0	22.9	25.7	28.7	28.7	28.5	
Minimum												
2002	18.7	18.3=	17.8	16.3	14.1	11.5	12.1	11.9	11.6	15.5	15.6	17.8
2003	18.9	19.3	18.1	16.6	14.1	11.2=	10.6=	11.8	11.3	15.9	17.0	18.0
2004	18.6	18.4	17.3	16.2	13.1	11.1	10.3	11.6	11.8	16.5	19.0	19.6
2005	20.0	19.7	18.2	16.8	14.9	14.1	12.2	14.7	15.9	16.7	17.8	

= Indicates that the mean for the month is unreliable due to missing daily values. (S.A.Weather Service 2005).

Table 6. Mean monthly rainfall (mm) data for Station [0679106A8] Grenshoek, Tzaneen.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2002	104.6	38.0=	91.6	40.6	12.4	32.0	1.2	9.8	17.4	58.4	14.6	93.6
2003	75.4	152.4	53.8	5.6	1.4	16.4=	1.6=	0.4	31.6	58.0	55.0=	117.6
2004	105.0	331.2	289.6	79.0=	6.8=	6.2	9.4=	14.8	11.2=	42.4	67.4	202.8
2005	110.8	23.0	100.6	89.4	0.0=	6.4	0.4	6.2	0.0	11.2	49.6	

= Indicates that the mean for the month is unreliable due to missing daily values. (S.A.Weather Service 2005).

Table 7. Mean humidity (%) data for Station [0679106A8] Grenshoek, Tzaneen.

8:00												
Year	Jan.	Feb.	Mar.	Ap.r	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2002	75.6	80.5=	77.4	77.4	64.7	72.1	58.4	74.5	67.3	72.7	71	79.5
2003	78.0	86.0	79.3	84.3=	#	75.0=	62.8=	62.5	66.8	75.6	80.9=	80.2=
2004	88.3=	88.0=	91.6	87.0=	83.1=	#	34.0=	69.1=	#	#	#	#
2005	#	#	#	#	#	#	#	#	#	#	#	#
14:00												
2002	56.5	63.8=	55	53.4	43.5	49.9	38.3	50.0	43.1	50.8	49.7	57.7
2003	52.4	58.1	54.6	57.3=	#	55.3=	39.2=	35.9	43.8	52.5	65.5=	63.2=
2004	68.5	66.6	80.2	69.7	57.1=	#	16.0=	45.5=	#	#	#	#
2005	#	#	#	#	#	#	#	#	#	#	#	#
20:00												
2002	68.4	74.1=	65.9	67.7	55.1	62.7	47.7	62.8	56.3	60.5	59.1	67.1
2003	66.6	72.7	70.6	80.6=	#	65.0=	51.9=	45.3	55.2	60.7	73.0=	74.9=
2004	79.3	76.9	91.9	86.3=	81.1=	#	70.0=	62.7=	#	#	#	#
2005	#	#	#	#	#	#	#	#	#	#	#	#

Data not available. = Indicates that the mean for the month is unreliable due to missing daily values (S.A.Weather Service 2005).

3.2 Sampling method

The research was conducted between July and September 2004. Field visits to the study site were undertaken three times a week between 10:00 am and 2:00 pm. Morning and afternoon temperatures were occasionally recorded at the site. Thirty leaves infested with *A. mopane* were randomly collected from each of 10 randomly selected *C. mopane* trees. North, south, east and west facing leaves as well as low, middle and upper canopy leaves were randomly collected. Trees were about 3 metres apart in the 0.6 hectare study area. The collected infested leaves were used for the following analyses under laboratory conditions.

3.2.1 Eggs

The length and width of 500 eggs were measured. The calculated mean number of eggs per leaf was used to determine the number per tree. To determine the number of eggs laid per female, 25 adult females were collected from the sampling site and transported to the laboratory. Each was placed in a transparent plastic bottle with 1 cm^3 of water, supplied with fresh uninfested *C. mopane* twigs with leaves. Stockings were used as lids to cover the bottles. The leaves and twigs were observed daily for egg deposition for 11 days.

3.2.2 Nymphs

3.2.2.1 Morphology and behaviour

Each lerp was opened with a pair of forceps and the nymphs under the opened lerps as well as those wandering on the leaflets were counted and measured. The nymphs were grouped into 5 instar stages based on body length; length of antennae; size and shape of wing pads and shape and spacing of darkly pigmented areas on the dorsal part of the thorax. Permanent slides were made of some of the specimens by mounting in glycerine jelly. The preparation was sealed with clear nail varnish. A total of 30 nymphs of each instar were measured. In both field and laboratory the behaviour of wandering nymphs as well as those whose lerps were opened was closely observed. The method of lerp construction was also observed.

3.2.2.2 Specimen preparation

Specimens (nymphs collected by the method described above) were ultrasonically cleaned for 10-12 seconds to remove mucus and debris. Specimens were dehydrated through graded ethanol series (70%, 80%, 96% and 100%), over a period of 3 hours, critical point dried (CPD) with CO_2 in absolute ethanol, mounted on aluminium stubs and sputter coated with gold–palladium. Specimens were viewed and micrographed in a Jeol 6100 Scanning Electron Microscope (SEM) at 7kV.

To investigate the feeding mechanism, leaves infested with *A. mopane* were fixed in formalin-acetate acid alcohol (FAA) (Johansen 1940) or Paraformaldehyde (PFA). Small sections infested with lerps from leaflets were dehydrated in alcohol with increasing concentrations, then in N-Propanol and N-butanol. These were then infiltrated with glycol methacrylate and thereafter placed into an oven (Feder & O’Brien 1968). Sections 3 µm thick were made with a Jung 2055 Multicut Rotary Microtonme. Staining of these sections was carried out according to the Periodic acid–Schiff’s reaction of Feder and O’Brien (1968) using 0.05% toludine blue O in benzoate buffer at pH 4.4 (Sidman *et al.* 1961) and mounted in ethylene.

3.2.3 Lerps

The number of lerps per tree was estimated using 300 leaves per tree. The structure of lerp was determined by placing a fresh 5th instar lerp in trichloroethalene (TCE) for five minutes. Soluble parts of the structure dissolved. The insoluble part was sputter coated with gold-palladium, and viewed with a Jeol 6100 Scanning Electron Microscope at 7kV. Lerps were sprayed with water to confirm their insolubility.

3.3 Carbohydrate and mineral analyses

Infested and uninfested *C. mopane* leaves and lerps were randomly collected from the 10 marked trees at the study site. Leaves were collected from lower, middle and upper canopies of the marked trees. Lerps, eggs and nymphs on the infested leaves were all completely removed before weighing and packaging. The leaves weighing 58 g each (i.e. 58 g infested leaves and 58 g uninfested leaves, fresh mass) and the empty lerps weighing 20 g DM was sent to ARC-Irene Analytical Services, and ARC-Institute for Soil, Climate and Water for mineral and carbohydrate analyses. These laboratories hold SANAS accreditation for analyses with an ASM number. The major mineral elements tested for were Nitrogen (N), Phosphorous (P), Potassium (K), Calcium (Ca), Magnesium (Mg), Sodium (Na), Iron (Fe), Zinc (Zn), Manganese (Mn) and Copper (Cu). The minerals tested for were compared with the mean values of a parallel project at the University of Limpopo from Musina Experimental Farm. Lerps were tested for starch with iodine solution.

3.3.1 Determination of Carbohydrates- HPLC method

Samples sent to ARC-Irene Analytical Services were used to determine the carbohydrates in lerps using the HPLC method. This method specifies a high performance liquid chromatographic (HPLC) technique for the determination of carbohydrates in feed and food products. In the HPLC method the protein in the test sample is precipitated with tungstate and the concentration of the different carbohydrates in the filtrate are determined by HPLC with refractive index detection (Smit & Nel 1987).

3.3.2 Mineral analyses

ARC-Institute for Soil, Climate and Water used samples sent to determine the various mineral elements as follows; two different methods were used in the determination of the following macro and micro elements; Ca, Mg, P, K, Na, Fe, Zn, Mn, Cu and N.

3.3.2.1 Method for nitrogen determination

The dried and milled sample was used directly for N determination on a Carlo Erba NA 1500 C/N/S Analyzer (Dumas Method). A few mg of the sample was weighed into a tin container and ignited at high temperature in oxygen (on a chrome oxide catalyst). The gases produced pass through silvered cobalt oxide, a column of copper (reducing the oxides of nitrogen to nitrogen gas and removing the excess O_2), and water vapour and CO_2 traps and are then separated by gas chromatography using a helium carrier gas and detected by a thermal conductivity detector. Ethyl ester of 4-Aminobenzoic acids, which contains 8.48% N, was used (Bellomonte *et al*. 1987).

3.3.2.2 ICP determination of macro- and micro- elements

An aliquot of the digest solution is used for the ICP-AES (Inductively Coupled Plasma Atomic Emission Spectrometer) determination of these elements. The ICP-ARS is a multi-element instrument that can determine all these elements effectively at the same time. The instrument used (JY Horiba Ultima) is sequential so the elements are not quite determined simultaneously. They are however, almost determined simultaneusly with only one or two seconds between each element so that the sample may be analyzed for all ten elements within two or three minutes. Each element is measured at an appropriate emission wavelength, chosen for high sensitivity and lack of spectral interferences. If necessary, one or more of the elements may be checked, either using a different wavelength on the ICP or by a different method. The instrument is set up and operated according to the recommended procedures in the instrument manual. It is calibrated against a series of standard solutions, containing all the elements of interest in the proportions found in typical leaf samples.

3.3.2.3 AAS determination of Ca, Mg, Fe, Mn, Zn and Cu

The digest solution was analyzed with flame atomic absorption spectrophotometry (AAS) for Fe, Mn, Zn and/or Cu using an Air-Acetylene Flame with wavelengths of 248.3 nm, 279.5 nm, 213.9 nm and 324.7 nm for Fe, Mn, Zn and Cu respectively. An aliquot of the solution is diluted for determination of Ca and/or Mg by AAS in a Nitrous Oxide-Acetylene Flame, using a wavelength of 422.7 nm for Ca and 285.2 nm for Mg (Antanasopoulos U.D.).

3.4 Analyses of organic constituents of lerps

The analytical technique of energy dispersive X-ray spectroscopy (EDS) in scanning electron microscope (SEM) was used to determine the constituents of lerps with analytical sensitivity of 0.1 wt %.

3.5 Presentation and analyses of results

Statistical analyses performed, included ANOVA (Analysis of Variance) and the Mann-Whitney Rank Sum Test. For ANOVA a desired type 1 error of 0.05 was specified. Graphs were constructed using Sigmaplot ver. 9.01, 2004 (Systat software Inc.).

CHAPTER 4

RESULTS

SECTION 1

ARYTAINA MOPANE

4.1 Life cycle features

The life cycle of *Arytaina mopane* consists of an egg, five nymphal instars, and an adult and thus constitutes an incomplete metamorphosis as in all Homoptera.

4.1.1 Eggs

4.1.1.1 Distribution and number recorded

Eggs were randomly laid on mature green and senescent leaves with no preference for north, south, east or west facing leaves. Eggs were deposited in the following areas of the leaflet: along veins, between veins, along leaf margins and on the pulvinus (Fig. 6 A and B). A few eggs were occasionally found on the leaf petioles but not on the twigs. Eggs also occurred randomly in the lower, middle and upper strata of the tree canopy. Seventy six percent of eggs were found along veins on both adaxial and abaxial leaflet surfaces. Egg packs were randomly placed on the leaflet. Very often, they were laid in clusters of various sizes and/or occasionally solitary on either surface of the leaflet. Eggs in a cluster were spirally arranged and touched one another (Fig. 7). Table 8 shows the differences in the numbers of clusters and eggs on abaxial and adaxial leaflet surfaces. The abaxial leaflet surfaces contained more eggs (68%) than the adaxial (32%).

The mean number of eggs per leaf comprising two leaflets was 1340. The calculated number of eggs per tree was 4 581 460 based on a tree with a mean of 3 419 leaves (n=5) bearing in mind that trees at the end of the dry season are senescent and that some leaves have already been shed. Under laboratory conditions, this study recorded a mean of 235 eggs laid by 25 females. The maximum number of eggs laid by a female was 320 and the minimum was 30 in the laboratory. However, some leaflets collected from the field contained more than two thousand eggs.

4.1.1.2 Morphology and attachment

Eggs in a cluster appeared to the naked eye as black spots on the leaflet (Fig. 8). Egg clusters could easily be distinguished from fungal black spot infections, which are common on leaflets. Fungal black spots penetrated the leaflet tissue and were visible on the direct opposite side of the leaflet, whereas the egg black spots did not penetrate the leaflet tissue and were subsequently not visible at the direct opposite end.

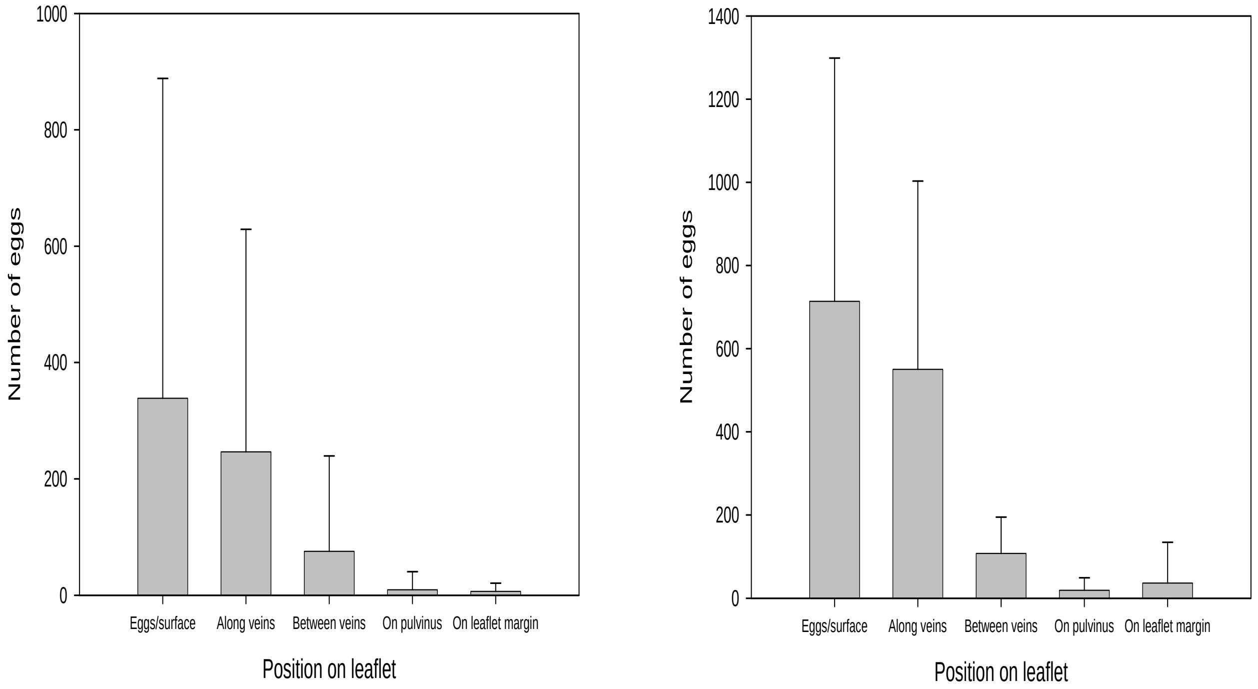
Eggs were conical in shape with a basal pedicel and an apical filament (Figs 9 & 10). Egg size ranged from 245-360 µm in length and 100-125 µm in width at its broadest part. Eggs laid in the laboratory and those found in the field were similar in size. The thickness of the eggshell varied from 1.0 µm to 1.34 µm (n=30). Under the light microscope, the eggs were black with smooth shiny grey spots closely spaced near the basal end of the egg. Scanning electron microscopy revealed the egg to be surrounded by a membrane (0.30 µm thick), which had a reticulate-sculpture (Fig. 11). The reticulate sculpture was 1.5 µm thick and 4.0 µm wide (Fig. 12). The black surface of the egg below the membrane was smooth (Fig. 13).

