

**SEASONAL DEVELOPMENT AND TRAPPING OF *CORYPHODEMA TRISTIS* IN
EUCALYPTUS NITENS PLANTATIONS**

by

Kayla Philippa Noeth

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SUMMARY

SEASONAL DEVELOPMENT AND TRAPPING OF *CORYPHODEMA TRISTIS* IN *EUCALYPTUS NITENS*

by

Kayla Philippa Noeth

Supervisor: Prof. Brett Hurley
Co-supervisor Prof. Bernard Slippers
Department: Department of Zoology and Entomology
University: University of Pretoria
Degree: M.Sc. Entomology
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Plantation forestry is a significant economic contributor in many countries around the world, accounting for approximately 0.9% of the global GDP according to a 2011 estimate. These exotic commodities are often at risk of being invaded by various pests and diseases, both native and exotic. In Brazil, for example, losses of up to US\$6.5 million per annum have been estimated due to infestations of the Sirex wood wasp (*Sirex noctilio*, Hymenoptera: Siricidae). Management of these biological risks is crucial to curb significant economic losses; however, management strategies can often be complicated and require a thorough understanding of the target pest's biology and ecology.

In South Africa, one of the more important pests in plantation forests is the cossid moth (*Coryphodema tristis*, Lepidoptera: Cossidae). This wood-boring moth was previously

described as a pest of quince and grapevines in the Western Cape region, but has recently been found to infest plantations of *Eucalyptus nitens* on the Mpumalanga Highveld. Despite its significant impact on *E. nitens*, few studies have investigated the biological and ecological characteristics of this pest, as well as aspects relating to its management, on this recent host. The aim of this study was to obtain a better understanding of the biological and ecological characteristics of *C. tristis* on *E. nitens*, and to use this knowledge to develop an effective management strategy.

The dissertation contains three chapters. The literature review in the first chapter provides a summary of wood-boring Lepidoptera as pests in commercial forestry plantations. The review draws on general characteristics present in the groups discussed and includes information on their diversity and distribution, life cycle characteristics, host associations, diet and nutrition, pathways of invasion and early detection mechanisms. Eradication as a control strategy, as well as other management tactics such as biological, chemical and behavioural control, is also discussed.

The aim of the first research chapter was to investigate the seasonal development and occurrence of *C. tristis* in association with *E. nitens*, on the Mpumalanga Highveld, and to compare these findings to those previously published for the Western Cape area on quince and vines. This was achieved through the regular felling of cossid infested *E. nitens* trees on the Mpumalanga Highveld over a 23-month period to investigate development of the immature stages, and through the trapping of *C. tristis* male adults to monitor the flight season(s). Since the previously recorded hosts and environment (quince and vines in the Western Cape) differ from the new host and environment (*E. nitens* on the Mpumalanga Highveld), differences in the life cycle of *C. tristis* between the two regions were expected.

The broad objective of the second research chapter was to optimise the management of *C. tristis* using behavioural control tactics. Specifically, we investigated the influence of

trapping density on moth captures, using pheromone-baited traps that have recently been used for an experimental mass trapping programme. Six different trap spacing treatments, ranging from 10 m to 60 m between traps, were investigated over a period of 23 months and the mean moth captures per trap and total estimated moth captures per hectare were compared between these treatments. It was expected that the lower trap densities would capture significantly more male moths than the higher trap densities, since inter-trap interference may occur at the higher trap densities.

This was the first study to investigate the seasonal development and occurrence of *C. tristis* on *E. nitens*. These results, together with results from the trapping density study, will be useful to inform future management strategies for this pest. In addition, this study made an important contribution to the knowledge on economically significant wood-boring moths.

RESEARCH OUTPUTS

Conference presentations:

Poster presentations

Investigating the development of the wood-boring moth *Coryphodema tristis* on *Eucalyptus nitens* in South Africa: Entomological Society of South Africa (ESSA) Annual General Meeting, 2-7 July 2017.

Investigating the development of the wood-boring moth *Coryphodema tristis* on *Eucalyptus nitens* in South Africa Essa 2017: Institute of Commercial Forestry Research (ICFR) 7th Forestry Symposium, 18-20 July 2017.

LIST OF ABBREVIATIONS

ARS	Argentinian peso
AUD	Australian dollar
BRL	Brazilian real
CAD	Canadian dollar
CLP	Chilean peso
CNY	Chinese yuan
CZK	Czech koruna
DBH	Tree diameter at breast height
DIP	Tree diameter at infestation point
EAR	Effective attraction radius
EUR	European euro
GDP	Gross domestic product
IDR	Indonesian rupiah
INR	Indian rupee
IPH	Tree height at infestation point
JPY	Japanese yen
NZD	New Zealand dollar
PCR	Polymerase chain reaction
PLN	Polish złoty
SEK	Swedish krona
THB	Thai baht
USD	United States dollar
ZAR	South African rand

DECLARATION

I, Kayla Phillipa Noeth, declare that the dissertation, which I hereby submit for the degree of Magister Scientiae at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature

Kayla Noeth

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CHAPTER 1

Wood-boring Lepidoptera in commercial hardwood plantations: A brief review

Plantation forestry is an important economic pillar in many countries around the world and wood-boring Lepidoptera are often serious pests of these important commodities. Because the majority of their life cycle is spent feeding within the wood, management of these pests is challenging. Semio-chemical based management strategies have been successful for many wood-boring moths, remaining the most promising method of control. This review discusses key aspects of their biology, diet and nutrition, invasion pathways, eradication prospects and management options. Chemical insecticides, biological control via parasitoids and entomopathogens, and behavioural control tactics such as mass trapping and mating disruption are some of the management options discussed.

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1.1 INTRODUCTION

Planted forests, defined as forests established through planting or deliberate seeding (Food and Agriculture Organization 2010), represent up to 7% of the global forested area (Brockerhoff et al. 2013). They can be based on either native or non-native species. These forests typically have lower biodiversity than natural forests (Barlow et al. 2007; Brockerhoff et al. 2008), but nevertheless remain important ecologically, especially considering the global decline in natural forests (Food and Agriculture Organization 2006, 2010). For example, plantation forests have the potential to mitigate the effects of climate change by acting as alternative carbon sinks to natural forests. A study in Sweden showed that if 400 000 ha of abandoned land were planted with willow (*Salix* spp.) and poplar (*Populus* spp.), the total annual carbon sequestration would equal approximately one tenth of the annual carbon emissions caused by anthropogenic activities (Rytter 2012). Similarly, a study in China found subtropical plantations (monocultures of *Eucalyptus urophylla* and *Acacia crassicarpa*) to be effective, large carbon sinks (Chen et al. 2011). In addition to this benefit, planted forests reduce the pressure on natural forests to satisfy growing timber needs (Sedjo 1999).

Planted forests are also an important economic pillar in many countries throughout the world (Table 1). In 2000, plantation forestry was responsible for supplying one third of the global industrial roundwood demand (De Groot and Van der Meer 2010). In South Africa, for example, the forestry sector contributed to approximately 0.7% of the total GDP in the 2014/2015 financial year, while also supporting manufacturing subsectors such as sawmilling, paper and pulp production, mining and construction. The forestry sector is further responsible for creating over 100 000 direct and indirect jobs (Department of Agriculture Forestry and Fisheries 2016a). The total investment in forestry in South Africa in 2014/2015 amounted to R25,6 billion (equivalent to US\$1,96 billion in 2015) and the forest products industry ranked

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among the top exporting industries in the country, accounting for approximately R19 billion (equivalent to US\$1,46 billion in 2015) for exported forestry products (Department of Agriculture Forestry and Fisheries 2016a). In addition, forests are of value to the local communities for firewood, fruits, honey and clean water production (De Groot and Van der Meer 2010). Planted forests face various abiotic and biotic risks, however, such as strong winds (Gardiner and Quine 2000), fire and climate change (Kirilenko and Sedjo 2007; Resco De Dios et al. 2007), but perhaps one of the greatest threats is the increasing incidence of pests and diseases (Wingfield et al. 2001, 2008; Chornesky et al. 2005; Garnas et al. 2012) where, for example, the rate of novel introductions of insect pests on *Eucalyptus* has globally increased five-fold since the 1980s (Hurley et al. 2016).

