

A Review of Leaf-mining Insects and Control Options for their Management, with Special Reference to *Holocacista capensis* (Lepidoptera: Heliozelidae) in Vineyards in South Africa

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Date of submission for publication: May 2020

Date of acceptance for publication: August 2020

Key words: Integrated pest management, leaf miner, biological control, grapevine

A leaf-mining pest occurring on commercial varieties of *Vitis vinifera* in South Africa was investigated due to the presence of cocoons on fruit. The leaf miner, *Holocacista capensis*, was reported on grapevines in 2012. Since its discovery on commercial grape varieties, control strategies have consisted solely of insecticide applications. Despite the fact that the leaf-mining habit is taxonomically diverse and considered ancient, little is generally known of leaf-mining larvae. A review was conducted in order to better understand the leaf-mining strategy and amalgamate the current knowledge of other leaf-mining insects. The general evolutionary history within the full complement of taxa that display the leaf-mining habit is discussed. The review focuses on lepidopteran leaf-mining pests and discloses the known information associated with the first report and the impact of *H. capensis* in the Western Cape, South Africa. As no control methods have been identified for *H. capensis* in vineyards, various chemical, biological and cultural control strategies adopted for other leaf-mining pests were investigated. Control options, including the use of entomopathogenic nematodes (EPNs), parasitoids, physical and cultural control measures, were considered and are discussed. Alternate control methods are pertinent for the grape-growing industry to avoid the development of the insecticide resistance that is common amongst leaf miners. This review aims to consolidate the available literature and therefore aid in the development of an integrated pest management strategy to effectively control *H. capensis* in infested vineyards in South Africa.

INTRODUCTION

Grapevines in South Africa are host to more than 35 insect pests, with the key pest orders being Hemiptera (mainly shield bugs, scale insects, mealybugs and planthoppers), Coleoptera (beetles) and Lepidoptera (butterflies and moths) (Allsopp *et al.*, 2015), which pose a threat to the industry.

In 2012, an unknown leaf-mining heliozelid was reported, infesting a table grape vineyard in the Western Cape province, South Africa. At the time, the known heliozelid fauna from Africa were limited to three species described in South Africa (Van Nieuwerkerken & Geertsema, 2015). Subsequent field visits indicated high larval/leaf mine abundances and cocoon casings of the leaf miner on the foliage, stems, trellises and grape bunches in vineyards. In 2015, the leaf miner was described by Van Nieuwerkerken and Geertsema (2015) as *Holocacista capensis* Van Nieuwerkerken & Geertsema (Lepidoptera: Heliozelidae). Since the discovery of *H. capensis* in 2012, a concomitant study by Wang *et al.* (2015), using gas chromatography-mass spectrometry, identified the sex pheromone (more accurately, a male attractant) of *H. capensis*. Baseline studies to better

understand the bio-ecology of *H. capensis* in the Western Cape were conducted by Torrance (2016).

Sustainable, effective control of the leaf miner is pertinent for the grape-growing industry in South Africa to avoid the development of resistance against commonly used insecticides. This review consolidates the available literature regarding the leaf-mining habit, lepidopteran miners as pests, and the effect of the environment on their infestation levels. Management options for leaf miners with regard to chemical control, the use of entomopathogenic nematodes (EPNs), parasitoids and other control measures were considered in the light of possible future control options for *H. capensis* on grapevines in South Africa.

LEAF-MINING INSECTS

Globally, little is known of leaf-mining insects (Vári, 1961; Auerbach *et al.*, 1995; Lees *et al.*, 2014). Leaf-mining insects are a taxonomically diverse group of endophagous insects and the larvae of leaf-mining taxa are, in most cases, concealed within the plant tissue of their hosts during larval

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Acknowledgements: Financial support for this work was provided by the National Research Foundation (NRF), the South African Table Grape Industry (SATI), and the Technology and Human Resources for Industry Programme (THRIP-TP14062571871).

development, or at least for part thereof (Hering, 1951; Kirichenko *et al.*, 2018). The duration of the leaf-mining stage varies between species and is not only associated with larval growth, but can also cover the development of pupae and the emergence of adult insects in taxa that pupate within the leaf mine (Connor & Taverner, 1997).

Despite the fact that the leaf-mining habit is ancient, it continues to be lost and acquired by a number of phytophagous insect lineages (Connor & Taverner, 1997) and has evolved independently numerous times (Auerbach *et al.*, 1995). The leaf-mining habit is known to occur in at least 57 families within four insect orders, accounting for more than 10 000 leaf-mining species (Connor & Taverner, 1997). The mines originating from the respective orders are classified into specific groups, namely lepidopteronome (Lepidoptera), dipteronomie (Diptera), coleopteronome (Coleoptera) and hymenopteronome (Hymenoptera) mines (Hering, 1951).

The geographical distribution of endophagous insects, like leaf miners, is inevitably dependent on the distribution of their larval host plants. In most cases, however, the distribution of a leaf miner is less extensive than that of its host plant (Hering, 1951). Amongst the herbivorous insects, many leaf miners pose a threat to a variety of forest and urban plant species, whilst others are regarded as important pests of agricultural crops and are considered an economically important group globally (Spencer, 1973; Nielsen & Common, 1991; Digweed *et al.*, 2009).

Over the last decade, an increase in incidents of leaf-mining insects has attracted the attention of the agricultural and horticultural industries due to their presence in commercial forests, agricultural landscapes and on ornamental plant varieties of high value (Van Nieukerken & Geertsema, 2015; Kirichenko *et al.*, 2018).