No pedicel puncture marks were observed on the leaflet surface (Fig. 13) to indicate egg attachment to leaflet surface via the pedicel. Eggs were rather glued to the leaflet surface in such a way that they could not be removed without breaking them. Eggs were not washed away by rain. Mean pedicel length was 84 µm and that of the filament 266 µm. The part of the egg where the pedicel was attached and the ventral part of the egg felt sticky to the touch. A small groove could be observed at the pedicel's attachment to the egg (Fig. 10). An egg felt gel-like and when crushed a colourless jelly-like liquid substance exuded.

4.1.1.3 Hatching

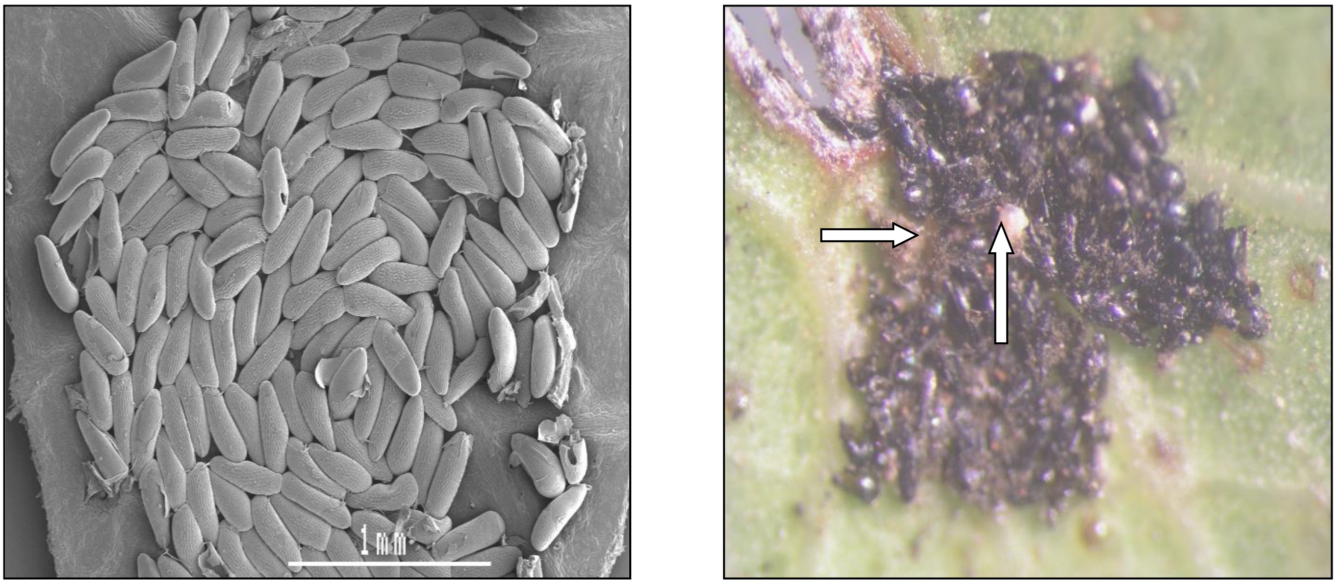
All eggs in a cluster hatched nearly simultaneously but independently of other clusters on the same leaflet. Unhatched eggs were found on dried shed leaves in the last week of September 2004 when *C. mopane* trees were completely leafless. Eggs from different clusters, either on the same leaflet or on other leaflets, hatched at different times throughout the period of investigation (July to September 2004).

During hatching, an egg opened longitudinally before splitting transversely (Fig. 14). It was found that a mean 86% of the eggs collected from the field hatched while none of the eggs laid by captive females in the laboratory hatched.



A. **B.**

Fig. 6. Distribution of eggs on adaxial, **A** and abaxial, **B** leaflet surfaces. (Vertical bars indicate standard deviation).



A **B**

Fig. 7. Cluster of eggs. **A**. Scanning electron micrograph showing the spiral arrangement of eggs, **B**. Light micrograph of eggs showing missing egg spots (arrows).

Table 8. Number of egg clusters and eggs per cluster.

	Number of egg clusters		Number of eggs per cluster	
	Abaxial	Adaxial	Abaxial	Adaxial
Mean	7.73	3.56	713.96	337.83
SD	± 5.64	± 4.61	± 584.57	± 550.25
Minimum	0	0	0	0
Maximum	29	17	2726	1903

Number of egg clusters; abaxial versus adaxial

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference ($P = < 0.001$), using the Mann-Whitney Rank Sum Test.

Number of eggs per cluster; abaxial versus adaxial

The difference in the median values between the two groups is greater than would be expected by chance; there is a statistically significant difference ($P = < 0.001$), using the Mann-Whitney Rank Sum Test.

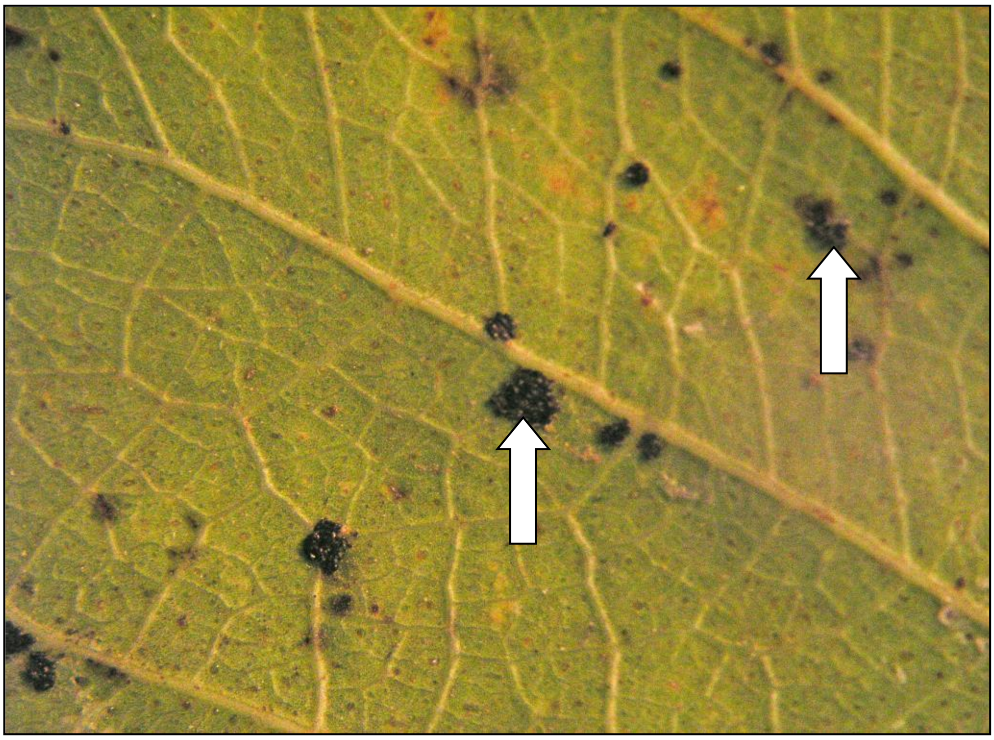


Fig. 8. Appearance of eggs to the naked eye (arrows).

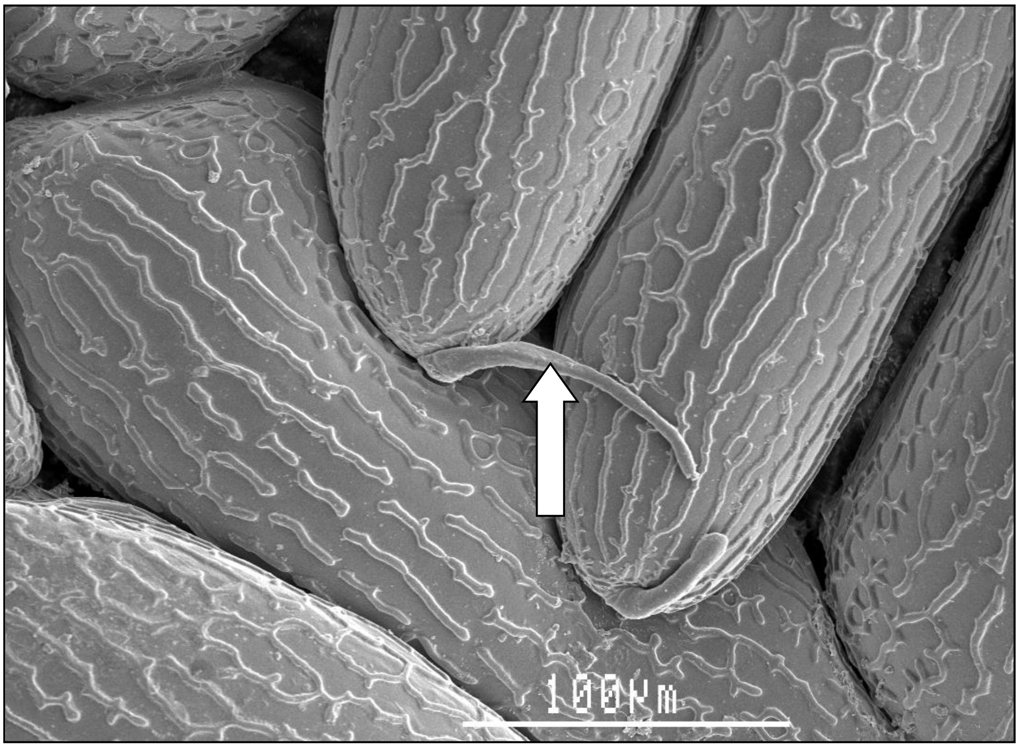
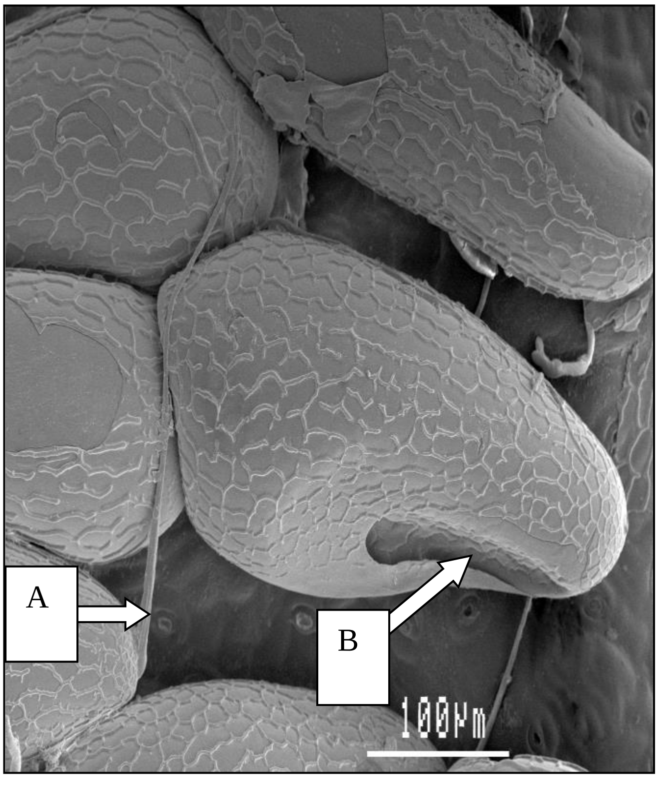


Fig. 9. Egg pedicel (arrow).



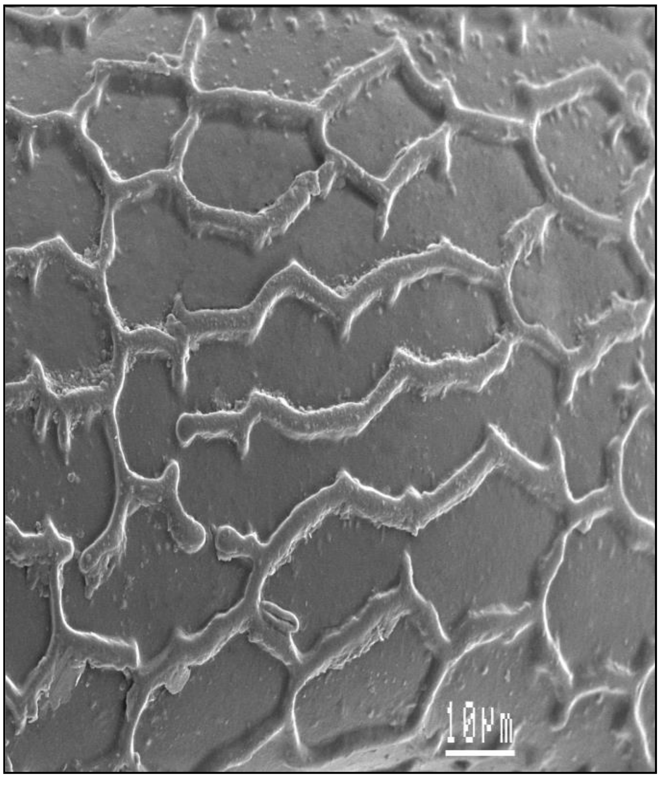


Fig. 10. Eggs with **A**. Filament, **B**. Pedicel groove.

Fig. 11. Egg membrane showing the reticulate sculpture in the form of ridges.

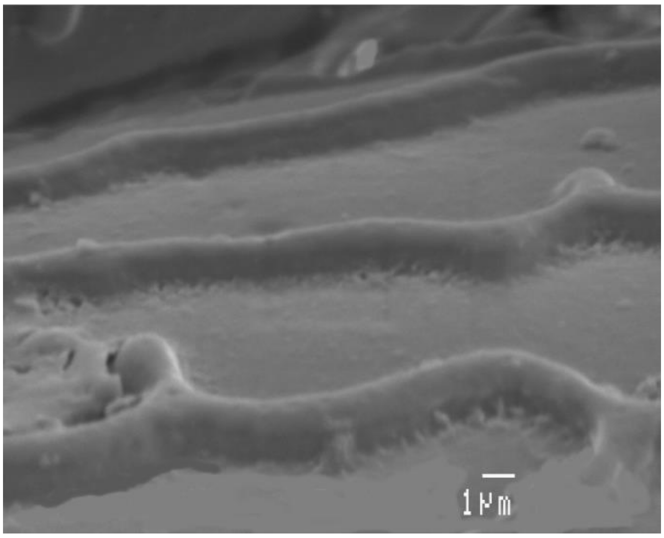


Fig. 12. High magnification of reticulate sculpture.