A number of different insect groups have been recorded as pests of planted forests, including leaf defoliators (e.g. pine processionary moth, *Thaumetopoea pityocampa*), gall formers (e.g. bluegum chalcid, *Leptocybe invasa*), sap suckers (e.g. bronze bug, *Thaumastocoris peregrinus*) and root feeders (e.g. white grubs, Scarabaeidae) (Collett 2001; Hóðar et al. 2003; Nadel et al. 2010; Ramanagouda et al. 2010; Echeverri-Molina and Govender 2016). However, many of the most important pests have been wood- and bark-borers. These include the emerald ash borer (*Agrilus planipennis*) (Poland and McCullough 2006; Kovacs et al. 2010; Herms and McCullough 2014), the mountain pine beetle (*Dendroctonus ponderosae*) (Safranyik and Carroll 2006; Brown et al. 2010) and the Sirex wood wasp (*Sirex noctilio*) (Talbot 1977; Hurley et al. 2007). The immature stages of these wood- and bark-borers typically penetrate the bark or tunnel into the wood of their host species, where they feed on either the phloem or xylem of the tree. When severe, borer activity significantly deforms trees and can lead to tree mortality due to water- and sap-conducting tissues being destroyed (Nielsen 1981). In Brazil, financial losses due to *S. noctilio* are estimated to be approximately US\$6.5 million annually (Oliveira et al. 2013).

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(2010) estimated the cost of treatment, removal and replacement of ash trees (*Fraxinus* spp.) in the USA due to losses caused by the emerald ash borer to equal approximately US\$10,7 billion over a ten-year period from 2009 to 2019. Aukema et al. (2011) estimated losses of US\$1,7 billion in governmental expenditures and US\$830 million in residential property values due to wood- and phloem-boring insects. Control of these insect pests, and especially wood-borers, is therefore critically important.

While extensive literature has been published on wood-boring beetles and wasps, comparatively little has been published on Lepidopteran wood-borers, despite the recent emergence of important species, such as *Coryphodema tristis* in South Africa (Gebeyehu et al. 2005; Boreham 2006), *Chilecomadia valdiviana* in Chile (Lanfranco and Dungey 2001) and *Endoclita signifer* in China (Yang et al. 2013; Zheng et al. 2016). This review provides a global overview of Lepidopteran wood-borers occurring on some of the important hardwood commercial forestry plantation species. Specifically, the diversity and distribution, biology and management of these species, including a brief discussion on early detection mechanisms and pathways of invasion will be discussed.

1.2 DIVERSITY AND DISTRIBUTION

The majority of the wood-boring Lepidopteran species that impact commercial forestry fall into three major families, namely the Cossidae (cossid moths), Hepialidae (ghost moths) and Sesiidae (clearwing moths), with few species occurring in other families. A notable exception is *Timocratica palpalis*, which falls in the newly defined Depressariidae (Heikkilä et al. 2014). These wood-boring families are highly diverse, with each family represented by over 500 described species recorded in between 50 and 100 genera (Van Nieukerken et al. 2011). Despite their widespread diversity, only a handful have been reported as serious pests

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on commercial forestry trees, and most of these species infest exotic host trees in the areas where they occur. Notable examples include *Chilecomadia valdiviana* (Cossidae), *Coryphodema tristis* (Cossidae), *Zeuzera coffeae* (Cossidae), *Indarbela quadrinotata* (Cossidae), *Tricophassus giganteus* (Hepialidae), *Sahyadrassus malabaricus* (Hepialidae), *Endoclita signifer* (Hepialidae), *Endoclita gmelina* (Hepialidae), *Endoclita sericeus* (Hepialidae), *Endoclita hosei* and *Aenetus virescens* (Hepialidae) (Table 2). Some species infest native commercial plantations, notably *Prionoxystus robiniae* (Cossidae), *Prionoxystus macmurtei* (Cossidae), *Duomitus* (= *Xyleutes*) *ceramicus* (Cossidae), *Endoxyla cinerea* (Cossidae), *Paranthrene robiniae* (Sesiidae), *Paranthrene tabaniformis* (Sesiidae), *Sesia sinengensis* (Sesiidae), *Sesia apiformis* (Sesiidae), *Endoclita excrescens* (Hepialidae) and *Endoclita signifer* (Hepialidae) (Table 2).

The distribution of wood-boring Lepidoptera impacting commercial forestry is global, with species occurring in the Australia, Brazil, Chile, China, Finland, India, Indonesia, Japan, New Zealand, Portugal, South Africa, Spain, Thailand and the United States of America (Figure 1). All species listed in this review are native where they occur. This is an interesting contrast to other insect pest invasions in commercial forests, which are often exotic insects (Brockerhoff and Liebhold 2017). Despite being capable of surviving long ocean voyages (Ciesla 2004), it would seem that wood-boring Lepidoptera are not as prone to utilising this invasion pathway as, for example, wood-boring Coleoptera are. Lepidoptera are seldom intercepted on logs (Meurisse et al. 2018), which is possibly due to their relatively short adult lifespan and that their larvae do not feed on decaying wood (Solomon 1995).

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1.3 BIOLOGY

The biological and ecological characteristics of wood-borers tend to be complex, due to the cryptic nature of the immature stages and the unique dietary preferences of the larvae. A brief biology of Lepidopteran wood-borers is outlined in this section, drawing on general characteristics present in most families and/or species. Notable exceptions are mentioned.

1.3.1 Life cycle characteristics

Depending on geographic location and climate, the complete life cycle from egg to adult varies between families and even within species. In general, a lengthy generational turnover is present within wood-boring Lepidoptera (Nielsen 1981), with most species completing a generation within one to three years. Cossidae exhibit variable life cycle lengths, for example *Chilecomadia valdiviana* (1–3 years) (Lanfranco and Dungey 2001), *Coryphodema tristis* (1–3 years) (Höppner 1991) and *Duomitus* (= *Xyleutes*) *ceramicus* (1–2) years (Chaiglom 1966). Sesiids generally have a generation every 1–2 years, and rarely every 4 years (Mifsud et al. 2003). Hepialidae also have variable life cycles, with *Aenetus virescens* 1–4 years (Grehan 1987), *Endoclita signifer* 1–2 years (Yang et al. 2013) and *Sahyadrassus malabaricus* 1 year (Nair 1982).

Female wood-boring moths typically lay a large egg complement (Powell 2009), as has been observed through the clutch sizes of, for example, *Prionoxystus robinae* (up to 318 eggs per female) (Forschler and Nordin 1989), *Endoclita signifer* (up to 9000 eggs per female) (Yang et al. 2013) and *Coryphodema tristis* (ranging between 104 and 318 eggs per female) (Gebeyehu et al. 2005). Eggs are usually laid in concealed locations such as under loose bark, in cracks and openings on the stem and within branch nodes and terminal shoots (Nielsen 1981; Mifsud et al. 2003; Powell 2009). However, some species, notably members of the Hepialidae,

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lay their eggs on the forest floor (Tobi et al. 1993; Powell 2009). The time taken for eggs to hatch varies between two to three weeks (e.g. *E. signifier*, Hepialidae (14- 15 days) (Yang et al. 2013) and *S. apiformis*, Sesiidae (approximately 20 days) (Martín-García et al. 2011)) to two months (e.g. *Coryphodema tristis*, Cossidae) (Höppner 1991). The variation in incubation time between the different species and families could partially be attributed to temperature, as it has been shown that temperature plays a key role in insect development (Ratte 1984).