THE LEAF-MINING HABIT

In the past, the concealed feeding environment of endophagous insects was speculated to provide a competitive advantage when compared to their exophagous counterparts (Hering, 1951; Nielsen & Common, 1991), and to protect feeding larvae from natural enemies (Hering, 1951; Price *et al.*, 1987). It also provides a buffer against the physical environment (Connor & Taverner, 1997), and enables the feeding larvae to avoid plant defences (Feeny, 1970) and thus facilitates selective consumption of more nutritious leaf tissue (Cornell, 1989). Price *et al.* (1987) and Connor and Taverner (1997) reviewed some of these hypotheses amongst various endophagous feeders and arrived at similar conclusions. Connor and Taverner (1997) suggest that the selective advantages inherent to the leaf-mining habit are to facilitate: 1) increased feeding efficiencies, which support some of the hypotheses and findings of Cornell (1989); 2) the avoidance of negative effects associated with disease, should it be present within a population or species, by internally feeding larvae; 3) the protection of larvae from the direct and indirect effects of photochemical changes in plant chemistry, for example due to UV radiation; and 4) the reduction of water loss and lessening the risk of desiccation by the presence of a buffered micro-environment within the feeding leaf gallery.

Connor and Taverner (1997) also highlight the

disadvantages of the leaf-mining habit. These include: 1) the loss of mobility, which thus cause larvae to be unable to escape parasitoids and predators; this is supported by statements made by Nielsen and Common (1991); 2) decreased species richness within leaf-mining lineages when compared to that of exophagous insects; 3) mortality associated with plant senescence, herbivory and premature abscission of leaves; and 4) reduced fecundity due to the small size of individuals.

From an evolutionary perspective, the disadvantages of the leaf-mining habit outweigh the advantages. The persistence of leaf-mining guilds in various insect orders and environmental niches in the present day, however, proves that, for some taxa, the leaf-mining habit is a feasible means of survival under certain circumstances (Connor & Taverner, 1997).

LEPIDOPTERAN LEAF MINES

Apodal or legless lepidopteran leaf-mining larvae (or “serpentine larvae”) consume the mesophyll between the upper and lower epidermal layers of a leaf (Stehr, 1992; Bernardo *et al.*, 2015), creating small blotch mines or galleries within the parenchymal tissues of host plants (Hering, 1951). These feeding channels, or cavities, serve as both living and feeding quarters for leaf-mining larvae (Hering, 1951).

The shape of a leaf mine and the presence of voluminous frass often presents a unique feeding pattern within an infested leaf, which can be used as a diagnostic tool for species-specific identification (Hering, 1951; Kirichenko *et al.*, 2018). Mines produced by any leaf-mining insect can be used to determine the order, family and, in many cases, the particular genus (Hering, 1951; Vári, 1961). Lepidopteran hyponomology (the study of mines) often provides a clear and more accurate indication of species identity than comparing fine differences in larval and adult morphology.

LEPIDOPTERAN LEAF-MINING PESTS

Lepidoptera account for the majority of leaf-mining insects (Kirichenko *et al.*, 2018). As a result, and due to the destructive qualities of the larval life stages of some of the leaf-mining species, these Lepidoptera are considered to be of great economic importance (Nielsen & Common, 1991). At least 40 lepidopteran families exhibit leaf-mining habits, with considerable variation between species. These lepidopteran leaf miners account for approximately 70% of all known insect families associated with leaf-mining activities (Connor & Taverner, 1997; Kirichenko *et al.*, 2018). Within the Lepidoptera, the leaf-mining families of economic importance include the Gelechiidae, major pests in the forestry and agricultural industries (Lee *et al.*, 2009); the Gracillariidae, notorious as invasive leaf-mining pests of woody plants (Kirichenko *et al.*, 2018); and the Heliozelidae, predominantly pests on trees and vines (Davis, 1998). A list of lepidopteran leaf-mining agricultural pests is presented in Table 1.

HELIOZELIDAE – THE “SHIELD BEARERS”

The Heliozelidae (Lepidoptera: Adeloidea) are a group of widely distributed, cosmopolitan, minute, diurnal micro-Lepidoptera (Davis, 1998; Powell, 2003, Van Nieukerken

TABLE 1
A (non-exhaustive) summary of agriculturally important leaf-mining lepidopteran pests

Family	Leaf-mining species	Common name	Commercial host	Native range	Region of invasion	Source
Bedelliidae	<i>Bedellia somnulentella</i>	Sweet potato leaf miner	Sweet potato	Eurasia	Cosmopolitan	Visser (2015a); Dos Santos <i>et al.</i> (2018)
Heliozelidae	<i>Holocacista capensis</i>	NA	<i>Vitis vinifera</i>	Southern Africa	Southern Africa	Van Nieuwerkerken & Geertsema (2015)
	<i>Holocacista rivillei</i>	European grapevine leaf miner	<i>V. vinifera</i>	Europe	Southern Europe, Western Asia	Van Nieuwerkerken <i>et al.</i> (2012)
	<i>Antispila oinophylla</i>	Grapevine leaf miner	<i>V. vinifera</i>	Eastern North America	Northern Italy	Van Nieuwerkerken <i>et al.</i> (2012)
	<i>Antispila uenoi</i>	Grapevine leaf miner	<i>V. vinifera</i>	Japan	Japan	Van Nieuwerkerken <i>et al.</i> (2012)
	<i>Antispila nysaefoliella</i>	Tupelo leaf miner	Black gum	Southeastern United States	United States	Low (2012)
	<i>Coptodisca splendorigerella</i>	Resplendent shield borer	Apples, cranberries	Unknown	North America	Boush & Anderson (1967)
Incurvariidae	<i>Protaephagus capensis</i>	Blotch leaf miner	Protea, <i>Leucaedendron</i> sp.	Southwestern Cape (South Africa)	Southern Africa	Wright (2015)
Gelechiidae	<i>Aproaerema modicella</i>	Groundnut leaf miner	Ground nut, soybean	South-South-East Asia	South, South-East Asia	Shanower <i>et al.</i> (1993)
	<i>Aproaerema simplexella</i>	Groundnut leaf miner	Groundnut, soybean, possibly lucerne	Africa and Australia	Africa, Australia	Buthelezi <i>et al.</i> (2012)
	<i>Bilobata subsecivella</i>	Groundnut leaf miner	Groundnut, soybean, lucerne	South-East Asia	Africa	Du Plessis (2015)
	<i>Tuta absoluta</i>	Tomato leaf miner	Tomato, potato	Western neotropics	South America, Afro-Eurasia	Siqueira <i>et al.</i> (2001); Biondi <i>et al.</i> (2018)
	<i>Phthorimaea operculella</i>	Potato tuber moth	Potato, tomato, gooseberry, brinjal, chilli, tobacco	South America	All tropical, subtropical potato-growing regions	Kroschel & Zegarra (2013); Visser (2015b)
	<i>Symmetrischema tangolias</i>	Andean potato tuber moth	Potato and tomato	South America	South America, New Zealand, Australia, United States	Kroschel & Zegarra (2013); Sporleder <i>et al.</i> (2017)
Gracillariidae	<i>Phyllocnistis vitegenella</i>	American grape leaf miner	<i>Vitis vinifera</i>	North America	Europe	Ureche (2016)
	<i>Phyllocnistis citrella</i>	Citrus leaf miner	Citrus	South-east Asia	Worldwide (all citrus-producing areas)	Kirichenko <i>et al.</i> (2018)
	<i>Acrocercops bifasciata</i>	Cotton leaf miner	Cotton and okra	Unknown	Southern Africa	Bennett (2015)