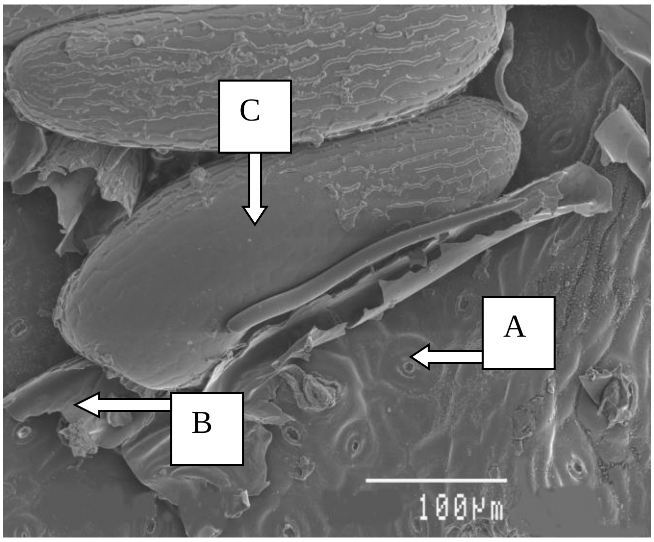


Fig. 13. Peeled egg membrane exposing the smooth egg surface. **A**. Stomatal opening, **B**. Membrane, **C**. Smooth egg surface.

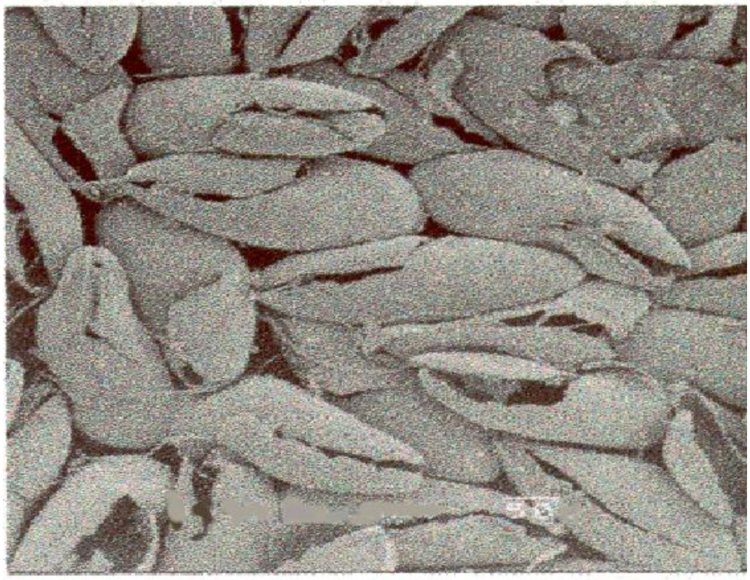


Fig. 14. Eggs showing longitudinal and transverse dehiscence.

4.1.2 Nymphs and lerps

4.1.2.1 Morphology

Two forms of nymphs, which vary conspicuously in colour and abdominal markings, were identified (Fig. 15). One form is yellowish with a v-shaped abdominal tip and no horizontal markings on the abdomen while the other is yellowish-brown with two dark-brown horizontal stripes on the dorsal abdomen and has a broader abdomen and two brown spots between the eyes. The yellowish nymphs constituted approximately 5% of the population, while the yellowish-brown nymphs made up the rest.

Five nymphal stages were identified with little morphological differences (Fig. 16). There was a significant increase from first to fifth instar in the body sizes and a considerable jump from second to third instar parameters (Tables 9 and 10). The duration between various instars could not be determined because development of the nymphs occurred under lerps and opening of the lerps would be a destructive method. Figure 17 illustrates the body length changes of the various instars depicting a significant increase from the first to the fifth instars. Figure 17 also shows an exponential increase in the body length from first to fifth instar. The eyes were distinctly reddish-brown, globular and compound. Wingpad development was first noted in the second instar and became marked in third fourth and fifth instars. Stylets of fifth instar nymphs were on average 5.55 µm thick and very flimsy. Due to the flimsy nature of the stylet no length measurements were taken.

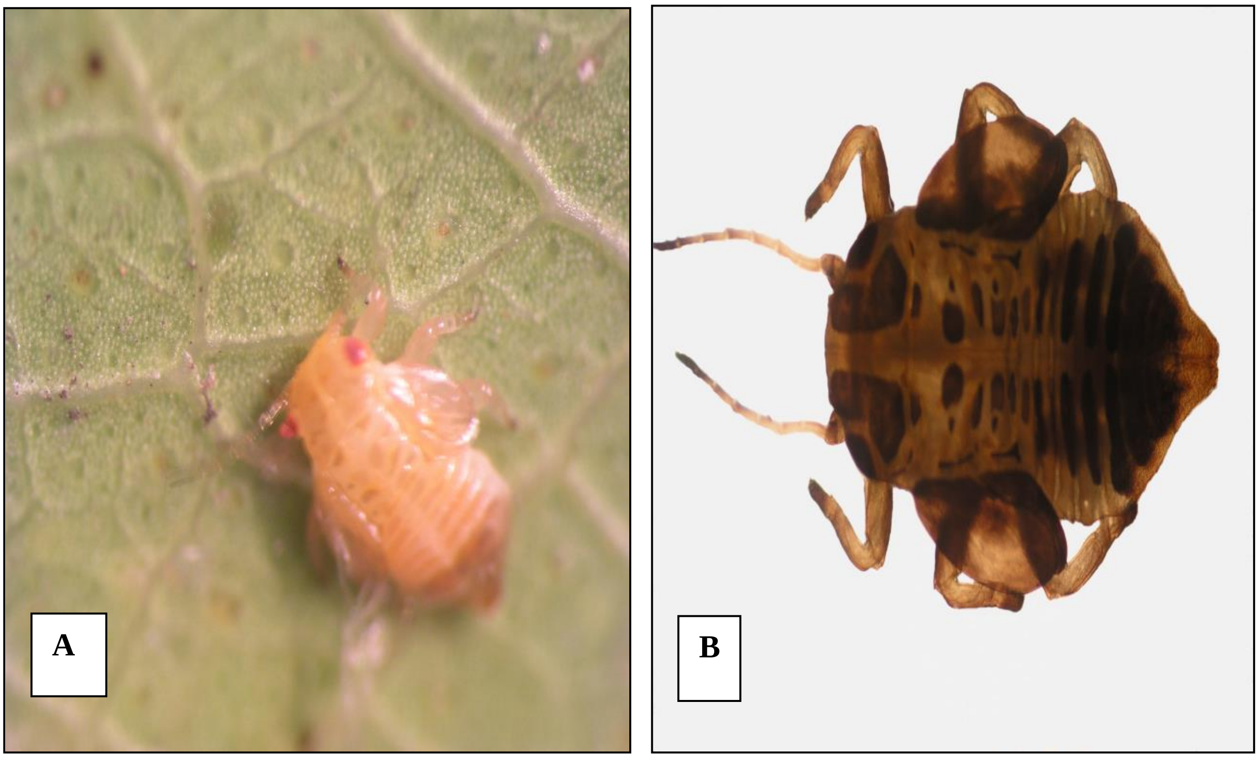


Fig. 15. Two forms of nymphs’, **A**. Yellow nymph, **B**. Yellowish-brown nymph.

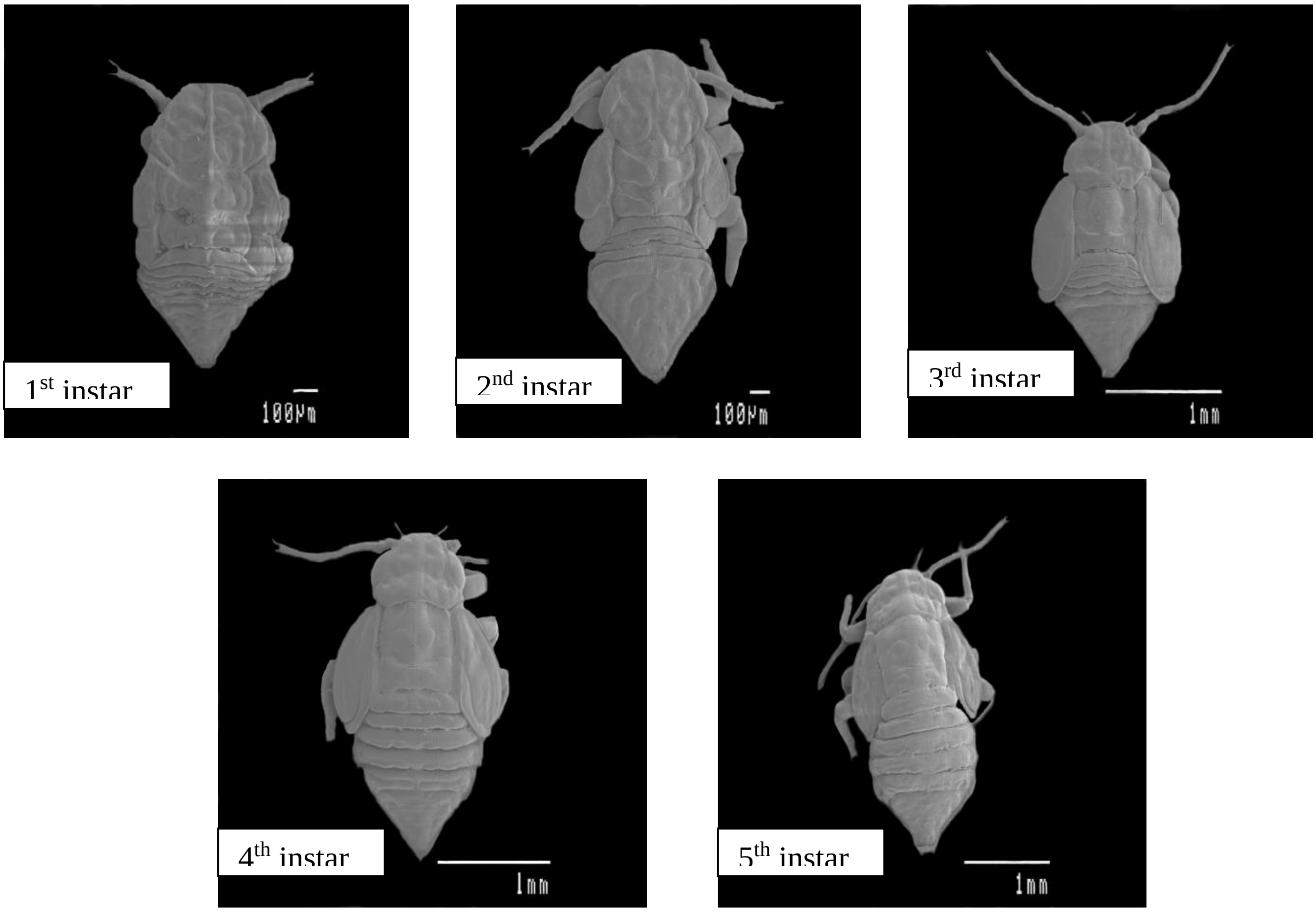


Fig. 16. Morphological features of various instars.

Table 9. Mean differences in wingpad, thorax and antenna of various instars (n=20).

Parameter (mm)	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Wingpad length	0.22	0.31	0.82	0.95	1.40
Wingpad width	0.13	0.18	0.37	0.39	0.42
Thorax length	0.23	0.18	0.43	0.55	0.72
Thorax width	0.36	0.35	0.52	0.65	0.75
Antenna length	0.23	0.63	0.95	1.13	1.16

Table 10. Body length of various instars (n=20).

Body length (mm)	First instar	Second instar	Third instar	Fourth instar	Fifth instar
Mean	0.72	1.22	1.74	2.32	2.82
SD	± 0.074	± 0.085	± 0.058	± 0.021	± 0.029
Minimum	0.60	1.09	1.66	2.29	2.78
Maximum	0.85	1.46	1.82	2.38	2.88

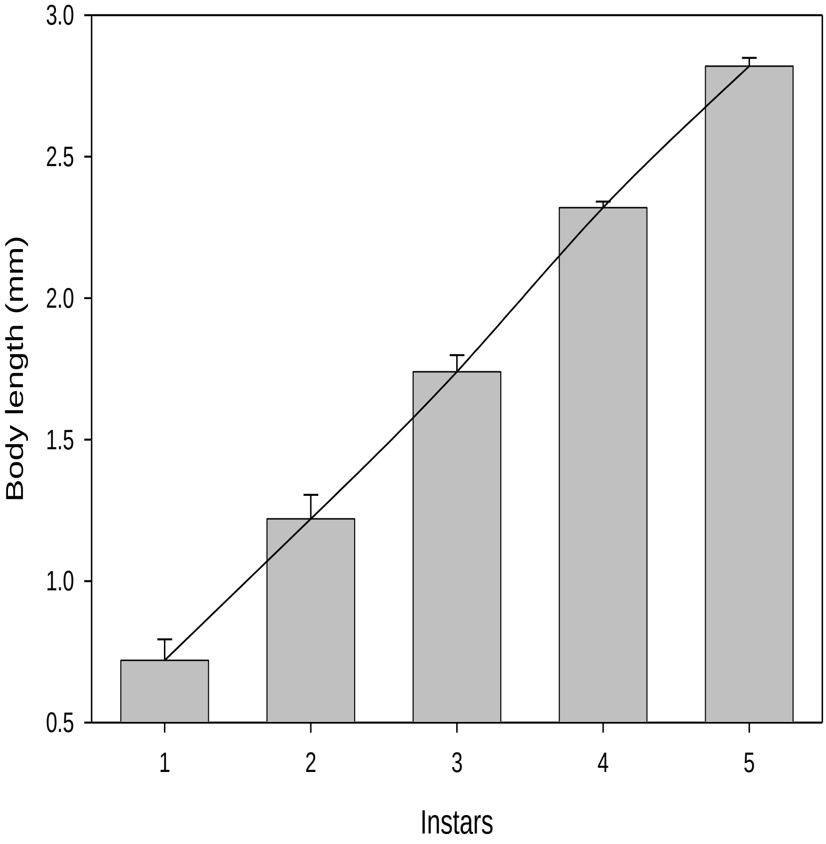


Fig. 17. Mean body length increases of the various instars. (Vertical bars indicate standard deviation).

4.1.2.2 Behaviour

Wandering nymphs did not show aggression towards each other no matter how close they came. They simply sensed each other by movement of the antennae and moved away in different directions from one another. First instar nymphs wandered approximately five minutes to select a suitable feeding site where they pierced the phloem tissue with their stylet to withdraw sap from the host plant. Nymphs then started to construct lerps over their bodies. The first and second instar nymphs preferred the areas between secondary veins whereas the older instar nymphs (third, fourth and fifth) settled on and along the main veins. Nymphs on petioles did not migrate to the leaflet; they remained to construct lerps. The feeding behaviour left stylet puncture marked in the guard cells of the stomata and on the epidermal cells of petioles but not on primary veins.

As nymphs developed, they enlarged their lerps by adding to the base of the existing one, ultimately resulting in a stack formation with the first (oldest) constructed lerp on top and the last at the bottom (Table 11 and Fig. 18). No two nymphs co-habited the same lerp even though lerps overlapped where the numbers were high per leaflet. The number of nymphs was fewer than the number of lerps on both adaxial and abaxial leaflet surfaces (Table 12).

When the lerp cover was removed, first and second instar nymphs quickly (within five minutes) started to construct a new lerp, but third to fifth instars took between four and six hours before constructing a new lerp. Fifth instar nymphs abandoned their lerps, which left them vulnerable to predation, but they stayed near it prior to moulting into an adult. This behaviour could last between one and three hours. Some nymphs abandoned their lerps only to construct a new one at a different site on the same leaflet.

Table 11. Mean values (mm) of changes in lerp dimensions as nymphs develop (n=30).