Neonate larvae of cossid and sesiid wood-borers either start boring immediately into the host plant or spend the first few months feeding on the inner bark. Thereafter, they will start boring into the xylophagous tissue where they construct a complex network of tunnels in which they will later pupate (Mifsud et al. 2003; Barnd et al. 2008; Buss and Foltz 2009). Neonate Hepialidae larvae often first feed on leaf litter and then later bore into woody stems (Grehan 1989; Tobi et al. 1993). The larval stage is typically the longest development stage in the life cycle of wood-borers, which spend several months feeding inside their constructed galleries (Nielsen 1981). When a larvae is ready to pupate, it will construct a silken cocoon within its gallery, often embedded with bits of wood, bark or frass (Grehan 1989; Mifsud et al. 2003; Barnd et al. 2008). The majority of the species spend two to three weeks developing into adults (Solomon 1995); however, some take up to six months, such as *Coryphodema tristis* (Höppner 1991).

Adults of wood-boring Lepidoptera are nocturnal or crepuscular, with the exception of the diurnal Sesiidae (Powell 2009). The adults are generally short-lived (10 days or less) (Solomon 1995) and are medium to very large in size, with forewing wingspans ranging between 4 and 70 mm for Cossidae, 5 and 28 mm for Sesiidae and 10 and 120 mm for Hepialidae adults (Powell 2009). Adults of the Cossidae and Hepialidae generally do not have specialised mouthparts and thus do not feed (Tobi et al. 1993; Powell 2009), while some adult Sesiidae feed on nectar (Powell 2009).

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1.3.2 Host associations

Many Cossidae species are polyphagous, often having very wide host ranges. For example, 20% of described cossid species are reported to be polyphagous (Powell 2009). Host plants of the larvae of sesiid moths include at least 40 families of angiosperms, and are often pests in the stems and trunks of important agricultural and forestry crops (Mifsud et al. 2003; Powell 2009). Most species of Sesiidae are oligophagous, however, and strict monophagy and polyphagy are rare (Mifsud et al. 2003). Larvae of Hepialidae feed on the roots, leaves, stems, branches, fungus and detritus (leaf litter) of many angiosperm families, with some larval species undergoing a dietary transition from one food source to another. For example, some *Aenetus* spp. and *Endoclita* spp. feed on leaf litter during the early instars and then transition to woody stems at later instars (Grehan 1989). Because of this behaviour, Grehan (1989) suggests that the Hepialidae fall somewhere between generalist and specialist feeders.

Several species, such as *Coryphodema tristis*, *Chilecomadia valdiviana*, *Timocratica palpalis* and *Endoclita signifera*, have undergone host expansions from native/indigenous vegetation to exotic commercial plantations, more specifically *Eucalyptus* species, where they cause significant economic damage (Zanuncio et al. 1990; Lanfranco and Dungey 2001; Boreham 2006; Yang et al. 2013). Several theories have been developed to explain host expansion events. One theory suggests that females fail to discriminate between host plants and novel plants and mistakenly oviposit on the novel plant (Larsson and Ekbohm 1995). This failure to discriminate has often been ascribed to the lack of time female insects have had to adjust their egg-laying behaviour or larval physiology to the novel plant (Chew 1977; Thompson 1988; Strong et al. 1993; Larsson and Ekbohm 1995). However, Fox and Lalonde (1993) suggested that insects are restricted in how sensitive they are when discriminating between hosts. Two different plant phenotypes may elicit similar chemical signatures, with the

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insect unable to discriminate between the two. Therefore, the novel host is retained within the insect's diet as a host plant, as excluding the signature would also exclude the chemical signature of the original host plant (Fox and Lalonde 1993). A phylogenetic study investigating the host expansion of the African maize stalk-borer, *Busseola fusca* (Lepidoptera: Noctuidae), from maize to sugarcane in Zimbabwe and South Africa showed a lack of genetic variation between maize populations and sugarcane populations (Assefa et al. 2015). This suggests that host plant expansion events are not necessarily a function of evolutionary genetics and that ecological opportunity may play a crucial role in these expansion events (Assefa et al. 2015). This may be important when climatic conditions are unfavourable and the reproductive urge of female insects to mate and lay eggs may further drive the oviposition on "non-hosts".

The relative lack of natural enemies in a novel host environment may be another explanation for these host shifts. Jeffries and Lawton (1984) explain that any change in an insect's behaviour that can reduce the risk of predation by natural enemies would be highly advantageous. This could be achieved through the utilisation of novel hosts, which offer an ecological refuge from their natural enemies. Singer et al. (2004) showed that the value of an enemy-free space far outweighs the value of host quality in relation to host plant preference of late-instar caterpillars of the saltmarsh caterpillar, *Estigmene acrea* (Lepidoptera: Arctiidae). Gratton and Welter (1999) showed that an enemy-free space does exist for a specialised leaf-mining fly, *Liriomyza helianthi* (Diptera: Agromyzidae), directly following a host shift event. Studies by Mulatu et al. (2004) on the potato tuber moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae) and by Murphy (2004) on the Old World swallowtail, *Papilio machaon* (Lepidoptera: Papilionidae), further support this hypothesis.

Phylogenetic relatedness of exotic tree species to native trees may also play a role in the colonisation of those tree species by native insects, as the dietary breadth of insect herbivores are usually restricted to hosts that are phylogenetically closely related (Goßner et

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al. 2009; Branco et al. 2015). However, this is not always the case as phylogenetically related plant species may have evolved in geographically distinct locations under different biotic and abiotic conditions, resulting in the adaptations of local herbivorous insect populations (Thompson 1999). Further, exotic tree species do not have a history of co-evolution with local herbivorous insect populations. This results in increased susceptibility of these exotic plant species to new herbivores due to the lack of development of appropriate plant defence mechanisms (Parker et al. 2006; Orians and Ward 2010). Finally, local adaptation processes may outweigh phylogenetic conservatism in relation to the development of host-plant defence mechanisms against insect herbivores, which may result in exotic and native plant species being equally susceptible to insect herbivory (Goßner et al. 2009). Phylogenetic analyses were carried out to investigate the relatedness of two cossid moths, *Coryphodema tristis* (South Africa) and *Chilecomadia valdiviana* (Chile), both of which underwent host range expansion to *Eucalyptus nitens* within a short period of time of each other. The results showed high genetic divergence between both species, suggesting that these independent evolutionary trajectories are likely a result of the characteristics and ecology of the host plant (Degefu et al. 2013).

The enemy-free space hypothesis might be an important factor for host shifts of native insects into exotic plantations when considering the environment which an exotic commercial plantation offers. Also, the oviposition on “non-hosts” due to chemical signature confusion, unfavourable climatic conditions and/or phylogenetic relatedness of exotic and native host trees likely also play an important role in host expansion events.

1.3.3 Diet/nutrition

Wood-boring larvae are unique in their dietary preferences, as they utilise a resource most other insects are unable to utilise, namely xylem tissue. As xylem consists primarily of

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cellulose (40-45% in hardwoods) and lignin (20-25% in hardwoods) (Sjöström 1993), digestion of this plant tissue is difficult due to the complex structure of these compounds (Myburg and Sederoff 2013) and typically requires other organisms such as fungi or yeasts to assist with the break-down process (Martin 1983). Some insects, such as termites and cockroaches, possess their own internal cellulases that digest the cellulose (Slaytor 1992). However, according to Kittelson (2006), there are no indications in the literature that wood-boring Lepidoptera make use of cellulases, or that they feed using fungi or yeasts for the breakdown of wood/ xylem. There are suggestions of an external source of cellulases in the case of *Prionoxystus robiniae*, due to the presence of cellulase enzymes in its gut contents, which it did not produce itself (Kittelson 2006). *Coryphodema tristis* also has an apparent symbiotic relationship with yeasts, which could be a source of external cellulases (Degefu 2013). A study showed that the clearwing borer, *Paranthrene robiniae* (Sesiidae), is capable of structural alteration and degradation of lignin within its gut (Ke et al. 2011). This provides valuable insight into how these borers are able to digest wood and indicates multiple mechanisms are used by wood-boring Lepidoptera.