TABLE 1 (CONTINUED)

Family	Leaf-mining species	Common name	Commercial host	Native range	Region of invasion	Source
	<i>Acrocercops gossypii</i>	Cotton leaf miner	Cotton	Unknown	Southern Africa	Bennett (2015)
	<i>Spulerina</i> sp.	Mango twig miner	Mango	Unknown	Southern Africa	Grové <i>et al.</i> (2015)
	<i>Phyllocnistis</i> sp.	Thin line leaf miner	Protea	Unknown	Southern Africa	Wright (2015)
Lyonetiidae	<i>Leucoptera coffeina</i> and <i>Leucoptera meyricki</i>	Coffee leaf miner	Coffee	Central, East, Southern Africa	Africa	Fragoso <i>et al.</i> (2002); Schoeman (2015)
	<i>Leucoptera coffeella</i>	Coffee leaf miner	Coffee	Africa	Neotropics, Mexico	Fragoso <i>et al.</i> (2002); Lomeli-Flores <i>et al.</i> (2010)

et al., 2011; Regier *et al.*, 2015; Milla *et al.*, 2018), present in all major faunal realms, with no representatives in New Zealand and Antarctica. One hundred and twenty-five described species comprise the Heliozelidae, placed in 12 genera (Van Nieukerken *et al.*, 2011; 2012; Van Nieukerken & Geertsema, 2015). The family is taxonomically poorly studied, although taxonomic revisions associated with heliozelids have been conducted by Van Nieukerken *et al.* (2011), Regier *et al.* (2015), Van Nieukerken and Geertsema (2015) and Milla *et al.* (2018) (Fig. 1) in recent years.

Heliozelid moths are typically small, with their forewings ranging from 1.7 mm to 7.0 mm in length (Regier *et al.*, 2015). Due to their small size, most heliozelids are rarely seen or collected, even when population abundances are high (Powell, 2003; Regier *et al.*, 2015). Most adult moths within the Heliozelidae possess fundamentally dark wing colouration with iridescent scaling (Scoble, 1992; Powell, 2003).

Larval instars are obligate leaf miners, with the exception of the final instar (Stehr, 1992; Regier *et al.*, 2015). A flat, lenticular case is constructed by the penultimate instar from the epidermal layers of a mined leaf, lined and bound with silk to form a firm, cocoon-type covering (Holloway *et al.*, 1987; Stehr, 1992; Regier *et al.*, 2015). The vernacular name, “shield bearers”, refers specifically to the oval, lenticular shape of the crafted casing (Scoble, 1992; Davis, 1998). The casing is either suspended by means of a silken thread,

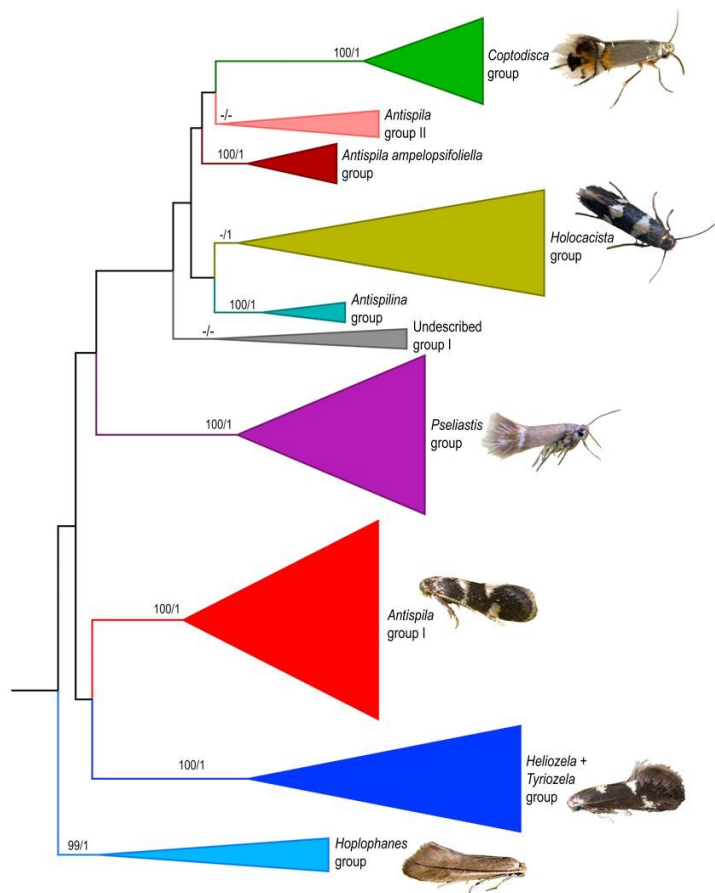


FIGURE 1

The maximum likelihood tree compiled by Milla *et al.* (2018) that represents the major genera within the Heliozelidae.

or carried or dragged from the infested leaf by the encased larvae (Scoble, 1992; Regier *et al.*, 2015). The larvae anchor themselves by weaving a silken mat onto objects with which they come into contact.