Instar number	1	2	3	4	5
Body length	0.72	1.22	1.73	2.30	2.82
Inner lerp diameter	0.78	1.52	2.65	2.84	3.20
Outer lerp diameter	1.01	1.83	3.25	3.10	4.82
Lerp height	0.81	1.20	1.82	2.13	2.63

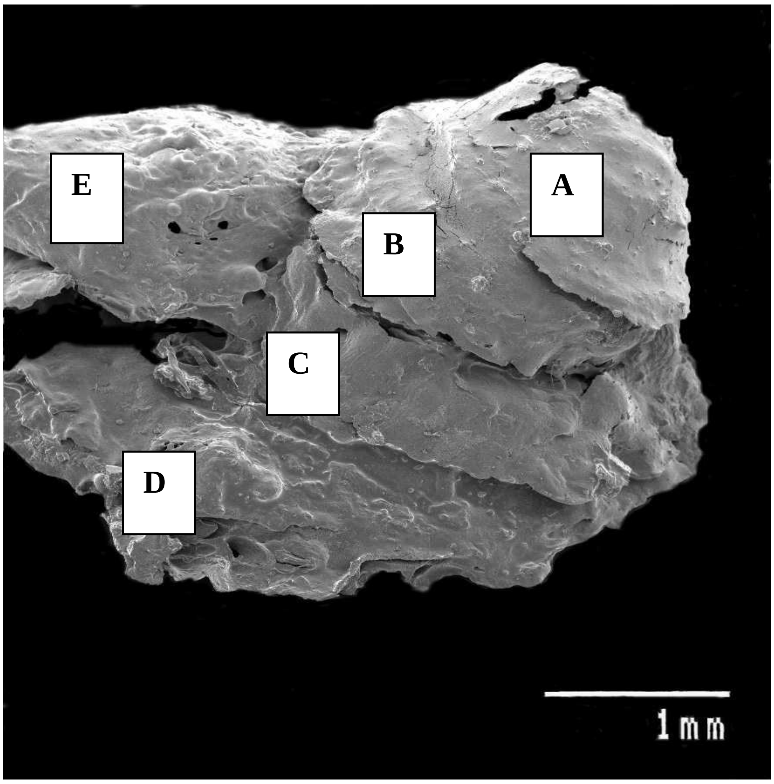


Fig. 18. Stacked structure of lerps. **A**. First stack, **B**. Second stack, **C**. Third stack and **D**. Fourth stack. **E**. Overlapping lerp of another nymph.

Table 12. Number of lerps and nymphs on abaxial and adaxial leaflet surfaces.

	Number of lerps		Number of nymphs	
	Abaxial	Adaxial	Abaxial	Adaxial
Mean	8.80	10.63	3.70	3.97
SD	± 6.71	± 8.20	± 3.48	± 4.14
Minimum	1	1	0	0
Maximum	23	36	14	16

Number of lerps; abaxial versus adaxial

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.408), according to the Mann-Whitney Rank Sum Test.

Number of nymphs; abaxial versus adaxial

The difference in the median values between the two groups is not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.888), using the Mann-Whitney Rank Sum Test.

4.1.2.3 Lerp construction

A nymph uses the tip of its abdomen to construct the lerp. During lerp construction, the stylet remained in a feeding position. The nymph pivoted its body in a semi-circle around the point of insertion of the stylet and excreted a light brown gelatinous liquid from the tip of the abdomen, which was deposited on the leaflet. The abdomen slowly moved clockwise, each movement corresponding to exudation of the gelatinous liquid adding to the base of the lerp. No marked construction pattern was observed in the structure of the lerp even though it seemed to have a lattice structure with some vents (Fig. 19). Lerps varied from single to multiple-layered structures depending on the instar stage of the nymph.

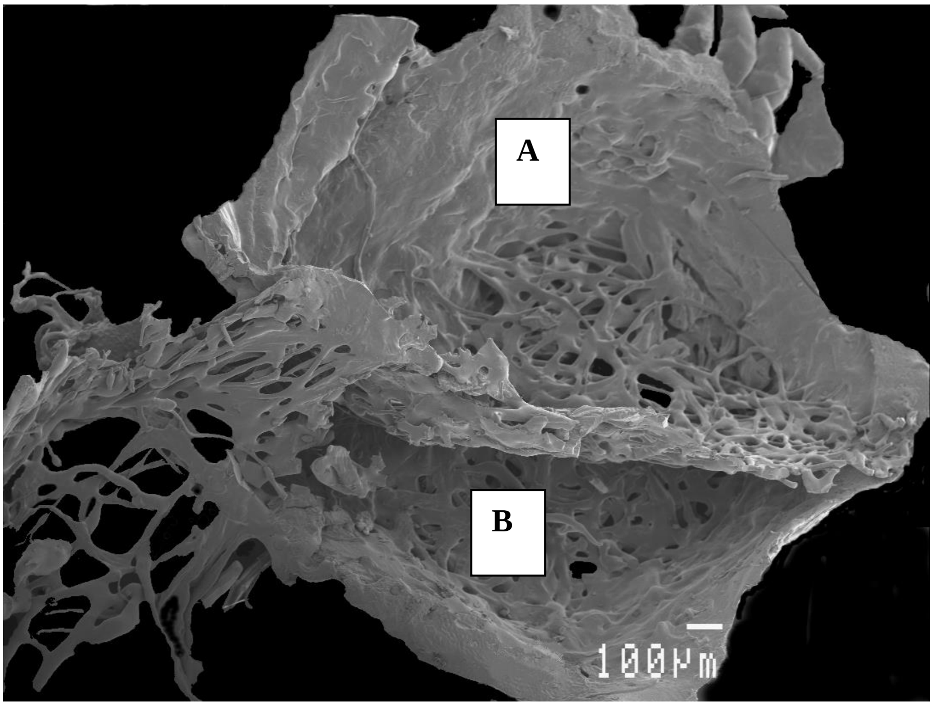


Fig. 19. Lerp structure showing no definite pattern. **A.** Outer surface, **B.** Inner surface.

4.1.2.4 Lerp distribution, abundance and appearance

The positions of lerps on the leaflets depended on the stage of development of the nymphs. First and second instar nymph lerps were placed along the smaller secondary veins whereas third and fourth instar nymphs placed their lerps along main veins on either surface of the leaflet. The first and second instar nymph lerps were much smaller in size but more numerous (ratio of 5:1) than the third and fourth instar nymph lerps.

When populations are large, lerps were observed on veins and occasionally along the leaf margins, pulvinus, on petioles and on flower buds (Fig. 20). Virtually all (94 %) (n=300) *C. mopane* leaves carried lerps and on many leaves (78 %) several lerps were joined together forming a chain up to 3 cm long. Lerps were found still attached to fallen *C. mopane* leaves while some were scattered on the ground under the trees. Tables 13 and 14 compare number of lerps in various positions on leaflets. Lerps were more common on the adaxial leaflet surface (55 %) than on the abaxial (45 %) (n=580) (Fig. 21).

Lerps covered approximately 0.2 % of the leaflet surface area. The mean number of lerps per leaflet was 19 (n=300) and the mean mass of a single lerp was 0.005 g (n=300). Most lerps (80 %) (n=300) were light brown; few (15 %) were white and still fewer (5 %) were grey to black. They are conical in shape and do not dissolve in water.

Lerps were glued at one end to the leaflet surface and loose at the opposite end. The loose end served as an opening for the fifth instar prior to moulting to adulthood. It was discovered that it was also a weak point where predators could lift the lerp and gain access to the nymphs.

Fig. 20. Lerps of different instars nymphs concentrated on main veins.

Table 13. Number of lerps on left and right leaflet surfaces (abaxial/adaxial).

	Abaxial surface		Adaxial surface	
	Left leaflet	Right leaflet	Left leaflet	Right leaflet
Mean	2.73	1.60	6.60	6.47
SD	± 5.21	± 2.98	± 8.25	± 7.88
Minimum	0	0	0	0
Maximum	26	11	42	35

Left leaflet versus Right leaflet (abaxial surface)

The difference in the mean values between the two groups is not great enough to exclude the possibility that the difference is due to random sampling variability; there is not a statistically significant difference (P = 0.894), using the Mann-Whitney Rank Sum Test.

Left leaflet versus Right leaflet (adaxial surface)

There was no significant difference in the mean values between the two groups (P = 0.314), according to the Mann-Whitney Rank Sum Test.

Table 14. Distribution of lerps on adaxial leaflets surfaces.

	Along veins	Between veins	Pulvinus	Petiole	Along leaflet margin
Mean	13	2.7	0.47	0.33	0.87
SD	± 10.87	± 3.78	± 0.78	± 0.96	± 1.33
Minimum	3	0	0	0	0
Maximum	54	15	2	4	5

Along veins versus between veins

The difference in the mean values between the two groups (along and between veins) is greater than would be expected by chance; there is a statistically significant difference (P = <0.001) using the Mann-Whitney Rank Sum Test.

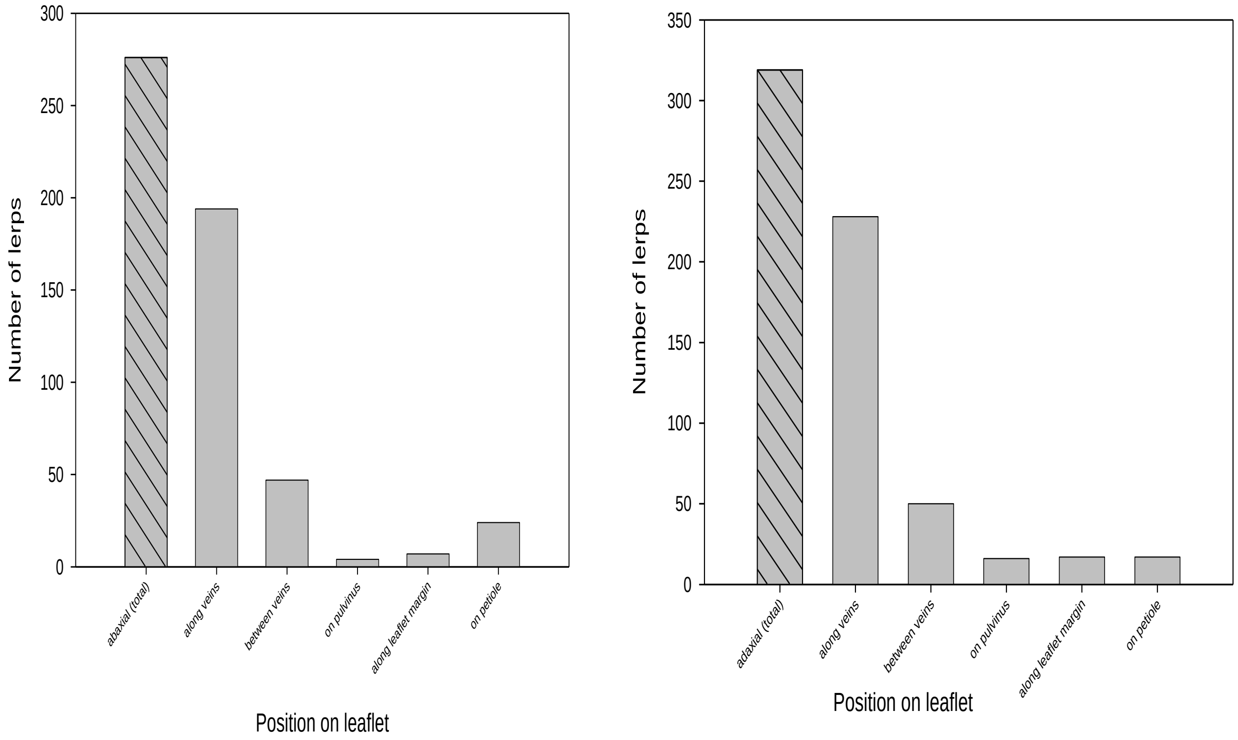


Fig. 21. Abundance of lerps on petiole and various positions of abaxial and adaxial leaflet.

4.1.2.5 Exoskeleton

Shed exoskeletons were observed both in some abandoned and occupied lerps (Fig. 22). In the same lerp different sizes of exoskeleton were observed. Dead nymphs, some with missing body parts and others with only the exoskeleton were also observed on the leaflet surfaces and inside lerps, however, not all abandoned lerps contained shed exoskeleton and body parts.

4.1.2.6 Damage caused by nymphs and lerps

Damage caused by nymphs and lerps was visible as black or reddish-brown patches around feeding sites (Fig. 23). Leaflet tissues around the base and edges of the lerps, but not covered by lerps appeared reddish-brown. Black sooty mould was observed on leaves in the vicinity of lerps. Sometimes the black sooty mould covered the entire lerp. A few curled leaflets enclosing lerps and nymphs were observed.

Fig. 22. Shed exoskeleton of nymphs in lerps.

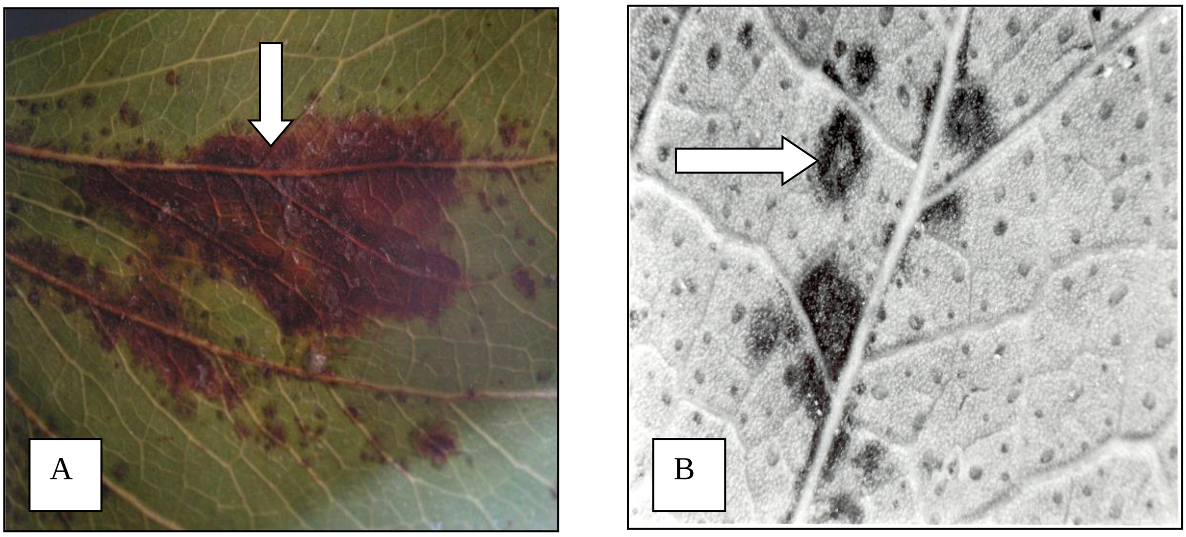


Fig. 23. Feeding damage on leaflets **A** and **B** caused by nymphs (arrows).

4.1.3 Adults

4.1.3.1 Field observation

Adults emerged when *C. mopane* leaves turned senescent to lay eggs (July to September 2004), but this study could not establish from where the adults emerged. When violently disturbed or threatened, by shaking the twig vigorously or trying to touch them, for instance, adults flew in a circular manner, approximately one metre away and returned to land on another branch of the same tree. They jumped about 50 cm away if a disturbance was not as violent and landed on another leaf. Adults sometimes walked on the same leaflet or to a neighbouring leaf when searching for new feeding sites. Adults rested almost motionless on the leaflets or petiole with the stylet withdrawn when not feeding. They folded their wings over their bodies when feeding. An adult could remain feeding at the same spot for 2 hours or more if not disturbed. Adults do not live in lerps. On the petiole and leaflets adults did not congregate, but rather stayed separately in the form of a queue. New adults developing from the fifth instars were pale yellowish-green with orange markings on the dorsal thorax, veins and wings (Fig. 24 A). Within 4-5 hours this colour changed to dark brown, which blended with the senescent *C. mopane* leaves (Fig. 24 B and C). During this time they remained motionless. No aggressive behaviour was observed amongst adults.