Moore and Navon (1966) suggested that the nutritional content in the diet of developing *Z. pyrina* larvae could affect their developmental time. *Zeuzera pyrina* raised artificially with a balanced diet had a generational turnover of four months, compared to the twelve months of field populations. The authors suggested that the nitrogen quantity and quality present in xylem may explain the differences observed, as xylem-based diets are low in protein and amino acids (Moore and Navon 1966). This was supported by Awmack and Leather (2002), who showed that host plant quality is an important factor in the fecundity of herbivorous insects and that the quality of the different components (such as carbon, nitrogen and defensive metabolites) directly affects insect reproductive strategies. *Prionoxystus robiniae* also showed differences in developmental time depending on host plant (Solomon 1988). These observations concur with

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the quantitative nutritional approach described by Scriber and Slanksy (1981), where a decline in host nutritional quality results in extended development.

Typically, wood has a low nutritional content. For example, the average nitrogen content of the wood and bark of *E. nitens* is reported to be 0.19% and 0.53% respectively (Madgwick et al. 1981). In comparison, the total nitrogen content (on a dry mass basis) in the wood of Chenin Blanc vines (*Vitis* spp.) varies seasonally between 0.36% and 0.67% (Conradie 1990). Leaves typically have a higher nitrogen content than that of wood; for example, the total nitrogen content in leaves of *E. nitens* varies between 1.34% (juvenile leaves) and 2.04% (mature leaves) (Madgwick et al. 1981). Nitrogen, while being one of many components that play a role in insect development, is critical in metabolic processes, cellular structure, genetic coding and overall growth (Mattson 1980). Immature insects subsisting on low-quality diets will therefore have slower developmental times and lengthier life cycles to procure enough nutrition for further development. This is supported with wood-boring insects, which have a smaller generational turnover per year (one generation per year or less) compared to insects that have higher quality diets (multiple generations per year) (Nielsen 1981).

1.4 MANAGEMENT

Management of wood-borers is challenging, since the larvae spend the majority of their life cycle concealed within inaccessible habitats (Nielsen 1981). In general, management of invasive insect pests involves an integrated approach, comprising three complementary strategies. These strategies include the identification and disruption of likely pathways of introduction, the eradication of invasive insects that have escaped early detection and prevention efforts, and the employment of long-term management strategies for the control of

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invasive insects that have successfully established via chemical, biological, cultural and behavioural control methods (Chornesky et al. 2005).

1.4.1 Pathways and early detection

Several pathways have been identified that facilitate the spread of invasive forest insects globally. The two most important pathways are the movement of wood (via roundwood imports, sawn timber trade, containerised cargo, ballast, wood packaging, dunnage and pallets), and through live plant trade (via ornamental plants, bonsais, nursery stock and other live plant imports) (Ciesla 2004; Humble 2010; Roques 2010; Brockerhoff and Liebhold 2017; Meurisse et al. 2018). “Hitchhiking” has also been identified as a major pathway. This involves the transport of organisms that are not associated with a particular commodity, but are rather transported accidentally as stowaways within sea containers, ships, vehicles or machinery (Brockerhoff and Liebhold 2017; Meurisse et al. 2018).

The movement of wood is a key pathway for the introduction of wood-borers (Haack et al. 2014; Brockerhoff and Liebhold 2017). The Asian long-horned beetle (*Anoplophora glabripennis*) and the emerald ash borer (*Agrilus planipennis*) are thought to have been introduced via this pathway from Asia to North America and Europe (Brockerhoff and Liebhold 2017). Since wood-borers feed directly on wood and have relatively long life cycles, they are capable of surviving long ocean voyages, making them particularly adept at spreading to other continents (Ciesla 2004).

The detection of these wood-borers relies primarily on phytosanitary inspections at border posts and shipping ports (Humble 2010; Roques 2010), but there are several limitations to this approach. Due to the large volume of material passing through these ports, it is impossible to screen all material (Humble 2010; Roques 2010). For example, in the USA approximately 2% of incoming material is inspected, and these inspections are also often biased

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towards known pests (Roques 2010). Inspections are also generally not based on random sampling techniques, but rather preferentially target high risk commodities and pathways (Humble 2010). Furthermore, negative inspections are not recorded, and the inspection process ceases once the first organism of quarantine significance has been identified (Humble 2010). Finally, organisms intercepted by the inspection process are often not fully identified to the species level (Humble 2010). In 2002, the International Standards for Phytosanitary Measures 15: Regulation of Wood Packaging Material in International Trade was adopted to provide guidelines to assist phytosanitary inspections and provide treatment standards for wood packaging material (Food and Agriculture Organization 2002; Haack et al. 2014). These and other phytosanitary measures are expected to decrease the introduction of invasive wood-boring insects. However, challenges still remain due to increasing trade, variation in quarantine standards between countries and continual changes in distribution networks (Meurisse et al. 2018). Recent advancements in technologies aimed at early detection of invasive insects show some promise in terms of more rapid and effective early detection. Techniques such as Polymerase Chain Reaction (PCR) screening, micro-array chips and DNA microprobes have been used successfully to identify pests and pathogens such as the Asian long-horned beetle and some species of *Phytophthora* root rot (e.g. *Phytophthora ramorum*) (Davidson et al. 2003; Kethidi et al. 2003; Chornesky et al. 2005). The development of expert systems that automate risk identification which integrate digital imaging and genetic information may prove to be even more effective (Chornesky et al. 2005). These techniques require equal advancement in DNA libraries, data development, archiving and delivery, but are arguably worth the investment (Chornesky et al. 2005).

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1.4.2 Eradication

Once an invasive pest population has become established in a non-native country, the next step in its management would be to attempt eradication (Chornesky et al. 2005). Successful eradication depends on several factors, namely the size of affected geographical area and cost of operations, the characteristics of the target species, surveillance and early detection, and the availability of detection tools (Brockerhoff et al. 2010). Various techniques have been utilised successfully in eradication programmes in New Zealand and North America. These include mass trapping, microbial pesticides, mating disruption, sterile insect technique, host destruction and systemic insecticides (Brockerhoff et al. 2006; Suckling et al. 2007; Liebhold et al. 2016). Eradication has been declared for only a few invasive pests, including the white-spotted tussock moth (*Orgyia thyellina*, Lepidoptera: Lymantriidae) and the painted apple moth in New Zealand (*Teia anartoides*, Lepidoptera: Lymantriidae) (Suckling et al. 2007; Glare 2009; Brockerhoff et al. 2010) and the Asian gypsy moth (*Lymantria dispar*, Lepidoptera: Erebidae) in North America (Brockerhoff et al. 2010).

Because of the cryptic nature of wood-borers, effective eradication tactics rely largely on trapping, mating disruption, host destruction or the use of systemic chemical insecticides. The Asian long-horned beetle has been successfully eradicated in parts of North America using a combination of host destruction and systemic insecticides (Brockerhoff et al. 2010; Liebhold et al. 2016). Eradication is generally aimed at exotic pests only, and since most, if not all, wood-boring Lepidoptera are native where they occur (see Table 2), eradication of these pests is unfeasible. Furthermore, the majority of the techniques used are not appropriate for the eradication of wood-borers, since host destruction or the large scale use of systemic insecticides is often not feasible (Liebhold et al. 2016). Eradication attempts of the Asian long-horned beetle in North America alone have exceeded US\$370 million (Haack et al. 2010; Liebhold et

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al. 2016). Management of wood-borers therefore focuses on long-term management and control, discussed in detail next.