Detailed accounts of the morphology of all the life stages of the Heliozelidae have been documented by Bourgogne (1951), Hering (1951), Holloway *et al.* (1987), Scoble (1992), Davis (1998), Powell (2003) and Patočka and Turčáni (2005). Keys in Mey (2011) and Patočka and Turčáni (2005) enable the identification of some genera and species within the Heliozelidae.

Almost all individual heliozelid species are hostplant-specific, confined to genus level or, at least, the plant family level (Regier *et al.*, 2015), which may lead to gregarious behaviour, depending on local plant assemblages. Within the agricultural context, a number of heliozelids are considered to be of economic importance (Table 1). Over the last three decades, four heliozelid species have unexpectedly been encountered on commercial grapevines. These are *Antispila oinophylla* Van Nieukerken & Wagner (reported in Northern Italy in 2007, one of the two species of North American origin), *Antispila uenoi* Kuroko (a pest native to Japan, reported on commercial vineyards (Kuroko, 1987; Ueno *et al.*, 1987) and *H. capensis* (a pest thought to be a native species, presently reported on commercial vineyards in South Africa) (Van Nieukerken & Geertsema, 2015).

HOLOCACISTA CAPENSIS

Holocacista capensis is a multivoltine (having several generations per year) pest present throughout a grapevine growing season (Van Nieukerken & Geertsema, 2015; Torrance, 2016).

Morphology and known biology

The adults are small, diurnal moths with a wingspan of ca. 3.9 mm to 4.9 mm (Van Nieukerken & Geertsema, 2015). The black ground colour of the wings is ornamented by silvery-white spots or fascia. The head and face are covered by silvery-white metallic, appressed scales. Male and female moths can be differentiated based on the colour of the posterior abdominal segments (lead-coloured in males, jet

black in females) and the markings on their forewings (in females the first costal and dorsal spots are joined to form a contiguous band) (Fig. 2). The adults of *H. capensis* closely resemble *Holocacista salutans* (Meyrick) and *Holocacista varii* (Meyrick). Eggs are laid singly in leaves by females after mating (Van Nieukerken & Geertsema, 2015).

The larvae develop through four feeding instars (Van Nieukerken & Geertsema, 2015). These larvae are unable to move to other leaves upon damage to the natal leaf or mine (Torrance, 2016). The heads of feeding larvae are usually characterised by dark, prognathous head capsules. Their bodies are yellow or whitish (Van Nieukerken & Geertsema, 2015). The larvae feed on leaf tissue only (Torrance, 2016) and completed mines reach 12 mm to 15 mm in length (Van Nieukerken & Geertsema, 2015). The fifth, final instar is non-feeding and constructs the cocoon casing in which it will pupate.

Symptoms of damage

The mining activities of larvae cause physical damage to the infested grapevine leaves. The effect of the mines on the photosynthetic ability of a grapevine is not yet known, although it appears to be limited (Van Nieukerken & Geertsema, 2015). The mines are predominantly present along the leaf margin. When high infestations are reported, it is usually later in a growing season, usually after harvest, or when leaf miner populations were left unmanaged.

The final instar larva in its cocoon casing descends from the leaf by means of a silken thread (similar to most other leaf-mining heliozelids) (Torrance, 2016). Upon landing on an object in its immediate surroundings (e.g. leaf, trellis post or grape bunch), the larva will move to an appropriate location and firmly attach itself to the object (Van Nieukerken & Geertsema, 2015; Torrance, 2016). It therefore is undesirable if the cocoon casings are present on fruit intended for consumption.

Bio-ecology

Larval and adult abundance tends to increase throughout a season, coupled with a rise in the prevailing temperatures (Torrance, 2016). February and March mark the peak in adult

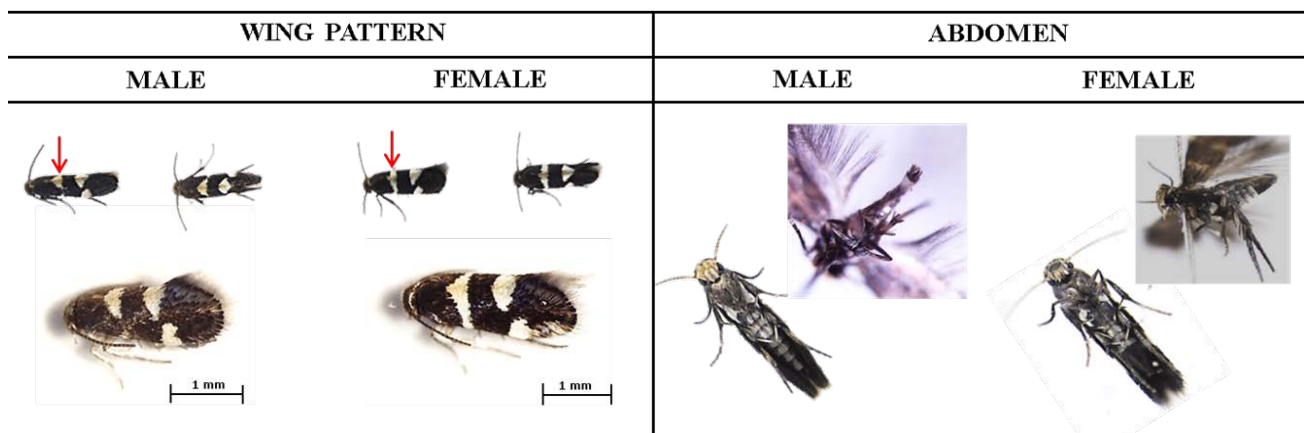


FIGURE 2

Different wing (indicated by red arrows) and abdominal patterns of male and female *Holocacista capensis* adults. Adapted from Torrance (2016).

and larval abundance (Van Nieuwerkerken & Geertsema, 2015; Torrance, 2016). According to Torrance (2016), temperature plays a vital role in leaf miner population abundance. Other variables (including trellis angle and block aspect) affecting leaf miner infestation were also investigated, but definite conclusions regarding their specific effect on population numbers could not be drawn (Torrance, 2016).