4.1.3.2 Adult morphology and life span

The mean adult body length from head to the tip of abdomen was 3.5 mm (n=30) (Table 15). Fifth instar nymphs observed moulting into adults lived between five and eight days with a mean life span of six days, but adults collected from the field lived between five and ten days with a mean life span of seven days under laboratory conditions (n=30). However, it could not be established how old they were in the field before being brought to the laboratory.

Head: Head depicts two prominent reddish-brown, globular, and slightly protruding compound eyes. Vertex had bristles of hair. Antenna with ten segments, the sixth and eighth segments longer than the rest. The sixth segment at 0.19 mm the longest. The last segment terminates with three unequal spines (Fig. 25). Adult mean antenna length was 2.06 mm (Table 15).

Thorax: Appears hatch backed with two pairs of wings. Fore-wings with dark brown spots along veins, hind-wings lack these spots. Veins more conspicuous in fore-wings than in hind-wings. Fore-wings are longer than hind-wings. Wings extend beyond the abdomen. Mean length of fore-wings is 3.27 mm and width 1.32 mm (Table 15). The first two pairs of legs are identical but smaller and less stout than the third (hind-) pair (Fig. 26).

Abdomen: Six abdominal segments present. The first five ring-like, the last segment v-shaped. The genitalia of the male has a cluster of long hairs (2.8 mm long) on the anterior of the ventral valve, the female genital segment is stout and has several short hairs (0.22 mm long) before the apex on the dorsal valve. A pair of cerci is located at the tip of the male genitalia but absent in the female (Fig. 27).

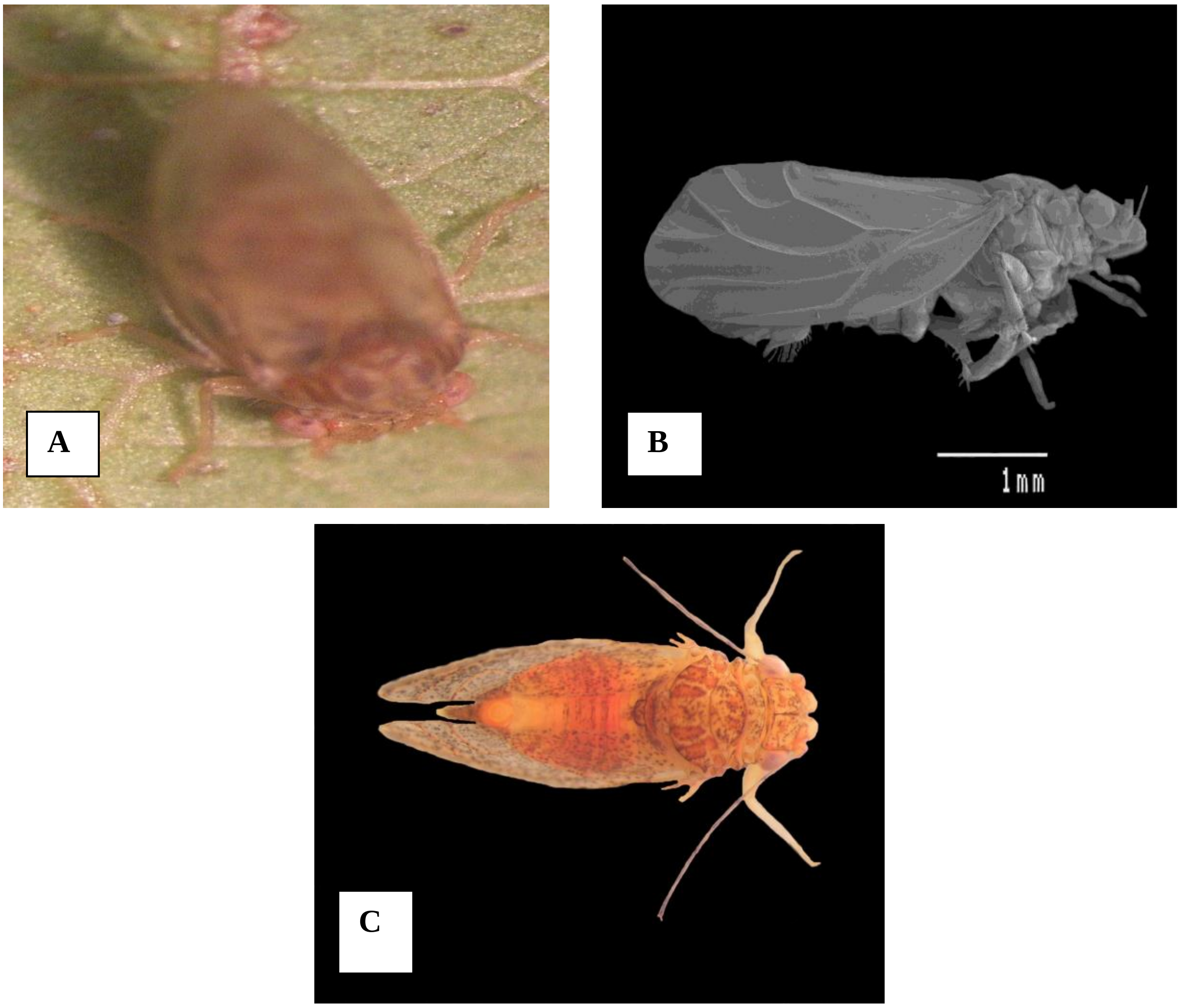


Fig. 24. Adults. **A.** Young adult, **B.** Mature adult side view, **C.** Mature adult top view.

Table 15. Measurements of body parts (n=30).

Body part (mm)	Mean	SD	Minimum	Maximum
Body length (head to abdomen)	3.50	± 0.03	3.46	3.55
Body length (head to tip of folded wings)	4.11	± 0.08	3.95	4.22
Body width (broadest part)	1.31	± 0.03	1.25	1.35
Fore-wing length	3.27	± 0.04	3.20	3.31
Fore-wing width	1.32	± 0.02	1.29	1.36
Hind-wing length	3.19	± 0.08	3.02	3.27
Hind-wing width	1.28	± 0.25	1.25	1.34
Antenna length	2.06	± 0.86	1.96	2.20

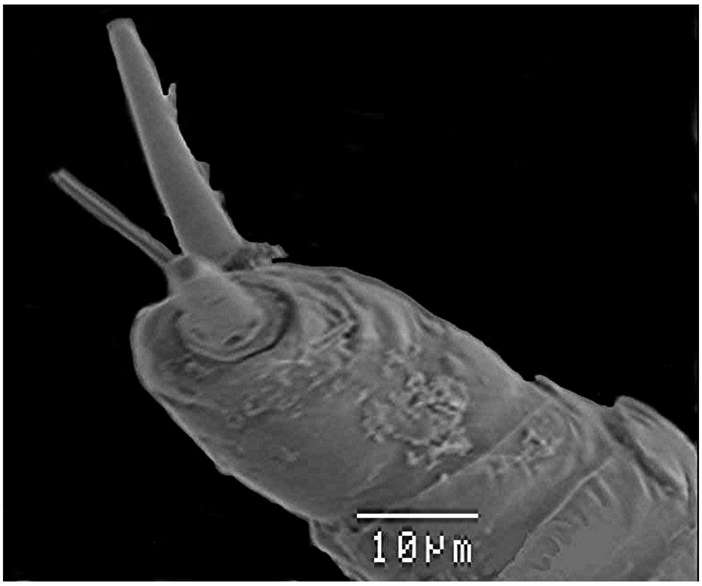


Fig. 25. The last segment of antenna with three spines.

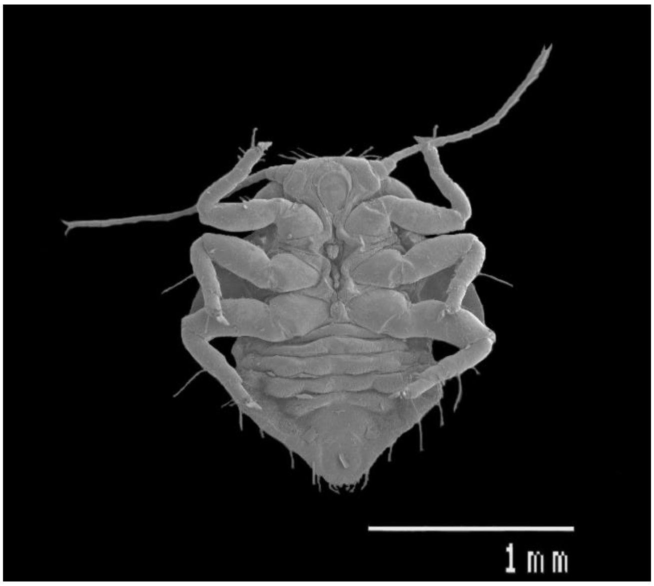


Fig. 26. Ventral view of fourth instar, indicating strong hind-legs.

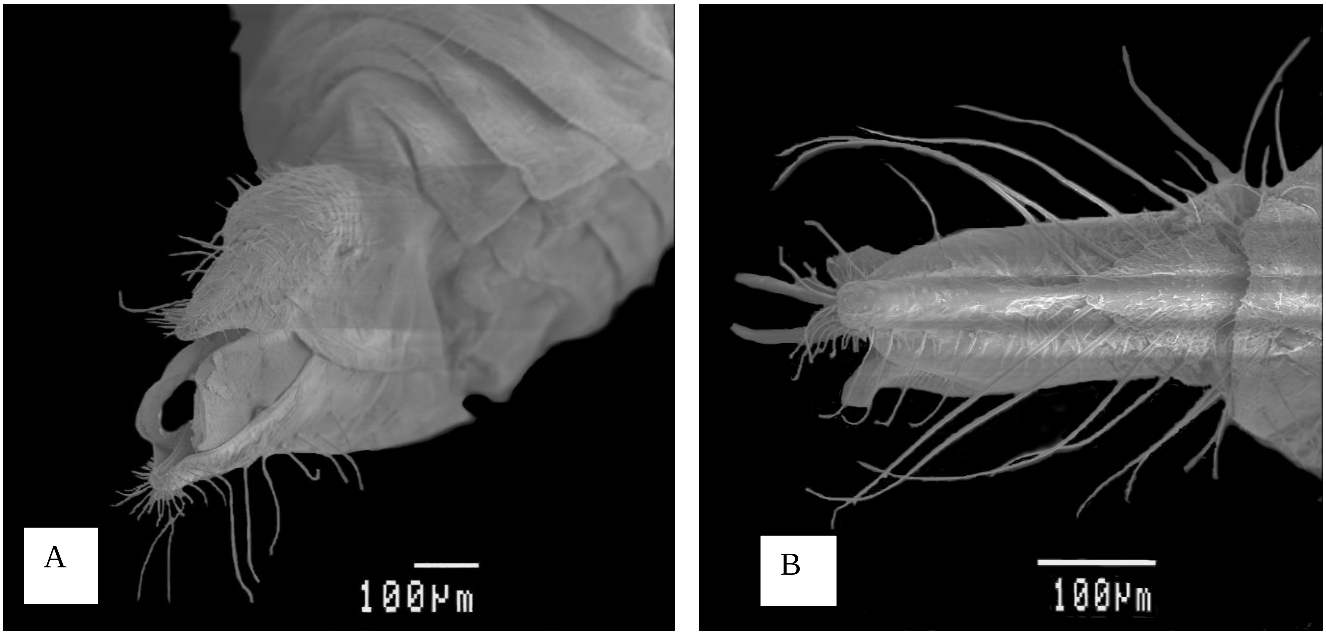


Fig. 27. Adult genitalia. **A.** Female, **B.** Male. (The shiny markings on B are due to excess carbon loading).

4.2 Predation

Red winged starling (*Onychognathus morio*) and Tawnyflanked prinia (*Prinia subflava*) were two species of birds observed preying on nymphs, adults and lerps on trees as well as on those lerps still attached to fallen leaves. The painted reed frog (*Hyperolius marmoratus taeniatus***)** (Fig. 28 A) was observed catching and feeding on exposed and wandering nymphs and adults on the tree. Brown lacewing larvae (Fig. 28 B) (Neuroptera: Hemerobiidae) were seen dislodging lerps from the leaflet surface and feeding on nymphs and leaving the exoskeleton of the nymph unconsumed. Another predator (Fig. 28 C), a suspected larva of the ladybird beetle (Coccinellidae), consumed the whole nymph. Ants (*Crematogaster* species) and Coccinellid larvae were observed in the vicinity with some feeding on lerps and nymphs. Ants (species unknown) were seen to aggregate around fallen *C. mopane* leaves with lerps on them (Fig. 29). Ants collected lerps and transported them to their nesting sites. The ants were specifically interested in the inner surface of the opened lerps. Silk-like treads, apparently woven by spiders were observed on some lerps (Fig. 29). No predation was observed on eggs but in some clusters, gaps were observed indicating missing eggs, which were marked by brown stains on the leaflet surface (Fig. 7 B).

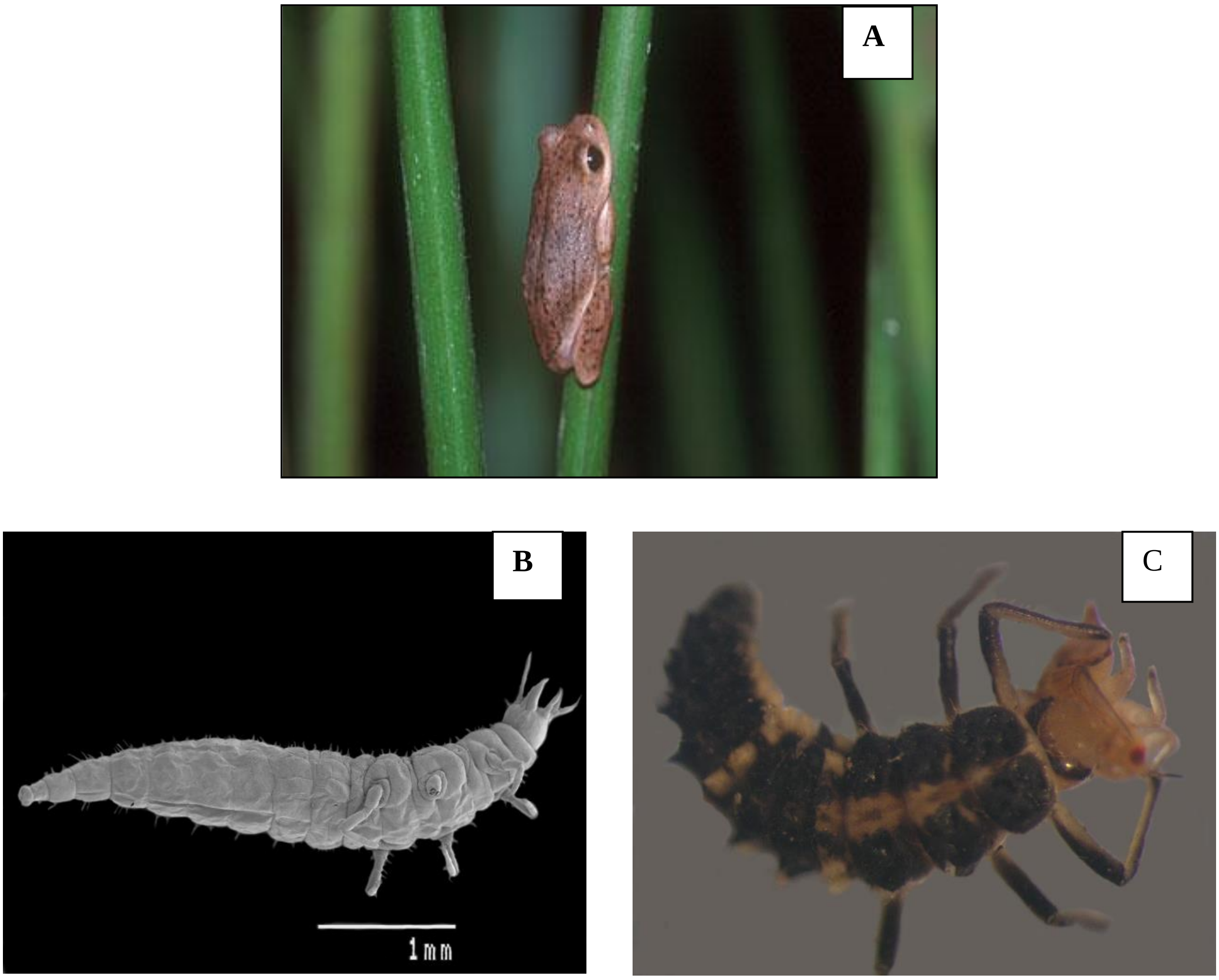


Fig. 28. Predators of *Arytaina mopane* **A**. Painted reed frog. **B**. Scanning electron micrograph of a Brown lacewing larva. **C**. Suspected Coccinellid larva.