1.4.3 Chemical control

Chemical control of wood-boring insects is challenging since the larvae spend the majority of their life boring within the wood or in other inaccessible habitats. The application of chemical insecticides are therefore applied either individually to each tree through trunk injections or via the application of soil drenches (Poland et al. 2006; Liebhold et al. 2016). In some cases, foliar sprays have been successful in controlling adult populations of the Asian long-horned borer, as the adults feed on the leaves of host plants (Poland et al. 2006). Active ingredients that proved successful in controlling the Asian long-horned borer on elms (*Ulmus* spp.), poplars (*Populus* spp.) and willows (*Salix* spp.) include azadirachtin (a tetranortriterpenoid insecticide), emamectin benzoate (a semisynthetic insecticide derived from avermectin), imidacloprid (a chloronicotinyl insecticide) and thiacloprid (a nicotinoid insecticide) (Poland et al. 2006). Significant control was achieved with mortalities of up to 64% on poplar trees treated with imidacloprid four months after the initial application, and 55% and 63% mortality on elms and poplars treated with imidacloprid respectively, nine months after the initial application (Poland et al. 2006). However, since most adult wood-boring Lepidoptera do not feed due to non-functional mouthparts, the application of foliar sprays is inappropriate. Systemic insecticides may, however, prove useful as these insecticides are taken up by the plant and transported throughout its tissues (Goulson 2013).

The use of chemical insecticides may have many non-target effects, especially when using broad-spectrum insecticides. These include the pollution of ground and surface water, residual activity in the environment and accumulation within the food-chain, as well as posing significant health risks to beneficial insects, humans and biodiversity (Pimentel 1995). More

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target-specific systemic insecticides such as neonicotinoids also pose serious risks in their application, as they persist in the soil and plant tissues (such as pollen or nectar), which could be lethal to other arthropods and birds feeding on these plant tissues (Goulson 2013). The use of environmentally friendly insecticides is therefore crucial, especially considering the public's attitude towards a greener, more sustainable future.

The application of chemical insecticides is also often very labour- and cost-intensive. Furthermore, the unpredictable translocation of systemic insecticides and asynchronous larval development of wood-borers may result in many larvae escaping treatment (Hajek and Bauer 2007). Finally, symptoms of wood-borer infestation may not always be clear visually, and therefore many trees may not be treated based on visual inspection of symptoms only.

1.4.4 Biological control

Biological control can be an effective strategy to curb invasive infestations. However, this strategy is not always effective for wood-borers, as the immature stages are cryptic and difficult to access (Nielsen 1981). Nevertheless, biocontrol agents are host-specific, non-toxic to mammals and other animals and environmentally friendly, making it one of the most desirable strategies to use (Lacey and Goettel 1995; Lacey et al. 2001; Hajek and Bauer 2007; Kenis et al. 2017). There are few reports of wood-boring Lepidoptera parasitoids in the literature. *Eriborus applicitus* (Hymenoptera: Ichneumonidae) has been reported to parasitise *Holcocerus insularis* (Cossidae) in China (Sheng and Sun 2006) and *Cossus insularis* in Japan (Konishi 2016). *Lissonota holcocerica* (Hymenoptera: Ichneumonidae) was found to parasitise *H. hippophaecolus* (Cossidae) in China (Zong et al. 2012). Kittelson (2006) found an unidentified parasitoid on larvae of *Paranthrene robiniae* (Sesiidae) and suspected it to be *Apanteles paranthrendis* (Hymenoptera: Braconidae), since previous literature had confirmed *A. paranthrendis* as a larval parasitoid of *Paranthrene robiniae* (Sesiidae).

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Entomopathogenic nematodes have been used successfully in the control of several cossid and sessiid wood-borers (Hajek and Bauer 2007). In China, *Steinerema carpocapsae* was found to successfully control *Z. multistrigata* with up to 93% larval mortality, *H. insularis* (Cossidae) with up to 90% larval mortality and *Cossus cossus* (Cossidae) with up to 80% larval mortality (Yang et al. 1993). Similarly, in the USA, *S. carpocapsae* was found to successfully control *Prionoxystus robiniae* (Cossidae), with larval mortality ranging between 70% and 100% (Forschler and Nordin 1988). *Paranthrene robiniae* (Sesiidae) showed 88.9% mortality with the application of *S. carpocapsae* on birch and poplar (Kaya and Lindegren 1983).

The use of entomopathogenic fungi such as *Beauveria* spp. has shown some promise towards control of wood-borers. In China, a paste consisting of *Beauveria bassiana* conidia, waste molasses and sweet potato starch was used in the control of *Z. multistrigata* in casuarina trees, and obtained larval mortality as high as 96% (Yang et al. 1990). The method was applied to approximately 580 ha of forests at a cost of US\$0.02 per hectare (equivalent to US\$0.04 per hectare in 2018), making it a relatively cheap method to use (Yang et al. 1990; Hajek and Bauer 2007). *Beauveria bassiana* has also been successful in Poland for the control of *Paranthrene tabaniformes*, where conidial suspensions injected into larval galleries showed larval mortalities of up to 96% (Hajek and Bauer 2007). Entomopathogenic bacteria can also be used to control wood-borers, but results have been inconsistent. For example, *Bacillus thuringiensis* (Bt) was largely ineffective against the control of wood-borers such as *Prionoxystus robiniae* (Cossidae) and *Paranthrene simulans* (Sesiidae), even when applied at high volumes (Solomon 1985).

The utilisation of entomopathogens can be challenging. Their increased use will require an increase in their aggressiveness, adaptability to changing environments and challenging environmental conditions, efficient methods of mass production, improved formulations that facilitate the ease of application to host trees, longer shelf life and increased persistence within

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the environment (Lacey et al. 2001). The development of resistance against these biocontrol agents is another aspect to consider, and these entomopathogens should therefore preferably be used in conjunction with other management strategies (Lacey and Goettel 1995).

1.4.5 Behavioural control

The use of semiochemicals has been instrumental in understanding insect-insect and insect-plant interactions over the last 50 years (Saha et al. 2017). Semiochemicals have been used widely in the monitoring, mass trapping and mating disruption of pest populations through sex pheromones, as oviposition deterrence pheromones and alarm pheromones and as activators of plant defence mechanisms (Witzgall et al. 2010). These tactics are considered to be more environmentally friendly alternative management approaches within integrated pest management strategies than the use of chemical pesticides. They pose little risk to beneficial arthropod communities in the environment and the development of resistance to these tactics is highly unlikely (Witzgall et al. 2010).

Behavioural control involving mass trapping baited with conspecific sex pheromones, mating disruption and lure and kill tactics has been used widely to successfully reduce the impact of Lepidopteran wood-borers below economic injury level (El-Sayed et al. 2006). Light traps and conspecific sex pheromones were shown to effectively control leopard moth, *Z. pyrina*, infestation in Egypt in olive orchards (Hegazi et al. 2010). *Prionoxystus robinae* was effectively controlled using a diamond carton trap design baited with sex pheromones in mixed hardwood forests in the USA (Doolittle et al. 1976; Dix et al. 1987). Sufficient control was likewise achieved for *Paranthrene robinae* (Sesiidae) in hybrid poplar plantations in the USA using a pheromone-based management tactic (Kittelson 2006). In Chile, a conspecific sex pheromone has been developed from *Chilecomadia valdiviana* with the aim of use within a trapping programme (Herrera et al. 2016). A conspecific sex pheromone blend was also

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developed for *Endoclita excrescens* in Japan (Marukawa and Mori 2002). More recently, a conspecific sex pheromone was developed for *Coryphodema tristis* in South Africa (Bouwer et al. 2015), and tested in field trials in 2015. Promising results allowed for the optimisation of the pheromone blend (Bouwer et al. 2017) and for its eventual use in a large scale mass trapping programme that was implemented on the Highveld region of the Mpumalanga province. Some 23 000 adult males were captured across 1 600 ha during a 17-week trapping period (Verleur et al. 2017, unpublished manuscript). Thus, semiochemical-based management tactics show a lot of potential for the management of wood-boring Lepidoptera within an integrated pest management strategy (El-Sayed et al. 2006).