It is estimated that the life cycle of the moth takes at least seven weeks to complete, and a minimum of four generations can be present within a growing season (Torrance, 2016). The leaf miner overwinters in the larval or pupal life stage within the cocoon casing that is sheltered from the elements (e.g. under the bark of a grapevine stem, in leaf litter or in the crevices of trellising posts) (Torrance, 2016). These individuals will eclose in the ensuing growing season and will produce the first generation in the new season (Van Nieuwerkerken & Geertsema, 2015; Torrance, 2016).

Holocacista capensis is widely distributed throughout the Western Cape, South Africa and has established itself in relatively high abundances in some of the major table grape-producing regions in southern Africa (Fig. 3) (Torrance, 2016). Synonymy amongst populations (molecular identifications) has not yet been confirmed.

VARIABLES AFFECTING LEAF MINER INFESTATION
Auerbach *et al.* (1995) state that the dominant cause of mortality or absence of leaf miner populations in suitable habitats can be attributed to vertical (interactions between miners, host plants and natural enemies) and horizontal interactions (including inter- and intraspecific interactions between miners and herbivores). This does not, however, account for environmental and abiotic factors affecting leaf

miner infestation.

Little is known of the direct effects of abiotic factors or variables on leaf miner abundance and survival (Auerbach *et al.*, 1995). Pereira *et al.* (2007) identified rainfall as an important factor affecting mortality of *Leucoptera coffeella* (Guérin-Méneville & Perrottet) (Lepidoptera: Lyonetiidae), and also considered that weather conditions could affect egg mortality. However, their study concentrated on the environmental factors operative between the two seasons (rainy vs. dry) and not necessarily on the factors influencing population abundances within a particular season. Potter (1992) excluded shade as an important factor affecting the abundance of *Phytomyza ilicicola* Loew (Diptera: Agromyzidae). A study by Johns and Hughes (2002) indicated a negative association between emergence success and adult weight of *Dialectica scariella* Zeller (Lepidoptera: Gracillariidae) in Paterson's curse, *Echium plantagineum* (Boraginaceae), and elevated CO₂ as a result of reduced foliar quality of *E. plantagineum*. The invasion ecology of the horse chestnut leaf miner, *Cameraria ohridella* Deschka & Dimić (Lepidoptera, Gracillariidae), on the other hand, has been found to be affected by long-distance dispersal and increased human population densities (increasing the probability of accidental transport of leaf miners as a result) (Gilbert *et al.*, 2004).

In the case of *H. capensis*, the average adult male abundance has been strongly correlated with the average minimum humidity (and thus also the average maximum temperature) (Torrance, 2016). Edge effects, the difference between externally located plots and internally located plots, did not affect leaf miner abundance. Spatial distribution and abundance in grapevine blocks have not been assessed,



FIGURE 3
Recorded distribution of *Holocacista capensis* (Van Nieuwerkerken & Geertsema, 2015; Torrance, 2016).

however, and require further investigation. Human-mediated means of dispersal have also been speculated (Torrance, 2016).

PEST MANAGEMENT

On a global scale, most commercial vineyards are protected against leaf-mining pests (as with a number of other pests) by the use of insecticides (Maier, 2001). However, various other control strategies have also been used to control pest populations. A summary of these strategies and their respective leaf-mining insect targets is given in Tables 2 to 4.

Chemical control

Chemical control can be achieved through the use of synthetic chemical insecticides or botanical insecticides (Isman, 2006) (Table 2). In terms of environment-friendly pest management, botanical insecticides pose an attractive alternative to the use of synthetic insecticides, being less of a threat to human health or to the environment. Generally speaking, synthetic pesticides exhibit some adverse effects, such as their toxicity for non-target organisms, contamination of groundwater and the development of pesticide resistance in pest populations (Isman, 2006).

Short-term (seasonal) control of *H. capensis* has been achieved in vineyards where dichlorvos and spinosad were applied (Torrance, 2016). Extensive research has been conducted on insecticide use and the corresponding insecticide resistance of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Biondi *et al.*, 2018), raising concern about long-term control strategies for other leaf-mining pests with similar generation times, including *H. capensis*.

Entomopathogenic nematodes

Of the various beneficial, parasitic groups within the nematode complex, entomopathogenic nematodes (EPNs) are used to control insect pests (Stock & Hunt, 2005; Stock, 2015). The genera within this group include members of the genera *Steinernema* Travassos (Steinernematidae: Rhabditida) and *Heterorhabditis* Poinar (Heterorhabditidae: Rhabditida) (Kaya *et al.*, 1993). Together with their associated pathogenic bacteria (from the genus *Xenorhabdus* and *Photorhabdus* for steinernematids and heterorhabditids respectively), EPNs kill their hosts within a few days (Dillman *et al.*, 2012, Lewis *et al.*, 2015).

For all EPNs there is a free-living, non-feeding stage known as the infective juvenile (IJ) or dauer (Griffin *et al.*, 2005). When an appropriate host is located, an IJ will enter through any natural opening (e.g., mouth or anus), the cuticle or spiracles in search of the nutrient-rich haemolymph. Here, the IJs will release their symbiotic bacteria from their intestines; these reproduce and release toxins. The infected insect usually succumbs within 48 h. Within the cadaver, the IJs feed on the bioconverted host tissues (and bacteria), grow and develop into adults. As the food source becomes scant within the cadaver, the nematodes develop in crowded conditions and become arrested as IJs. The new IJs, with their specific symbiotic bacteria, will emerge from the cadaver in search of a new host (Griffin *et al.*, 2005).