Fig. 29. Ants collecting lerps.

SECTION 2

PHYSIOLOGICAL INVESTIGATIONS

4.3 Carbohydrate and other organic content analyses

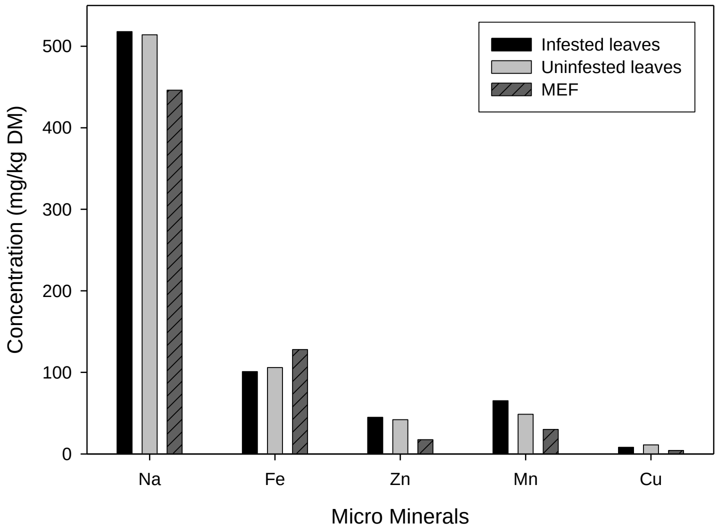
The carbohydrate constituent of the lerps and leaves (infested and uninfested) occur in the form of glucose, fructose and raffinose (Table 16). Raffinose was absent from the infested leaves. Lerps tested with iodine solution gave a negative result, which indicated absence of starch. Lerps were found to be organic in nature containing mainly carbon and oxygen and waxy substances as yet of unidentified constituents. Trace elements were below the analytical sensitivity of the technique used.

Table 16. Carbohydrate content of leaves and lerps.

Sample	Glucose	Fructose	Raffinose
Uninfested *C. mopane* leaves (g/100g)	0.86	5.88	0.25
Infested *C. mopane* leaves (g/100g)	1.30	8.07	Not detected
Lerps (g/100g)	0.94	6.21	0.31

4.4 Mineral content of leaves

Infested leaves contained significantly higher amounts of calcium, zinc and manganese than uninfested leaves. The concentrations of nitrogen, phosphorous, potassium, iron, and copper were higher in uninfested than infested leaves (Fig. 30).



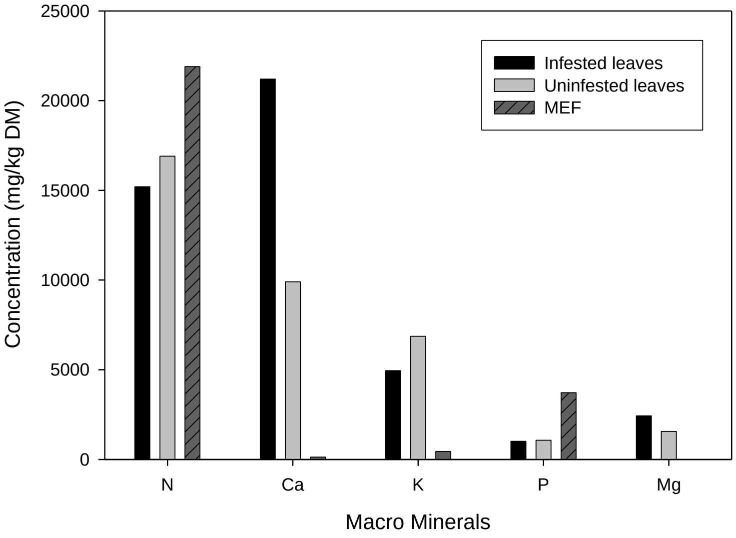


Fig. 30. Comparative concentrations of mineral elements in infested and uninfested *C. mopane* leaves (micro and macro minerals) with MEF project.

CHAPTER 5

DISCUSSION

5.1 Life cycle features

5.1.1 Eggs

According to Urquhart and Stone (1995), psyllids generally lay yellow, brown or black-stalked eggs, which conform to *A. mopane*'s black eggs. It is speculated that the black colour of the eggs is an evolutionary development to blend in with the black fungal spots, which are common on leaflets as a camouflage or to absorb enough heat to enhance hatching. The latter speculation is supported by Watmough's (1968b) report that hatching in *Arytaina spartiophila* was delayed until April because of prolonged cold, which generally occurs in Europe.

According to White (1968a), water in the form of cell sap is absorbed through the pedicel and eggs quickly desiccate if the water source is removed. This statement by White (1968a) is valid when the pedicel penetrates the tissue, which is not the case with *A. mopane.* The question then is how do *A. mopane*'s eggs avoid desiccation? *Colophospermum mopane* leaflets fold together to present the smallest surface area toward the sun, thereby reducing exposure of the leaf surface in the heat of the day to conserve water (Prior 1996; Aubrey 2004). This could be to the advantage of *A. mopane* eggs to prevent over exposure to high temperatures and possibly from desiccation. Perhaps this is the reason why most eggs are distributed on the abaxial surface of the leaflets as a means to reduce desiccation. However, future investigation into this aspect is required.

The long filament at the tapering end of the egg, whose function is currently unknown, may be a modification of the reticulate-sculptured egg membrane in accordance with Gaino and Rebora's (2001) finding, that eggs of mayfly (*Siphlonurus lacustris*) are wrapped in a thick coat composed of a network of tightly entwined filaments.

In this study, no pedicel-punctured marks were observed on the leaflet surface to indicate attachment of the egg to the surface. However, the sticky nature of the place where the pedicel is attached could facilitate egg attachment to the leaflet surface. Gaino and Rebora (2001) state that covering of eggs of *Siphlonurus lacustris* (Ephemeroptera) interact with water to promote marked cohesion of the eggs and leading to their firm adhesion to the substrate. They then postulate a trophic function and protection from shear stress as additional functions. Similarly the reticulate sculpture might assist in enlarging the surface area of the egg to which the glue can adhere. The glue may also serve as an antipredatory substance as only a few eggs were missing from some clusters. The fact that eggs are laid superficially on the leaflet surface of *C. mopane* tree might be an indication that predatory pressure is not very high which further explains why only a few eggs were missing in some clusters.

Some variation in how eggs are placed on the leaflet surface occurs in *Arytaina*. In *Arytaina spartii*, the egg can be deeply embedded in the leaf tissue (Hodkinson 1974). This is in contrast with *A. mopane*, whose eggs are laid superficially on the leaflet and petiole surfaces. It would seem that embedding its eggs in the leaf tissue is an indication of behaviour adaptation to the very cold conditions of England, where *A. spartii* occurs. In the lowveld region where *A. mopane* occurs, the winters are mild (temperatures range between 11.4 and 23.5°C, Table 5) but dry (mean humidity values at 8:00, 14:00 and 20:00 being 61.9 %, 38.9 % and 56.5 % respectively, Table 7) (S.A. Weather Service 2005). Values were calculated from mean values of July to September 2002 to 2004 of the respective tables.

The spiral arrangement of *A. mopane* eggs in a cluster is in contrast to that of Australian psyllids, which generally lay their eggs in rows or circles (Urquhart & Stone 1995). There are no reports on the arrangement of any *Arytaina* eggs for comparison. Perhaps eggs in a cluster assist to maintain the optimum temperature for hatching. Furthermore, eggs in a cluster may present a large surface to confuse would be predators. *Arytaina mopane* also differs from *A. genistae* regarding the timing of deposition. Eggs are laid on mature green and senescent *C. mopane* leaves, which normally occur between July and September when temperatures are between 11.4°C and 23.5°C (S.A. Weather Service 2005). During this period (July to September) there is very little (10.8 mm calculated from mean values of July to September 2002 to 2004, Table 6) or no rainfall and humidity is also low during day (38.9 %) and night (56.5 %), which contribute to dry conditions (S.A. Weather Service 2005). It thus seems that climatic conditions determine emergence and subsequent oviposition by *A. mopane* compared to *Arytaina genistae*, which can lay eggs anytime of the year in England (Watmough 1968b).

A mature female psyllid could deposit over 500 eggs (Anonymous 2004). This study recorded a mean of 235 eggs laid by an individual female under laboratory conditions. However, leaves collected from the field could contain more than two thousand eggs. This suggests that many females could lay eggs on the same leaflet, which is in agreement with Clark's (1962) statement that when females are numerous, hundreds and occasionally thousands of eggs may be placed on the same leaf. The low number of eggs laid by captive females in the laboratory could be that the females had already laid eggs in the field. That eggs were mostly laid in clusters may be an indication that different females either avoided mixing their eggs with other females' or a single female oviposited at different times at different sites on the same leaflet. The former may be supported by the fact that eggs in a cluster hatched simultaneously and independent of neighbouring clusters.

Dobson (1851) states that psyllid eggs hatch by opening longitudinally. Similarly, the eggs of *A. mopane* dehisce longitudinally from the tapering side and then cross-wise half way around the egg's circumference. None of the eggs laid in the laboratory hatched, compared to the 86 % hatching of the field laid eggs. It was most likely that temperature and shading affected the non-hatching of the eggs laid in the laboratory, which is an idea supported by Watmoughs' (1968b) statement that hatching in *Arytaina spartiophila* was retarded in shady positions. Field temperatures during the day could rise to 25°C (14:00) and fall to 15°C in the morning (10:00), with leaf temperatures between 25 and 26°C, whereas the laboratory temperatures were fairly constant ranging between 18°C and 22°C (own data from random temperature recordings). However, it must be stated that correlations between temperature changes and hatching percentage was not one of the objectives of this study and can form the basis for further studies. The non hatching of the eggs laid by the captive insects in the laboratory could also be due to the eggs being infertile as no prior mating was observed.

Watmough (1968b), in his studies of the biology of *A. spartiophila* and *A. genistae*, found that *A. spartiophila* has a protracted hatching period continuing for several weeks spanning from February to May. He further observed that the eggs of *A. spartiophila* showed a wide range in the amount of heat required for hatching in spring, which results in a long hatching period and a wide overlap of nymphal stages. In this study *A. mopane* also showed continues hatching for several weeks, stretching for twelve weeks. Newly hatched nymphs were observed throughout the period of research, which suggests some similarity between *A. mopane* and *A. spartiophila,* however this could also mean that new adults that emerged earlier have started reproducing.

5.1.2 Nymphs

5.1.2.1 Behaviour and lerp construction

The younger nymphs (1st and 2nd instars) were very quick (5 minutes) to construct lerps immediately after emergence from the egg and when disturbed from the existing lerp as compared to older nymphs

(3rd and 4th instars). According to several authors (Catling & Annecke 1968; Atwal *et al*. 1970; Green & Catling 1971), psyllid nymphs are highly susceptible to desiccation, particularly at high temperatures. This behaviour of first and second instar *Arytaina mopane* nymphs to quickly construct lerps is assumed to escape desiccation as field temperatures during the day could rise to 25°C (14:00) and fall to 15°C in the morning (10:00) with fluctuating air humidity. Furthermore, this behaviour to quickly construct lerps further emphasizes presumably, an innate vulnerable fear that nymphs have in terms of possible predation. Third and fourth instar nymphs do not quickly construct lerps over their bodies when exposed, which suggests possible acclimatization but this leaves them vulnerable to predation. The latter may explain the relative lower number of lerps on leaflets as compared to the percentage of hatched eggs. Whereas more eggs were distributed at the abaxial leaflet surface than at the adaxial surface, the opposite occurred with the lerps, which is consistent with the protection offered by lerps against predators and direct rays of the sun and also suggests feeding preference of nymphs to the adaxial surface. The fact that no two nymphs co-habited the same lerp perhaps minimizes competition for food and consequent aggressive behaviour.

Nymphs seemed to escape through the loose ends of lerps, which is in contrast to *Psylla eucalypti,* which eats its way out of the lerp through a round hole except when the base of the lerp is not too firmly attached to the leaf (Dobson 1851).

5.1.2.2 Forms of *A. mopane*

Pettey (1925) described two adult females differing from each other whereas this study identified two forms of nymphs based on colour variation and markings of the abdomen. These nymphs might have hatched from eggs laid by the two different female morphotypes in accordance with Pettey's finding. It is also speculated that the variation could be due to gender differences or just a natural variation, however, this warrants further research.

5.1.2.3 Feeding

Limonene is a toxin, which when present in large quantities is known to deter feeding by insects on plant sap (Sturgeon 1979). Limonene is present only in the young green leaves and not in older mature *C. mopane* leaves (Styles 1993). If it is indeed such an active deterrent to feeding then it could be the possible reason why *A. mopane* feeds on senescent *C. mopane* leaves.

According to White (1971), nymphs of *Cardiaspina albitextura* insert their stylets through the stomates of the leaf and "plug-in" to the phloem cells of the fine ultimate branches of vascular tissue.

This study observed possible stylet puncture marks on the guard cells of stomata and the petiole epidermal cells, which is consistent with White's (1971) finding. This suggests that the nymphs stylet cannot puncture hard tissues such as the bundle sheath cells, made of hard fibres and may be the reason why the younger nymphs (1st and 2nd) instars preferred settling between and along secondary veins, where they could proably feed directly from the major phloem vessels of the secondary veins. This suggestion is supported by the fact that *C. mopane* leaves have a fibre sheath around the vascular bundle, which must be penetrated to reach the phloem (Potgieter & Wessels 1998).

According to White (1970a) psyllid nymphs induce nitrogen release through salivary secretion, which causes a breakdown of the mesophyll tissue, resulting in the liberation of copious amounts of soluble nitrogen at the feeding site. Perhaps this is the feeding mechanism employed (secretion of chemical substance, that soften plant tissue resulting in leakage of nutrients) by *A. mopane* with regard to nymphs occurring on main veins, which contain no stomata and could also account for the absence of stylet punctured marks on primary veins. The suggestion is supported by the lack of stylet puncture marks at such sites, however, this could be considered for future research.