1.5 CONCLUSIONS

Wood-boring Lepidoptera are global pests of important forestry commodities such as teak (*Tectona grandis*), gum (*Eucalyptus* spp.), poplar (*Populus* spp.), gamhar (*Gmelina arborea*) and sengon plantations (*Paraserianthes falcataria*). They are capable of invading both native and exotic plantations and having a significant economic impact. No exotic wood-boring Lepidoptera have been reported, suggesting that they are not as prone to utilising invasion pathways, such as wood packaging, as wood-boring Coleoptera are, for instance.

Because of their complicated life history traits, wood-boring Lepidoptera pose unique management challenges. Chemical control may be an option; however, it remains a labour- and cost-intensive operation that also has a negative environmental impact. Biological control strategies through the use of entomopathogens such as fungi, bacteria and nematodes may be effective in controlling insect pest populations. However, the immature stages of wood-boring insects are often cryptic and difficult to access, rendering these tactics difficult to implement. Semiochemical-based management tactics are likely the most promising strategy for the control

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of wood-boring insect pests, since these tactics often target the adult stages and are host-specific, environmentally friendly and cost-effective. The combination of multiple strategies, coupled with efficient early detection mechanisms, will greatly aid in the management of destructive wood-boring insect pests.

1.6 PROJECT RATIONALE

The cossid moth of South Africa, *Coryphodema tristis*, was first reported as a significant pest of quince in 1917, and later on vines in 1977. In recent years, the cossid moth has expanded its host range again to *Eucalyptus nitens* plantations on the Mpumalanga Highveld. Only a few studies have been published that detail the life history of *C. tristis*, and these focused solely on populations in the Cape region on vineyards and quince trees, where there is a Mediterranean climate. No studies have yet investigated the life history of *C. tristis* in a temperate environment on *E. nitens*. In addition, no formal management strategies are currently in place, despite the significant economic impact *C. tristis* has on plantation forestry. Knowledge on seasonal development and emergence period is important to inform management strategies, including when to implement control measures for the best results.

1.7 PROJECT AIM AND OBJECTIVES

Aims:

1. Investigate the life-cycle of *Coryphodema tristis* in *Eucalyptus nitens* on the Mpumalanga Highveld.
2. Optimize the use of traps to catch male *C. tristis*, with the intention of moving towards a mass trapping approach.

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Objectives:

1. Investigate seasonal occurrence and development of the immature stages of *C. tristis* through regular felling of infested *E. nitens* trees on the Mpumalanga Highveld.
2. Investigate the possibility of multiple flight seasons of the adults through lure-based trapping.
3. Optimise the trap to trap distance of lure-based traps by investigating six different trap spacing treatments.

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1.8 TABLES AND FIGURES

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Table 1. Annual GDP income generated from the forestry sector from the top 20 industrial roundwood producers from planted forests (Food and Agriculture Organization 2015). The list of the top 20 industrial roundwood producers was obtained from Payn et al. (2015). The monetary value equivalent in USD\$ is shown for each country relative to the year of latest information, with the 2018 monetary value in USD\$ indicated in brackets.

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	Major commercial species	National GDP contribution in millions	US\$ equivalent in millions	Year of latest information
Argentina	<i>Pinus</i> spp., <i>Eucalyptus</i> spp., <i>Nothofagus</i> spp.	ARS \$ 1,040	211.52 (232.98)	2012
Australia	<i>Pinus</i> spp., <i>Araucaria cunninghami</i> , <i>E. globulus</i> , <i>E. nitens</i>	AUD \$ 1,265	1,314.84 (1,448.22)	2011-2012
Brazil	<i>E. benthamii</i> , <i>E. camaldulensis</i> , <i>E. grandis</i> , <i>E. pellita</i> , <i>E. robusta</i> , <i>E. saligna</i> , <i>E. tereticornis</i> & <i>E. urophylla</i>	BRL R\$ 17,028	9,138.08 (10,273.38)	2011
Canada	Various <i>Pinus</i> , <i>Picea</i> , <i>Populus</i> , <i>Abies</i> , <i>Tsuga</i> & <i>Pseudotsuga</i> spp.	CAD \$ 4,292	4,307.88 (4,744.89)	2012
Chile	<i>E. globulus</i> , <i>E. nitens</i> , <i>E. camaldulensis</i> , <i>E. delegatensis</i> , <i>E. viminalis</i>	CLP \$ 2,716,340	5,671.72 (6,247.08)	2012
China	<i>Cunninghamia lanceolata</i> , <i>Pinus yunnanensis</i> , <i>E. exceria</i> , <i>E. citriodora</i> , <i>E. urophylla</i> , <i>E. grandis</i> , <i>E. grandis x urophylla</i>	CNY ¥ 3,945.1	633.15 (697.38)	2012
Czech Republic	<i>Picea</i> , <i>Pinus</i> , <i>Fagus</i> & <i>Quercus</i> spp.	CZK Kč 25,714	1,352.56 (1,520.60)	2011
Finland	<i>Pinus sylvestris</i> , <i>Picea abies</i> , <i>Betula pubescans</i> , <i>B. pendula</i> , <i>Populus tremula</i> , <i>Alnus incana</i> , <i>A. glutinosa</i> , <i>Salix caprea</i> , <i>Sorbus aucuparia</i> , <i>Prunus padus</i>	EUR € 2,857	3,766.95 (4,149.09)	2012
Germany	<i>Pinus</i> , <i>Picea</i> , <i>Quercus</i> & <i>Fagus</i> spp.	EUR € 2,400	3,212.16 (3,725.22)	2010
India	<i>Tectona grandis</i> , <i>E. grandis</i> , <i>E. camaldulensis</i> , <i>E. globulus</i> , <i>Gmelina arborea</i> , <i>Paraserianthes falcataria</i>	INR ₹ 1,134,880	21,381.14 (24,037.49)	2010-2011
Indonesia	<i>T. grandis</i> , <i>P. falcataria</i> , <i>Hevia brasiliensis</i>	IDR Rp 44,952,100	4,764.92 (5,616.64)	2009
Japan	<i>Cryptomeria japonica</i> , <i>Chamaecyparis obtusa</i>	JPY ¥ 159,200	2,069.6 (2,326.72)	2011
New Zealand	<i>Pinus radiata</i>	NZD \$ 1,022	682.19 (791.14)	2010
Poland	<i>Pinus sylvestris</i> , <i>Quercus</i> spp., <i>Picea abies</i> , <i>Fagus sylvatica</i> , <i>Betula</i> spp., <i>Alnus</i> spp., <i>Abies</i> spp.	PLN zł 5,410.2	1,568.69 (1,763.58)	2011
Portugal	<i>Pinus pinaster</i> , <i>Eucalyptus</i> spp., <i>Quercus suber</i> , <i>Q. ilex</i> , <i>Pinus pinea</i> , <i>Castanea sativa</i>	EUR € 172.86	231.36 (268.31)	2010
South Africa	<i>E. grandis</i> , <i>E. nitens</i> , <i>E. dunnii</i> , <i>E. grandis x urophylla</i> , <i>Pinus radiata</i> , <i>P. patula</i> , <i>P. taeda</i> , <i>P. elliotii</i> , <i>Acacia mearnsii</i>	ZAR R 10,155	1,486.25 (1,723.64)	2010
Spain	<i>Pinus pinaster</i> , <i>P. sylvestris</i> , <i>P. halepensis</i> , <i>P. nigra</i> , <i>P. radiata</i> , <i>F. sylvatica</i> , <i>Quercus ilex</i> , <i>Q. pyrenaica</i> , <i>Q. petraea</i> , <i>Eucalyptus</i> spp.	EUR € 1,623	2,186.76 (2,568.47)	2008
Sweden	<i>Picea abies</i> , <i>Pinus contorta</i> , <i>P. sylvestris</i> , <i>Betula</i> spp.	SEK kr 35,557	5,280.21 (6,123.59)	2010
Thailand	<i>H. brasiliensis</i> , <i>T. grandis</i>	THB ฿ 8,144	270.38 (313.57)	2010
USA	Various <i>Pinus</i> , <i>Populus</i> , <i>Quercus</i> , <i>Fraxinus</i> , <i>Larix</i> , <i>Salix</i> , hybrid <i>Populus</i> & <i>Salix</i> spp.	USD \$ 2,659	3083.71	2010