In a study by Steyn *et al.* (2019), high mortality of

TABLE 2
A (non-exhaustive) summary of chemical control strategies used against leaf-mining pests.

Order/Family	Scientific name	Common name	Active agent/species	Success	Source	
Diptera/ Agromyzidae	<i>Liriomyza trifolii</i>	Celery leaf miner	Abamectin	Yes	Hara <i>et al.</i> (1993)	
	<i>L. trifolii</i>	Celery leaf miner	Abamectin, cyromazine	Yes ¹	Trumble (1985); Ferguson (2004)	
	<i>L. trifolii</i>	Celery leaf miner	Spinosad	Yes ¹	Ferguson (2004)	
	<i>L. trifolii</i>	Celery leaf miner	Methomyl	No	Trumble (1985)	
	<i>Liriomyza huidobrensis</i>	Potato leaf miner	Abamectin, cyromazine	Yes ²	Weintraub & Horowitz (1998)	
	<i>Chromatomyia horticola</i>	Pea leaf miner	Acetamiprid, methamidophos, imidacloprid, <i>Bacillus thuringiensis</i> and abamectin mixture	Yes	Khan <i>et al.</i> (2015)	
	Lepidoptera/ Gelechiidae	<i>Tuta absoluta</i>	Tomato leaf miner	Abamectin, chlorantraniliprole	Yes	Pereira <i>et al.</i> (2014)
		<i>T. absoluta</i>	Tomato leaf miner	Chlorpyrifos	Yes ¹	Haddi <i>et al.</i> (2017)
		<i>T. absoluta</i>	Tomato leaf miner	Diamide	Yes ¹	Roditakis <i>et al.</i> (2017)
		<i>T. absoluta</i>	Tomato leaf miner	Indoxacarb, spinosad	Yes ¹	Pereira <i>et al.</i> (2014); Roditakis <i>et al.</i> (2018)

TABLE 2 (CONTINUED)

Order/Family	Scientific name	Common name	Active agent/species	Success	Source
	<i>T. absoluta</i>	Tomato leaf miner	Methamidophos, phenthoate, cartap hydrochloride, chlorfenapyr	Yes ³	Pereira <i>et al.</i> (2014)
Lepidoptera/ Gracillariidae	<i>Phyllocnistis citrella</i>	Citrus leaf miner	Permethrin, methidathion, fenoxycarb	Yes	Beattie <i>et al.</i> (1995a)
	<i>P. citrella</i>	Citrus leaf miner	Petroleum spray oil	Yes	Beattie <i>et al.</i> (1995b)
	<i>P. citrella</i>	Citrus leaf miner	Polysaccharides	No	Beattie <i>et al.</i> (1995b)
	<i>Cameraria ohridella</i>	Horse chestnut leaf miner	Harpin protein, potassium phosphite, salicylic acid derivative	Yes	Percival & Holmes (2016)
	<i>C. ohridella</i>	Horse chestnut leaf miner	Benzothiadiazole, propanazole, deltamethrin	No	Percival & Holmes (2016)
Lepidoptera/ Lyoneutiidae	<i>Perileuoptera coffeella</i>	Coffee leaf miner	Chlorpyrifos, disulfoton, ethion, methyl parathion	Yes ¹	Fragoso <i>et al.</i> (2002)

¹ Resistance reported; ² Negative effects on parasitoids; ³ Effect on natural enemies

H. capensis larvae was obtained for *Heterorhabditis baujardi* Phan, Subbotin, Nguyen & Moens (92%), *Heterorhabditis noenieputensis* Malan, Knoetze & Tiedt (85%) and *Heterorhabditis indica* Poinar, Karunakar & David (83%). Almost double the number of *H. noenieputensis* (34 nematodes/insect) penetrated the insect larvae in comparison with the other two EPNs. However, the relative potency of *H. baujardi* was 3.56 times higher than it was for *H. indica*, whilst that of *H. indica* was 2.57 times higher than it was for *H. noenieputensis*. These authors concluded that the results obtained in the laboratory were encouraging, especially with regard to the nematodes' ability to penetrate the leaf-mining galleries and to infect the larvae successfully.

A variety of EPNs have successfully controlled certain leaf-mining pest populations (Table 3). In the case of *T. absoluta*, leaf bioassays conducted on leaves infested with larvae, using concentrations of 1 000 IJs/ml (equivalent to a 60 IJs/cm² dose) of *Steinernema carpocapsae* (Weiser, 1955) Wouts, Mráček, Gerdin & Bedding, *Steinernema feltiae* (Filipjev, 1934) Wouts, Mráček, Gerdin & Bedding and *Heterorhabditis bacteriophora* Poinar caused high levels of mortality (88.6%, 92% and 76.3%, respectively) after 72 h of exposure to the respective EPNs (Batalla-Carrera *et al.*, 2010). These results revealed that the EPNs were able to find and kill larvae, despite their relative position on or within a leaf (i.e. outside of or within leaf galleries). Field trials conducted by Gözel and Kasap (2015) with the same EPNs on netted plants, using a conventional airblast-sprayer at an application rate of 50 IJs/cm², confirmed these results (ca. 46%, 92% and 82% total mortality, respectively). Similar results were obtained by Van Damme *et al.* (2015), who applied a concentration of 27.3 IJs/cm² of each of the three EPN species to infested leaves by means of an automated spray boom. Beattie *et al.* (1995b) tested *S. carpocapsae* against the larvae of *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae) at concentrations of 5 x 10⁶, 10 x 10⁶ and 30 x 10⁶ IJs/l water. A significant increase in mortality was only obtained at the highest dose, resulting in 35% mortality.