5.1.2.4 Feeding damage

Feeding damage to the host was observed as a black stain and reddish-brown rough patches on the leaflet surface. This could possibly be a result of damage caused by the stylet to cells by its penetration through various tissues or perhaps due to the release of secretions to facilitate nymph feeding. The first possibility is supported by Clark's (1962) statement that *Cardiaspina* species nymphs insert their stylets through stomata in order to reach their food supply. Results by Annecke and Cilliers (1963) suggest that feeding damage is mostly caused by the nymphal stages and that some psyllid nymphs inject small amounts of toxic salivary secretion into the phloem, which diffuses into the surrounding tissue (Crawford & Wilkens 1996). The toxic salivary secretion induces a breakdown of the mesophyll tissue (White 1970a). It therefore seems that the discolouration on the leaves is caused by the death of mesophyll tissue. This may be one of the reasons for nymphs to move to new feeding sites. Another reason contributing to the tendency of nymphs' movement to new feeding sites might be due to restrictions in the transport of phloem sap by a too small vein. Movement to a site closer to or on a main vein presumably will provide more phloem sap.

According to Urquhart and Stone (1995), when feeding, the nymphs of *Cardiaspina* species secrete substances that cause necrosis. Initially the affected area appears reddish-purple but later turns brown. They further state that in Sydney blue gum, *Eucalyptus saligna*, large populations of *Glycaspis baileyi* can sometimes cause a general purplish discolouration of the foliage and sooty moulds may develop on the sugary secretions, blackening the leaves and reducing the rate of photosynthesis. This study showed similar observations on *C. mopane* leaves suggesting that *A. mopane* nymphs, like *Cardiaspina* species also secrete substances that cause necrosis. The presence of black sooty mould on the leaves in the vicinity of the nymphs and lerps of *A. mopane* is supported by the statement by Dreistadt *et al*. (2004) that all psyllids produce honeydew on which blackish sooty mould grows. *Arytaina mopane* also shows similarity with *Glycaspis baileyi* of Australia in that the honeydew secretions attract ants and other insects that feed on the secretions (Fig. 30).

The nymphs of *A. mopane* exhibit only a limited tendency to disperse, have little ability to maintain a foothold on foliage if they leave their lerps and in this way they resemble the Australian psyllid *Cardiaspina albitextura* (Clark 1962). The fact that nymphs were found beneath their lerps on petioles suggests that feeding was taking place there. White (1971) reported that unless some catastrophe (such as the death of leaf) overtakes them, psyllid nymphs remain in the same place until adulthood. That *A. mopane*'s nymphs feed on leaves as well as petiole is supported by the notion that although most psyllids feed on the leaves of plants, some do feed on fruits, flowers, stems or even trunks (White 1971).

The observed curling of *C. mopane* leaflets enclosing lerps and nymphs could be due to morphological changes in the cells of the leaflet as a result of feeding by nymphs. This is supported by the finding that *Pachypsylla celtidis-mamma* nymphs feeding on hackberry causes morphological changes in the cells of the leaf of the hackberry which results in the growth of a pouch or a gall that grows up around the nymphs (McDermott *et al.* 1996). The finding by Valterová *et al.* (1997) that *Trioza apicalis* injects saliva during feeding that causes curling of the host leaves provides further support.

5.1.3 Exoskeleton and development

According to Dobson (1851), the fifth instar nymph of *Psylla eucalypti* abandons its lerp leaving the cast exoskeleton within. This study observed shed exoskeleton in some lerps (Fig. 22) and thus supports Dobson's (1851) finding that the shed exoskelton is left in the lerp. This further suggests, in addition to the fact that the observed shed exoskeletons in the lerps represented different stages of nymphs, that development of nymphs and ecdysis till adulthood occurs inside lerps.

5.1.4 Adults

It is a belief of the local inhabitants that when local climatic conditions are hot and dry, *A. mopane* do not emerge. This seems to be supported by the data (Tables 5, 6 and 7 with special reference to the months of May, June and July) because a visit to the current study area in July 2005 revealed some infestation on *C. mopane*, but in smaller numbers compared to that of the previous year. During the study period (July to September 2004), a visit to a mopani veld in Giyani, 130 km further east of the study area showed an absence of *A. mopane* on *C. mopane* trees. The distribution of *A. mopane* appears to be sensitive to climatic differences, which needs to be further investigated.

5.1.4.1 Morphology

The mean adult length of 3.5 mm recorded for *A. mopane* fell within the 2.5 to 4.0 mm cited by Pettey (1924) and Driestadt *et al.* (1999). In his description, Pettey (1925) reported the presence of two short and unequal spines at the end of the last segment of the antenna from his Musinacollection. However, this study showed the last antenna segment to have three sub-equal spines (Fig. 16A). This could mean a morphological diversity, which may be another morphological difference between the two forms of adults, described by Pettey (1925) and may require further investigation.

5.1.4.2 Behaviour and life span

The fact that adults do not stay in groups minimizes the effects of competition especially for food, and this, probably contributed to the non-aggressive behaviour among adults. The respective mean life spans of six and seven days under laboratory conditions for adults emerging from fifth instar nymphs and those captured from the field fall within the recorded 3 to 10 days life span of Psyllid adults (Erbilign *et al.* 2004). However, it has been reported that *Paratrioza cockerelli* adults can live for between 15 and 30 days in the field (Anonymous 2004).

5.1.4.3 Hibernation

In the northern hemisphere, some psyllids overwinter as adults on their host-plant. Most, however, disperse onto shelter plants and move back onto their true host-plant to mate and oviposit in the spring, usually prior to bud opening (Schaefer 1949). Others survive the winter in the form of eggs and still others hibernate in the nymphal forms (Heslop-Harrison 1937). *Arytaina spartiophila* overwinters in the egg stage while *A. genistae* does so as a mature adult (Watmough 1968b). Survival strategies used by adults of *A. mopane* during the leafless winter months of *C. mopane* are still unknown and needs further investigation. It is likely that adults hibernate in some surrounding grass or herb species or in crevices of the rough bark of *C. mopane*. It must be noted that *A. mopane* emerge during the winter and therefore oversummer, unlike the northern hemisphere psyllids, which overwinter.

5.1.4.4 Number of generations

This study could not establish the number of generations per year for *A. mopane*, but it is suspected that there could be more than one. The presence of young nymphs throughout the study period and the additional egg clusters observed suggest that newly matured adults started reproducing. This could be possible as they have a short life span (only live for five and eight days) and must reproduce fast It may also be argued that delayed hatching attributed to the presence of young nymphs, which could be refuted with the simultaneous hatching of eggs in a cluster. However, this warrants further investigation.

5.2 Lerps

5.2.1 Distribution

More lerps were present at the adaxial than the abaxial leaf surfaces contrary to the distribution of eggs on the leaflet surfaces. This confirms the migration of nymphs from hatching sites to feeding sites, where lerp construction commences. Lerps were mostly positioned along veins where nymphs mostly remain feeding at a feeding site unless some catastrophe such as death of the leaflet overtakes them (White 1971; Urquhart & Stone 1995).

Lerps of *A. mopane* occupied approximately 0.2 % of leaflet surface area, which is in contrast to Van Wyk's (1972) suggestion that lerps can cover the whole leaflet surface, thereby reducing photosynthetically active light penetration. Besides, lerps were placed mostly along veins, which left most of the lamina uncovered. Furthermore, *C. mopane* leaflets are isobilateral, resulting in photosynthesis taking place from both sides of the leaflet (Potgieter & Wessels 1998).

5.2.2 Construction and attachment

Although there is no report on the method of lerp construction for other *Arytaina* species, lerp construction by *A. mopane* follows a pattern similar to that described by Wooster (1880) for lerp construction psyllids and White (1972) for *Cardiaspina albitextura*. Albeit the construction method of *C. albitextura* and *A. mopane* is the same, it results in two totally different structures. The lerp of *Lasiopsylla rotundipennis* is solid with a surface structure of repeated parallel arcs. The lerp of *C. albitextura* is an open lace-like structure similar to that of *C. densitexta* (White 1972) as opposed to the lerp of *A. mopane*, which shows no marked pattern.

Lerps sometimes fell from the leaves and could be seen lying scattered under *C. mopane* trees even though they were glued to the leaflet surface. This may be due to drying out and loosening from the leaves or dislodged by predators. Alternatively emerging adults as well as nymphs abandoning lerps for better feeding sites may destroy the glues' adhesiveness.

5.2.3 Appearance

Lerps appeared mostly (80%) light brown (15%) white and (5%) black. According to Ernst and Sekhwela (1987), the light brown appearance may be due to the presence of water-soluble phenolics, which makes up 1.06 mg/g lerp dry weight. The black appearance is probably due to fungal colonization. It is not known what contributes to the white appearance, but the unidentified constituents of the waxy substance present in the lerp could contribute to this. According to Dekker *et al*. (1994), waxes form waterproof layers on many stems, leaves and fruits. Furthermore, waxes are fat-like substances, which serve as insulators against cold and help regulate body temperatures. In view of the aforementioned, it could be speculated that the wax probably forms a waterproof layer on the lerp. As lerp contains sugar this (wax) would prevent it from dissolving in water, thereby depriving nymphs of their shelter. This speculation is supported by the fact that lerps do not dissolve in water. It would also seem that the wax absorb a high amount of heat in the day to keep the lerp cool and release the heat slowly in the night to warm the nymphs thereby assisting in temperature regulation. This would be to the advantage of the nymphs as winter temperatures (June to September 2004), range from 11.4 to 23.5°C (Table 5). The thermoregulatory role of lerps can be considered for future research.

5.2.4 Damage

The leaf tissues at the edges of lerps appeared stained, which could probably be attributed to the pressure exerted on the tissues by the lerps or glue that attaches lerps to the leaflet surface, or death of mesophyll cells, however this could be investigated in future. Lerps attract humans, baboons, birds and other organism, which utilize them to supplement their food. For instance, local people use lerps to sweeten bread in addition to eating them directly from the leaflets. These organisms in the process of removing lerps might cause secondary damage by plucking leaves off trees.

5.3 Predation

The presence of dead nymph body parts on leaflet surface and in both abandoned and occupied lerps suggests possible predation on the nymphs, which probably occurred during the period of exposure such as when eggs first hatched and when fifth instar nymphs abandoned their lerps prior to moulting into adults. The fact that the number of nymphs fell short of the number of lerps could also be explained in terms of predation and the moulting of nymphs into adults. It might also be due to migration of nymphs especially the 1st and 2nd instars to new feeding sites thereby abandoning their lerps. Predators such as the suspected Coccinellid beetle and the Brown lacewing larva, which were observed lifting lerps in search of nymphs might have contributed to the death of nymphs found in the lerps. Predation by other insects, frogs, birds, baboons could be the reason for the comparatively low population of third to fifth instar nymphs in relation to the first and second instars. The colour of adults which blend with that of *C. mopane* leaves may be a way of escaping predation through camouflage.

Many animals including baboons, monkeys, birds and frogs consume nymphs and lerps. These animals benefit from the transfer of metals such as Cu, Mn, Fe and Ca, which the nymphs accumulate (Glowacka *et al.* 1997). Based on the manner in which the local native African people selectively lick lerps from the leaflet surface, chances are high that they unknowingly consume some nymphs together with the lerps.

5.4 Physiology

5.4.1 Carbohydrate analyses

In Botswana, Ernst and Sekhwela (1987), state that *A. mopane* lerps are composed of fructose, glucose and raffinose, which is in agreement with the findings of this study (Table 17). This study confirms that fructose and glucose are the predominant sugars in the *A. mopane* lerps with traces of raffinose. The absence of starch in the lerps of mopane psyllids differs from lerps of Australian psyllids feeding on *Eucalyptus* species, which is largely composed of starch (White 1972; Gilby *et al*. 1976).

Table 17. Carbohydrate contents of uninfested *C. mopane* leaves and *A. mopane* lerps from Botswana and South Africa.

Carbohydrate (g/100g)	Uninfested leaves		Lerp	
	Botswana *	South Africa	Botswana*	South Africa
Glucose	0.33	0.86	4.20	0.94
Fructose	0.18	5.88	10.3	6.21
Raffinose	0.01	0.25	0.41	0.31

Converted figures from Ernst and Sekhwela (1987).

The presence of water-soluble monosaccharides may be an indication that honeydew is used for the construction of lerps. According to Meyer (2001), in most of the Homoptera, a portion of the digestive system is modified into a filter chamber, which allows the insect to ingest and process large volumes of plant sap. Excess water, sugars and certain amino acids bypass most of the midgut and are shunted directly into the hind-gut for excretion as honeydew. This suggestion that honeydew is used for the construction of lerps is supported by the high concentration of potassium, contributing to 90% of the ash content of lerps of *A. mopane* (Ernst & Sekhwela 1987). Potassium is a typical constituent of phloem sap and is closely linked to sugar transport in plants (Halt 1970).

It is possible that the hydrolysis of raffinose into glucose and fructose led to the increase in these substances and the consequent absence of raffinose in the infested *C. mopane* leaves. This suggestion is supported by Hartmann-Petersen and Pigford's (1984) finding that completely hydrolyzed raffinose is broken down to the monosaccharides glucose, fructose and galactose.

From the results on carbohydrate analyses (Table 16, p 54), the following calculations can be made. A 100 g of lerps contain 0.94 g of glucose and 6.21 g of fructose. The mean mass of lerp is 0.005 g and the mean number of lerps per leaflet is 19, which translates to 0.095 g (i.e. 19 x 0.005) mean mass of lerps per *C. mopane* leaflet. Thus a leaf comprising 2 leaflets could contain 0.19g lerps (i.e. 0.095 x 2). But 100 g of lerps contain 0.94 g glucose and 6.21 g fructose. Therefore, 0.19 g lerps on a leaf will produce 0.002 g glucose (i.e. 0.19 x 0.94/100) and 0.012 g fructose (i.e. 0.19 x 6.21/100). Consequently 100 g lerps will yield 1.05 g glucose (i.e. 0.002 x 100/0.19) and 6.32 g fructose (i.e 0.012 x 100/0.19). Thus a browser consuming 100 g infested *C. mopane* leaves and lerps is likely to gain 2.35 g glucose (i.e. 1.30 + 1.05) and 14.39 g fructose (i.e. 8.07 + 6.32). Compared with the 0.86 g glucose and 5.88 g fructose gained if 100 g uninfested leaves were consumed, it could be speculated that infestation of *C. mopane* leaves is a source of added sugar (energy) for browsers.

This is consistent with the finding that browsers are adapted to food with higher contents of soluble, readily fermentable nutrients like sugars and starches, measured as nitrogen-free extracts in classic proximate nutrient analyses (Clauss *et al*. 2003). According to Hall (2002) glucose and fructose are the simple sugars most commonly found in plants. Sugars ferment very rapidly in the rumen producing various organic acids. Studies report relatively higher butyrate and similar to slightly lower propionate production and greater potential for lactate production with sugars than with starch (Strobel & Russell 1986; Cullen *et al*. 1986; Heldt *et al.* 1999). Implications of the rate and type of organic acid production from sugars relate to their ability to meet specific animal requirements and affect urinal pH. Butyrate is metabolized by the gut epithelium and is preferentially utilized as an energy source for colony epithelial cells (Bergman 1990). Butyrate is also more effective than propionate or acetate in eliciting development of rumen papillae (Van Soest 1994). Accordingly, sugar feeding has the possibility of enhancing rumen papillae development as compared to other carbohydrate sources. Development of rumen papillae assists in the retention of ingesta particles in the rumen, which leads to an increased ability to digest fibre (Clauss *et al*. 2003). Increased intake noted with sugar feeding may be related to improved diet palatability or increased rates of solid or liquid passage from the rumen (Broderick *et al*. 2000).