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Table 2. Major and minor wood-boring Lepidoptera occurring in the world's top 20 industrial roundwood producers. The table is not an exhaustive list, but rather a summary of species reported in the literature. The list of the top 20 industrial roundwood producers was obtained from Payn et al. (2015). ‡ indicates a species is exotic respective to the country where they occur, while † indicates a species native respective to the country where they occur.

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Country	Species	Family	Commercial forestry trees affected	Reference
USA	<i>Prionoxystus robinae</i> †	Cossidae	<i>Quercus</i> spp. (oak)†, <i>Populus</i> spp. (poplar)†	Solomon (1988)
	<i>Prionoxystus macmurtei</i> †	Cossidae	<i>Quercus</i> spp.†	Barnd et al. (2008)
Brazil	<i>Paranthrene robinae</i> †	Sesiidae	<i>Populus</i> spp.†	Brown et al. (2006); Kittelson (2006)
	<i>Trichophassus giganteus</i> †	Hepialidae	<i>Eucalyptus</i> spp. (gum)‡	Tobi et al. (1993); Schühli et al. (2016)
	<i>Timocratica palpalis</i> †	Depressariidae	<i>E. saligna</i> ‡, <i>E. urophylla</i> ‡	Pereira et al. (2001)
China	<i>Endoclita signifer</i> †	Hepialidae	<i>E. grandis x urophylla</i> hybrids‡	Yang et al. (2013); Zheng et al. (2016)
	<i>Sesia sinengensis</i> †	Sesiidae	<i>Populus</i> spp.†	Zhenguo et al. (1984)
India	<i>Sahyadrassus malabaricus</i> †	Hepialidae	<i>Tectona grandis</i> (teak)†, <i>Paraserianthes falcataria</i> (sengon)‡	Nair (2001); Varma et al. (2007)
	<i>Zeuzera coffeae</i> †	Cossidae	<i>T. grandis</i> †	Varma et al. (2007)
	<i>Duomitus (= Xyleutes) ceramicus</i> †	Cossidae	<i>Gmelina arborea</i> (gamhar)†	Kumar and Chandra (2017)
	<i>Alcterogystia cadambae</i> †	Cossidae	<i>T. grandis</i> †	Nair (2001)
	<i>Indarbela quadrinotata</i> †	Cossidae	<i>G. arborea</i> †	Kumar and Chandra (2017)
Chile	<i>Chilecomadia valdiviana</i> †	Cossidae	<i>E. nitens</i> ‡, <i>E. globulus</i> ‡, <i>E. camaldulensis</i> ‡, <i>E. delegatensis</i> ‡, <i>E. viminalis</i> ‡	Lanfranco and Dungey (2001)
New Zealand	<i>Aenetus virescens</i> †	Hepialidae	<i>E. saligna</i> ‡, <i>E. delagatensis</i> ‡	Grehan (1984)
Australia	<i>E. cinerea</i> †	Cossidae	<i>E. teretricornis</i> †, <i>E. grandis</i> †	Lawson and Debus (2016)
	<i>Culama</i> spp.†	Cossidae	<i>E. teretricornis</i> †, <i>E. grandis</i> †	Lawson and Debus (2016)
Finland	<i>Sesia bembeciformis</i> †	Sesiidae	<i>Salix</i> spp. (willow)†, <i>Populus</i> spp.†	Vuola and Korpela (1977)
	<i>Paranthrene tabaniformis</i> †	Sesiidae	<i>Salix</i> spp.†, <i>Populus</i> spp.†	Vuola and Korpela (1977)
South Africa	<i>Coryphodema tristis</i> †	Cossidae	<i>E. nitens</i> ‡	Boreham (2006)
Thailand	<i>D. ceramicus</i> †	Cossidae	<i>T. grandis</i> †	Chaiglom (1966)
	<i>E. signifer</i> †	Hepialidae	<i>T. grandis</i> †	Nair (2001)
	<i>Z. coffeae</i> †	Cossidae	<i>Acacia mangium</i> (black wattle)‡	Nair (2001)
Japan	<i>E. signifer</i> †	Hepialidae	<i>Populus</i> spp.†, <i>Salix</i> spp.†, <i>Alnus</i> spp. (alder)†, <i>Castanea</i> spp.	Tobi et al. (1993)
	<i>E. excrescens</i> †	Hepialidae	(chestnut)†, <i>Quercus</i> spp.†	
Indonesia	<i>Prionoxystus</i> spp.†	Cossidae	<i>G. arborea</i> saplings‡	Nair (2001)
	<i>E. gmelina</i> †	Hepialidae	<i>T. grandis</i> †	Kalshoven (1965); Tobi et al. (1993)
	<i>E. sericeus</i> †	Hepialidae	<i>T. grandis</i> †	Kalshoven (1965); Tobi et al. (1993)
	<i>I. quadrinotata</i> †	Cossidae	<i>P. falcataria</i> ‡	Nair (2001)
	<i>Z. coffeae</i> †	Cossidae	<i>Eucalyptus</i> saplings‡	Nair (2001)
Spain	<i>Paranthrene tabaniformes</i> †	Sesiidae	<i>Populus</i> spp.†	Templado (1964)
	<i>Sesia apiformis</i> †	Sesiidae	<i>Populus</i> spp.†	Martín-García et al. (2011)
Portugal	<i>P. tabaniformes</i> †	Sesiidae	<i>Populus</i> spp.†	Laštůvka and Laštůvka (2001)

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Table 3. Summary of management tactics used to control wood-boring Lepidoptera.