Parasitoids

In contradiction to the inferences made by Ayabe and Hijii (2016) regarding the study by Connor and Taverner (1997), the leaf-mining habit does not allow leaf miners to escape predation. According to Connor and Taverner (1997), the loss of mobility, and thus escape strategies, in leaf-mining insects has led to higher mortality rates associated with hymenopteran parasitoids than in exophagous insects. This has led to the evolution of more species of associated parasitoids than in any other insect-feeding guild. In the case of *H. capensis*, several parasitoids have been found to attack the larval and pupal life stages, although these parasitoids have not yet been identified. The use of parasitoids against leaf-mining insects is a popular alternative to the use of insecticides.

A few case studies with promising results are listed in Table 4. Trichogrammatidae, Encyrtidae and Eulophidae (all of which belong to the superfamily Chalcidoidea) have been found to parasitize lepidopteran leaf-mining pests (Table 4). The species within the Chalcidoidea are generally less than

TABLE 3
A (non-exhaustive) summary of the entomopathogenic nematodes (Steinernematidae and Heterorhabditidae) used as control strategies against leaf-mining pests.

Order/Family	Common name	Scientific name	Species/Active agent	Success	Source	
Diptera/ Agromyzidae	Celery leaf miner	<i>Liriomyza trifolii</i>	<i>Steinernema bicornutum</i> ; <i>Heterorhabditis indica</i>	Yes	Jacob & Mathew (2016)	
	Celery leaf miner	<i>L. trifolii</i>	<i>Steinernema carpocapsae</i>	Yes	LeBeck <i>et al.</i> (1993); Jacob & Mathew (2016)	
	Celery leaf miner	<i>L. trifolii</i>	<i>Steinernema feltiae</i>	Yes**	Hara <i>et al.</i> (1993)	
	Potato leaf miner	<i>L. huidobrensis</i>	<i>S. feltiae</i>	Yes	Williams & Walters (2000)	
	Potato leaf miner	<i>L. huidobrensis</i>	<i>S. feltiae</i> - *trichlorfon, *dimethoate	Yes	Head <i>et al.</i> (2000)	
	Potato leaf miner	<i>L. huidobrensis</i>	<i>S. feltiae</i> - *trichlorfon, *dimethoate	No	Head <i>et al.</i> (2000)	
	Tomato leaf miner	<i>Liriomyza bryoniae</i>	<i>S. feltiae</i>	Yes	Williams & Walters (2000)	
	Chrysanthemum leaf miner	<i>Chromatomyia syngenesiae</i>	<i>S. feltiae</i>	Yes	Williams & Walters (2000)	
	Hymenoptera/ Tenthredinidae	Amber-marked birch leaf miner	<i>Profenusa thomsoni</i>	<i>S. carpocapsae</i>	No	Progar <i>et al.</i> (2014)
Tomato leaf miner		<i>T. absoluta</i>	<i>Heterorhabditis bacteriophora</i>	Yes	Batalla-Carrera <i>et al.</i> (2010); Gözel & Kasap (2015); Van Damme <i>et al.</i> (2015); Kamali <i>et al.</i> (2017)	
Tomato leaf miner		<i>T. absoluta</i>	<i>Steinernema affine</i>	Yes	Gözel & Kasap (2015)	
Tomato leaf miner		<i>T. absoluta</i>	<i>S. carpocapsae</i>	Yes	Batalla-Carrera <i>et al.</i> (2010); Gözel & Kasap (2015); Kamali <i>et al.</i> (2017)	
Tomato leaf miner		<i>T. absoluta</i>	<i>S. feltiae</i>	Yes	Batalla-Carrera <i>et al.</i> (2010); Gözel & Kasap (2015); Van Damme <i>et al.</i> (2015)	
Tomato leaf miner		<i>T. absoluta</i>	<i>Steinernema kariii</i> ; <i>Heterorhabditis</i> sp.	Yes	Mutegi <i>et al.</i> (2017)	
Citrus leaf miner		<i>P. citrella</i>	<i>S. carpocapsae</i>	Yes	Beattie <i>et al.</i> (1995a)	
Lepidoptera/ Heliozelidae		NA	<i>Holocacista capensis</i>	<i>Heterorhabditis indica</i> ; <i>Heterorhabditis noeneputensis</i> ; <i>Heterorhabditis bajardi</i>	Yes	Steyn <i>et al.</i> (2019)
				<i>Heterorhabditis bacteriophora</i> ;	No	Steyn <i>et al.</i> (2019)
				<i>Heterorhabditis zealandica</i> ; <i>Steinernema jeffreyense</i> ; <i>Steinernema yirgalemense</i>		

* Added independently ** Dependent on relative humidity

TABLE 4

A (non-exhaustive) summary of parasitoids used as control strategies against leaf-mining pests.