It has been reported (Anonymous 2005) that when animals eat feed of relatively low energy value (low digestible energy), its passage through the digestive system of the animal is slow compared with feed that is easily digestible. The effect of this slow passage is to reduce the appetite of the animal. The combined effect of reduced appetite, reduced feed intake and slow release of digestible energy, which results from feeding poor quality feed, reduces weight gain, milk production and/or work output of the animal (Anonymous 2005).

5.4.2 Mineral analyses

5.4.2.1 Mineral deficiency

Mineral deficiencies are a potential constraint for herbivore productivity throughout Africa (Schillhorn van Veen & Loeffler 1990). Clinical signs and behaviours consistent with mineral deficiencies have been reported in several wild ungulates (Langman 1978). Wilson and Hirst (1977) concluded that mineral deficiencies were among the factors responsible for the low rate of increase of roan (*Hippotragus equines*) and sable (*H. niger*) antelope populations introduced into nature reserves in the northern parts of South Africa. Despite the apparent importance of minerals, however, there is little published information on the mineral status of ungulates and the factors, which influence mineral status (Gallivan *et al*. U.D.).

A report on the serum magnesium and zinc status of wild ungulates in Swaziland’s lowveld by Gallivan *et al*. (U.D.) showed a decline in serum zinc and magnesium from June to August, with the small browser (duiker) having a higher magnesium level than the large browser (kudu). According to Tolsma *et al*. (1987), the low zinc level may be due to low zinc availability in browse as soluble minerals are translocated out of the leaves. This study observed significant increases in the two mineral elements, zinc and magnesium, in the infested *C. mopane* leaves as compared with uninfested leaves (Fig. 30). In line with the statement by Tolsma *et al.* (1987), it could be speculated that infestation compensated for the translocation of soluble minerals out of the leaves in the infested leaves thereby making magnesium, manganese and zinc more available to browsers. The translocation of mineral out of leaves might have contributed to the decline of soluble minerals in the uninfested leaves. Zinc is an enzyme activator and deficiencies are manifested by salivation, parakeratosis of the rumen and loss of hair on the snout, manganese is required for hair pigmentation and magnesium improves milk production (Bothma 2002).

The significantly higher concentration of potassium, iron and copper in the uninfested leaves suggest these elements may be present in the honeydew (not tested in this study) used for the construction of lerps, which resulted in their decline in the infested *C. mopane* leaves. This suggestion is consistent with Glowacka *et al.* (1997) stating that *Psyllopsis fraxini* eliminated large amounts of aluminum, iron, copper, manganese and cadmium with honeydew. Ernst and Sekhwela (1987) detected a high concentration of potassium in *A. mopane* lerps in Botswana, which further substantiates the suggestion.

5.4.2.2 Nutritional quality

Browse usually has higher crude protein content than grasses (Dube & Ncube 1993). The nutritional quality of semi-deciduous leaves decreases with maturity, largely because mature leaves generally contain fewer nutrients than immature leaves (Mattson 1980; Schultz *et al*. 1982; Schroeder 1986). It has also been reported that plants on average resorb about half of the nitrogen and phosphorous from a leaf before it is shed (Chapin & Kedrowski 1983; Pearcy *et al.* 1996). Nutrient resorption is important to the nutrient economy of a plant, because it allows nutrient redistribution either to reproductive structures and new leaves or to storage over winter (Pearcy *et al.* 1996).

The large increase in Ca, Mn, and Mg in infested mature leaves perhaps increases the nutritional quality of *C. mopane* leaves in contrast to the above reports of Mattson (1980), Schroeder and Malmer (1980) and Schultz *et al*. (1982) calcium plays an important role as a constituent of cell walls in the form of calcium pectate (Devlin 1975). According to Ernst (1975), the concentrations of calcium and manganese increase with maturation of the leaves of some miombo woodland trees of the Leguminosae family. It is also reported that Ca is not resorbed (Epstein 1972). These findings of (Epstein 1972; Ernst 1975) together with the fact that infestation occurred on mature *C. mopane* leaves probably contributed to the high increase in calcium and magnesium in the infested leaves.

Leaves accumulate starch in the absence of calcium (Curtis & Clark 1950). It has been suggested that calcium has some role to play in the sugar transport or is directly concerned in the starch-sugar change over (Curtis & Clark 1950). In view of this suggestion it could be speculated that *A. mopane*'s infestation enhances sugar transport in *C. mopane* since infested leaves contain a significantly higher amount of calcium than uninfested leaves.

Ernst and Sekhwela (1987) report the presence of N, P, K, Ca, Mg, Mn, and Zn in *A. mopane* lerps although this study did not perform such analyses. If browsers really consume lerps together with the browse then the nutritional quality of browse is enhanced by the lerps in terms of natural minerals.

Plant physiologists (Devlin 1975; Bannister 1976) have shown that there is an increase in the amount of nitrogen in the aerial parts of both perennial and annual plants when subjected to water stress (water-logging and drought), and especially so for the soluble nitrogen in their phloem sap. Nitrogen is transported to sites of synthesis and away from senescing tissue as amino acids in the phloem (White 1969). This means that water stress causes an increase of these amino acids in the phloem sap. This study was conducted during the dry winter period and this possibly contributed to the higher amount of nitrogen in the uninfested leaves. Furthermore, Melillo *et al*. (1982) report that invasion by fungi often causes an increase in the nitrogen content of the leaf. Fungal colonization of *C. mopane* leaflets was also a common sight, which probably added to the nitrogen content in the leaves in line with the findings of Melillo *et al*. (1982).

On the other hand, comparing the results of this study (August 2004) with the mean values of a parallel project at the University of Limpopo from Musina Experimental Farm (MEF) for August 2002 to 2003 (Fig. 30), the infested *C. mopane* leaves of this study contained more nitrogen than the uninfested leaves. This suggests differences in the concentration of minerals in *C. mopane*, which may be due to different environmental conditions in different years. Probably these changes on the mineral concentrations contribute to the presence or absence of *A. mopane* in a particular location of *C. mopane* in a specific year. The results of this study could not be compared with that of Ernst and Sekwhela (1987) (Table 3, p 24) because convertion of that (Table 3) to dry mass values produced insignificant figures.

According to White (1970a), *Cardiaspina* nymphs appear to inject small amounts of a toxic salivary secretion into the phloem, which diffuses into surrounding tissues. This substance induces a breakdown of the mesophyll tissue resulting in the liberation of great amounts of soluble nitrogen at the feeding site. Thus psyllids with their salivary secretions are able to mobilize nutrients from the leaf cells as their food supply (White 1970b; Morgan 1984; Crawford & Wilkens 1996). Young insects (like all young animals) grow very fast and must have an abundant and balanced supply of amino acids in their diet. This is needed for the production of body proteins or they will suffer from malnutrition and die (White 1970b). Nymphs feeding on nitrogen in the form of amino acids may account for the decrease in the concentration of nitrogen in the infested *C. mopane* leaves. As utilization of browse is positively correlated with nitrogen content (Jachmann & Bell 1985; Kursar & Coley 1991), ruminant browsers are likely to benefit from the available nitrogen at the feeding sites of the nymphs, which they are able to recycle into the rumen as ammonia via the blood or as urea via the saliva according to Van Soest (1994). This is consistent with the report (Jones *et al*. 1998) that adequate nitrogen must be supplemented to the rumen to avoid starving fibre digesters, especially if rapidly growing non-fibre carbohydrate bacteria are scavenging available nitrogen. Deficiencies or excesses of nutrients or other constituents may reduce digestibility of foods. In ruminants, deficiencies in rumen of ammonia nitrogen or of sulphur will restrict microbial growth and thus reduce fibre digestibility (McDonald 1995). Higher digestibility yields more available nutrients for passive or active transport in intestinal absorption and furthermore, less food is needed to meet energy and nutrient requirements (EZNC 2005), which is what is required especially in the dry winter period when browse is scarce in mopani veld.

Potassium, a typical constituent of phloem sap is closely linked to sugar transport in plants (Halt 1970; Läuchli & Schwander 1966). It is thought (Ernst 1975) that psyllids feeding on phloem sap might cause a depletion of potassium in the leaves. Ernst and Sekhwela (1987) report on the selective accumulation of potassium and phosphorous in *A. mopane* lerps and the large amounts of lerps on heavily infested *C. mopane* leaves. They speculated that these (large infestation and the accumulation of potassium and phosphorous in lerps) might affect the mineral and carbohydrate metabolism of the leaves. This study is in support of the aforementioned reports in view of the fact that *A. mopane* feeds on the phloem sap of *C. mopane* and that there is large infestation of lerps.

5.5 Ecology: game farming, browse and animal condition

5.5.1 Game farming

Wildlife in the Limpopo Province plays an important role in the income and employment of the area. Impala (*Aepyceros melampus*), greater kudu (Tragelaphus strepsiceros), steenbok (*Rhapicerus campestris*), grey duiker (*Sylvicapra gimmia*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis*), and occasionally even wildebeest (*Connochaetes taurinus*) and zebra (*Equus *burchlli*) feed on *C. mopane* (Styles 1993). This means that the mortality of game species especially in winter would have a negative influence on the local economy. Contrary to reports that considerable reduction in leaf production, leaf size and even seed production are known to occur in plants infested with homopterans (Newberry 1980; Becerra &Venable 1989), it appears that *A. mopane*'s infestation increases the energy value and probably the palatability of *C. mopane*, which could favour game farming.

5.5.2 Browse and animal condition

Plants infested with sap sucking insects are known to allocate more macro elements such as calcium, phosphorous and sodium as well as organic material such as carbohydrate and protein to the leaves, often at the expense of the roots. This condition would result in a decrease in both the value and palatability of the browse (Vranjic & Gullan 1990). So it appears that homopterans not only confer protection on plants through their association with ants, but also through reducing browse quality (Styles 1993). In this study *A. mopane* was not found in association with any specific ant species, and therefore does not confer protection on *C. mopane,* contrary to Styles's (1993) statement. The sugary secretions in the form of lerps increase the energy value and also seem to increase the palatability of *C. mopane* leaves, which is not in agreement with the statement by Vranjic and Gullan (1990). Virtually, all *C. mopane* trees infested by *A. mopane* had lerp covered leaves scattered over most of their canopies. Within stands of *C. mopane* these trees could be regarded as patches for consumption by browsers (Astrom *et al.* 1990). This could have an important impact in the winter browsing areas of the Limpopo and Mpumalanga Provinces of South Africa, when most plant species are leafless. Consequently, the infestation of *A. mopane* on *C. mopane* could translate into a direct economic value for the region in terms of improved animal condition. Its major benefit is increasing the energy content of *C. mopane* browse and in providing a supplement to the diet of native African people, baboons, birds, and some insects.

5.6 Future research

Time constraints coupled with a lack of appropriate equipment in some instances made it impossible for a complete investigation of the biology of *A. mopane.* The following aspects need to be considered for future investigations with the hope that a complete account of the biology of *A. mopane* can be written.

- The number of generations per year, adults' life span in the field, the duration between instars, how *A. mopane* survives the period when it is not seen on *C. mopane* (between October and June), how many females is a male capable of inseminating and how many times does a female mate to produce eggs to her full capacity.

Other aspects that require further investigations are:

- The two forms of nymphs observed to ascertain if they originate from the two females described by Pettey (1925).

- The three spines that terminate the antenna (in contrast to the two reported by Pettey 1925) need to be examined to explain their function and also its taxonomic implications.

- The true function of the pedicel in *A. mopane* as it does not attach egg to the leaflet surface contrary to literature.

- The eggs possess filaments whose function is currently unknown.

- The higher quantities of calcium and manganese in the infested leaves to ascertain if they result from soil conditions, infestations or both.

- Trace elements and other chemical contents of lerp material need to be analyzed by more suitable techniques such as atomic absorption.

- The potential of brown lacewing larvae and the suspected Coccinellid larvae as biological control agents for other psyllids as crop pests.

- The chemical structure of the active salivary substance secreted by psyllid nymphs.

- The substance(s) contributing to the white appearance of lerps.

- The thermoregulatory role of lerps.

- The mechanism of nymph feeding on petioles and flower buds.

- The utilization of lerps in view of the sugary nature by game and human as food.

- Infestation on *C. mopane* by *A. mopane* is an annual occurrence in winter. What happens to *A. mopane* before and after winter? This needs to be investigated to find out where these insects hibernate.

- Courtship, mating behaviours and lifespan of adults in the field to complete the life cycle features of *A. mopane*.

Conclusion

Arytaina mopane occur and feed on *C. mopane* leaves probably due to lack of alternative hosts plants as the emergence of *A. mopane* coincides with the dry winter period of South Africa, when other trees are leafless. Seemingly, there are sporadic localized occurrences of *A. mopane* with rainfall, temperature and humidity differences between the years.

Eggs are not attached to the leaflet surface by a pedicel (contrary to literature) but glued to it. This suggests some kind of evolution with glue replacing the pedicel function. Whereas eggs are mostly placed on the abaxial leaflet surface, nymphs prefer the adaxial leaflet surface.

Among the nymphs, two morphotypes differing in colour and abdominal markings were identified, which could be linked to the two differing female specimen described by Pettey (1925). Nymphs produce lerps, which partially protect them against predators and desiccation. Lerps are, however, used by different animal species as a source of additional nutrients. Neither nymphs nor adults showed aggression towards each other. Nymphs do not co-habit same lerp. The high infestation of *A. mopane* probably affects the mineral metabolism of the host tree.

There seems to be more than one feeding mechanism by nymphs. Stylet puncture marks have been observed in the guard cells of stomata when nymphs occur in-between veins and stylet penetration through epidermis into parenchyma tissues when nymphs occur on the petiole. When nymphs occur on veins where no stomata exist, a different feeding mechanism may be employed. Perhaps nymphs secrete chemical substances that soften plant tissue, which may result in leakage of nutrients.

Visible damage caused by nymphs on the host plant includes discolouration of leaflets around feeding sites and occasional curled leaflets.

Every organism has its natural enemies and *A. mopane* is no exception. Baboons, Red winged starling, Tawnyflanked prinia, painted reed frog, brown lacewing larvae, suspected larva of the ladybird beetle, spiders and some ants prey on nymphs and lerps.

Ecologically, Badenhorst (2003), citing research done by Ian du Hoven, shows that plants have the ability to defend themselves from browsing pressure. By producing more condensed tannins, leaves lose their taste after a while, which “signals” to the animals the necessity for moving on to other trees. *Colophospermum mopane* trees, utilized by *A. mopane* had lerp covered leaves scattered over most of their canopies, and such trees could be regarded as patches for consumption within stands of *C. mopane* browsers (Astrom *et al*. 1990). Lerps are a source of added sugar (energy) and possibly also increase the palatability of the leaves. In this regard, *A. mopane* may play a vital role in improving the browse quality and thus impacts positively on game farming in the winter browsing areas of the Limpopo and Mpumalanga provinces of South Africa. In southern Africa, the long dry winter season is a period of several nutritive stresses for livestock and game, leading to loss of weight. During this drought period other woody tree species are still leafless and the quality and quantity of natural grasses are poor and scarce (Macala 1996). However, in areas where *C. mopane* is common and particularly in shrub or low tree form, game avidly feed on the leaves, still attached to the plant and on those that have fallen to the ground leading to reduce weight loss in the winter months (Timberlake 1999).

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