Order/family	Common name	Scientific name	Species/Family	Success	Source
Diptera/ Agromyzidae	Celery leaf miner	<i>Liriomyza trifolii</i>	<i>Chrysocharis flacilla</i> (Eulophidae)	Yes	Muchemi <i>et al.</i> (2018)
	Celery leaf miner	<i>L. trifolii</i>	<i>Diglyphus isaea</i> (Eulophidae)	Yes	Minkenbergen & Van Lenteren (1986)
	Potato leaf miner	<i>L. huidobrensis</i>	<i>C. flacilla</i>	Yes	Muchemi <i>et al.</i> (2018)
	Potato leaf miner	<i>L. huidobrensis</i>	<i>D. isaea</i>	Yes	Maharjan <i>et al.</i> (2017)
	Potato leaf miner	<i>L. huidobrensis</i>	<i>Opius dissitus</i> (Braconidae)	Yes	Wei & Kang (2006)
	Vegetable leaf miner	<i>Liriomyza sativae</i>	<i>O. dissitus</i>	Yes	Wei & Kang (2006)
	Vegetable leaf miner	<i>L. sativae</i>	<i>C. flacilla</i>	Yes	Muchemi <i>et al.</i> (2018)
	Holly leaf miner	<i>Phytomyza ilicis</i>	<i>Chrysocharis gemma</i> (Eulophidae)	Yes	Heads & Lawton (1983)
	Holly leaf miner	<i>P. ilicis</i>	<i>Opius ilicis</i> (Braconidae)	Yes	Kirichenko <i>et al.</i> (2018)
Hymenoptera/ Tenthredinidae	Amber-marked birch leaf miner	<i>Profenusa thomsoni</i>	<i>Lathrolestes thomsoni</i> (Ichneumonidae)	Yes	Soper <i>et al.</i> (2015)
	Birch leaf miner	<i>Fenusa pumila</i>	<i>Lathrolestes nigricollis</i> (Ichneumonidae), <i>Grypocentrus albipes</i> (Ichneumonidae)	Yes	Langor <i>et al.</i> (2000)
Lepidoptera/ Gelechiidae	Tomato leaf miner	<i>T. absoluta</i>	<i>Trichogramma euproctidis</i> , <i>Trichogramma achaeae</i> (Trichogrammatidae)	Yes	El-Arnaouty <i>et al.</i> (2014)
	Tomato leaf miner	<i>T. absoluta</i>	<i>Trichogramma pretiosum</i> (Trichogrammatidae)	Yes	Parra & Zucchi (2004)
Lepidoptera/ Gracillariidae	Citrus leaf miner	<i>P. citrella</i>	<i>Ageniaspis citricola</i> (Encyrtidae)	Yes	Hoy <i>et al.</i> (2007)
	Citrus leaf miner	<i>P. citrella</i>	<i>Citrostichus phyllocnistoides</i> (Eulophidae)	Yes	Garcia-Marí <i>et al.</i> (2004)

3 mm in length, making it rather difficult to collect and study individuals (Noyes, 2003).

Cover cropping

Ingels and Klonsky (1998) describe a cover crop as a crop (or secondary plants) of little to no economic significance that is grown in intra- and inter-rows of vineyards, the presence of which, however, provides numerous other potential benefits. Parolin *et al.* (2012) provide an extended definition of barrier plants, as "... a plant which is used within or bordering a primary crop for the purpose of disease suppression and/or interception of pests and/or pathogens". In terms of their potential to harbour pests and pathogens, the effect of barrier plants or cover crops on population numbers of most leaf-mining pests is not known and should be investigated, as the use of different cover crops to reduce pests in vineyards is regarded as an option in the future.

OTHER PEST MANAGEMENT METHODS

Entomopathogenic fungi (EPF) have been used successfully in a variety of integrated pest management (IPM) strategies

against many leaf-mining pests of economic importance (Shah & Pell, 2003). Various strains of *Metarhizium anisopliae* (Metschnikoff) (Sorokin) (Hypocreales: Clavicipitaceae) and *Beauveria bassiana* (Balsamo) (Vuillemin) (Hypocreales: Cordycipitaceae) have been used to control the pea leaf miner, *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) (Migiro *et al.*, 2010; 2011); and the tomato leaf miner, *T. absoluta* (Rodríguez *et al.*, 2006; Allegrucci *et al.*, 2017).

Mating disruption implies the use of a formulated female pheromone to disrupt or regulate the mating habits of a target pest species (Cardé & Minks, 1995). Amongst the leaf-mining Lepidoptera, mating disruption has only been explored and successfully achieved against *P. citrella* (Stelinski *et al.*, 2008; Stelinski *et al.*, 2010; Willett *et al.*, 2015). Mating disruption studies on *T. absoluta* have only proved successful under greenhouse conditions (Vacas *et al.*, 2011; Cocco *et al.*, 2013).

The practice of bagging grapes (as a physical measure of control) using a bunch cover/bag dates back to 1919 (Signes *et al.*, 2007). After ripening, bunches are typically

covered with a cover/bag which is only removed during harvest. Bagging has been used to promote uniform colour development within a bunch, reduce the incidence of blemished fruit, reduce the incidence of disease, delay the ripening process (ideally when harvest needs to be delayed for increased market access), increase hygiene (reduced contact with pesticides sprays and other contaminants), protect grape bunches against adverse environmental variables (e.g. moisture, hail, sunburn and cracking/bursting of fruit), and to provide protection against attack by birds and insects (Signes *et al.*, 2007; Sharma *et al.*, 2014). Pre-harvest fruit bagging has been used to avoid insect infestation in a variety of crops (Sharma *et al.*, 2014).

The use of netting (overhead netting, vineyard layover netting and zone netting) in vineyards has become widespread in recent years (Suvočarev *et al.*, 2013). Netting is used to reduce the number of pests (reduced immigrant invasion from surrounds), leading to a reduction in the number of pesticide applications; reduce radiation exposure of plants during hot summer months; and minimise hail and bird damage (Suvočarev *et al.*, 2013). Neither bagging of grapes nor netting, however, has been tested to exclude leaf-mining pests.

RECOMMENDATIONS

The discovery of a newly recognised pest in an industry that contributes to a country's economy requires novel and baseline studies to understand the pest's ecology and distribution so that pest populations can be controlled adequately. The use of dichlorvos and spinetoram has been used to reduce the density of *H. capensis* populations in infested vineyards. When studying and considering the various control options, however, it is important to consider the restrictions imposed on growers regarding the use of harmful chemical insecticides and the effect of insecticides on the evolution of insecticide resistance. The investigation of alternative control strategies therefore is pertinent in enhancing IPM strategies. It is clear that there is potential for the use of parasitoid wasps and EPNs to control *H. capensis*. The review highlights the need to commercialise smaller, native EPN species and to test a variety of parasitoids (especially the trichogrammatids, encyrtid and eulophid species identified in this review) against *H. capensis* in the laboratory and field environments. Furthermore, continued research will increase the current knowledge of *H. capensis* and the use of chemical and biological control options that potentially could be used as a reference for studies focused on other emerging leaf-mining pests, such as *T. absoluta*, in South Africa.

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