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Species	Management tactic	Location	Reference
<i>Acosus centerensis</i> (Cossidae)	Traps baited with semiochemicals	USA: North Dakota	Doolittle et al. (1976)
<i>Chilecomadia valdiviana</i> (Cossidae)	Semiochemical developed	Chile	Herrera et al. (2016)
<i>Coryphodema tristis</i> (Cossidae)	Traps baited with semiochemicals	South Africa	Bouwer et al. (2015)
<i>Cossus cossus</i> (Cossidae)	Parasitic nematode: <i>Steinerema carpocapsae</i> (Rhabditida: Steinernematidae)	China	Yang et al. (1993)
<i>Cossus insularis</i> (Cossidae)	Parasitoid: <i>Eriborus applicitus</i> (Hymenoptera: Ichneumonidae)	China	Konishi (2016)
<i>Endoclita excrescens</i> (Hepialidae)	Semiochemical developed	Japan	Marukawa and Mori (2002)
<i>Holcocerus hippophaecolus</i> (Cossidae)	Parasitoid: <i>Lissonota holcocerica</i> (Hymenoptera: Ichneumonidae)	China	Zong et al. (2012)
<i>H. insularis</i> (Cossidae)	Parasitoid: <i>Eriborus applicitus</i> (Hymenoptera: Ichneumonidae)	China	Sheng and Sun (2006)
<i>Paranthrene robinae</i> (Sesiidae)	Chemical insecticide applied to entire trees	USA: California	Bentley et al. (1994)
<i>Paranthrene robinae</i> (Sesiidae)	Parasitic nematode: <i>Steinerema carpocapsae</i> (Rhabditida: Steinernematidae)	USA: California	Kaya and Lindegren (1983)
<i>Paranthrene simulans</i> (Sesiidae)	Entomopathogenic bacteria: <i>Bacillus thuringiensis</i> (Bacillales: Bacillaceae)	USA, Mississippi	Solomon (1985)
<i>Paranthrene tabaniformes</i> (Sesiidae)	Entomopathogenic fungus: <i>Beauveria bassiana</i> (Hypocreales: Clavicipitaceae)	Poland	Hajek and Bauer (2007)
<i>Prionoxystus robinae</i> (Cossidae)	Entomopathogenic bacteria: <i>Bacillus thuringiensis</i> (Bacillales: Bacillaceae)	USA: Mississippi	Solomon (1985)
<i>Prionoxystus robinae</i> (Cossidae)	Traps baited with semiochemicals	USA: Nebraska, Mississippi	Dix et al. (1987)
<i>Prionoxystus robinae</i> (Cossidae)	Parasitic nematode: <i>Steinerema carpocapsae</i> (Rhabditida: Steinernematidae)	USA: Kentucky	Forschler and Nordin (1988)
<i>Zeuzera multistrigata</i> (Cossidae)	Parasitic nematode: <i>Steinerema carpocapsae</i> (Rhabditida: Steinernematidae)	China	Yang et al. (1993)
<i>Z. multistrigata</i> (Cossidae)	Entomopathogenic fungus: <i>Beauveria bassiana</i> (Hypocreales: Clavicipitaceae)	China	Yang et al. (1990)
<i>Z. pyrina</i> (Cossidae)	Semiochemicals, light traps	Egypt	Hegazi et al. (2010)

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Figure 1. Global distribution of wood-boring Lepidoptera reported as pests on commercial forestry plantations.

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CHAPTER 2

**Seasonal development and occurrence of
Coryphodema tristis (Lepidoptera: Cossidae) on
Eucalyptus nitens in the Mpumalanga Highveld,
South Africa**

CHAPTER 2: SEASONAL DEVELOPMENT AND OCCURRENCE OF *CORYPHODEMA TRISTIS* (LEPIDOPTERA: COSSIDAE) ON *EUCALYPTUS NITENS* IN SOUTH AFRICA

2.1 ABSTRACT

A native wood-boring moth, *Coryphodema tristis* (Drury, 1782) (Lepidoptera: Cossidae), was reported to infest *Eucalyptus nitens* trees in plantations on the Mpumalanga Highveld in 2004. While it has had significant impacts on commercial forestry operations, little is known about its seasonal phenology and ecological traits. This study aims to investigate the seasonal development and occurrence of *C. tristis* in *E. nitens* plantations. One hundred and twenty-three trees were felled across eight sites over a 23-month period to investigate the seasonal development. Two thousand and seventy-nine larvae were extracted from these felled trees and their head capsules were measured as an indication of developmental stage. Tree height and diameter for each infestation point were recorded and correlated against larval size. Finally, flight period(s) was investigated throughout the year by using cross-vane yellow bucket funnel traps baited with the *C. tristis* sex pheromone. Larvae feeding beneath the bark and within the wood were present throughout the year, with some very young under-bark larvae occurring late in August. Pupation generally started in May and pupae were present until November, although some pupae started to spin only in August. Tree diameter and height were found not to be an indicator for larval size, and only one flight period in 2017 was detected. Endogenous cues may regulate the life cycle of *C. tristis*, and successive invasions of *C. tristis* into *E. nitens* plantations likely took place. The implications of these results, particularly for management purposes, are discussed in detail.

2.2 INTRODUCTION

Wood-boring insects have been reported from numerous countries as pests of forestry trees. Many of these are in the order Coleoptera, such as the emerald ash borer (*Agrilus plannipennis*) and the Asian long-horned beetle (*Anoplophora glabripennis*). These latter

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beetles have spread from Asia to parts of North America and Europe via pathways involving the transport of wood or wood-packaging material, and have caused significant economic losses in their introduced range (Haack et al. 2010; Herms and McCullough 2014). Native wood-boring insects can also cause major economic losses. For example, the mountain pine beetle (*Dendroctonus ponderosae*) has caused significant losses in lodgepole pine plantations in its native North American range (Vorster et al. 2017). Wood-boring Lepidoptera are perhaps less known than their Coleopteran counterparts, but can also have a negative impact on growth and survival. These wood-boring moths fall into three families within the Lepidoptera, namely cossid moths (Cossidae), clearwing moths (Sesiidae) and ghost moths (Hepialidae).

The Cossidae, in particular, are some of the most serious wood-boring pests of woody ornamental trees, agricultural crops and commercial forestry plantations. For instance, the leopard moth (*Zeuzera pyrina*), which is a significant pest of olive, apple and pear trees in Egypt and Israel (Hegazi et al. 2015). The teak beehole borer, *Duomitus* (= *Xyleutes*) *ceramicus*, has caused extensive losses in the teak plantations of Thailand and Malaysia (Chaiglom 1966; Gotoh et al. 2003). Likewise, *Chilecomadia valdiviana* has become an important forest pest in the *Eucalyptus nitens* plantations of Chile (Herrera et al. 2016).

Coryphodema tristis is a native cossid moth in South Africa, which has been reported from eight native tree host families in the country (Gebeyehu et al. 2005). *Coryphodema tristis* was first reported on commercial agricultural crops such as apples, pears and quince in the Cape region in 1917 (Petty 1917). In the 1980s it was discovered to also infest vineyards in the Cape region (Höppner 1991). In 2004, *C. tristis* further expanded its host range and was reported to infest *E. nitens* in plantations of the Mpumalanga Highveld of South Africa (Gebeyehu et al. 2005; Boreham 2006). The feeding of the larvae on the xylem and their tunnelling throughout the stem cause disruptions in the host's conducting tissue. The result is

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crown death, loss of structural integrity, growth of secondary pathogens such as *Botryosphaeria* spp. and, eventually, tree death (author's own observations).

Coryphodema tristis has caused significant losses to the plantation industry, with up to 77% mortality in some *E. nitens* stands (Boreham 2006). *Eucalyptus nitens* is an important species for the forestry industry since it has excellent snow tolerance (Swain and Gardner 2003) and is of particular value in the heavy snow fall areas of KwaZulu-Natal. Due to the negative impact from *C. tristis*, many *E. nitens* plantations are currently being felled before reaching rotation end and replanted to *E. macarthurii* and *E. benthamii* at considerable cost to the plantation forestry industry. Of further concern, Degefu (2013) showed that *Eucalyptus* species have no inherent physiological barriers preventing *C. tristis* from utilising xylem as a food source, with plant defences influencing the successful or unsuccessful infestation of host trees. It is possible that *C. tristis* may yet adapt to these plant defences and colonise other *Eucalyptus* species in time, especially if their preferred host has been completely replaced on the Mpumalanga Highveld.

Due to the value of *E. nitens* as a plantation species, and the ability of *C. tristis* to expand its host range, the development of an effective management strategy is crucial. However, management of *C. tristis* in *E. nitens* plantations has proven difficult. Since *C. tristis* was first reported on *E. nitens*, no natural enemies have been collected from *E. nitens* or from any of the reported native host species (author's personal observation). The lack of natural enemies on *E. nitens* possibly indicates that unknown factors have prevented the natural enemies from following *C. tristis* to its new host, while the collection of natural enemies on native hosts has been limited due to difficulties to find infestations of *C. tristis* on reported native hosts. The use of insecticides to control *C. tristis* is also challenging due to the wood-boring nature of the larvae, although systemic insecticides and targeting the adult moths with a contact insecticide during the flight season may provide an option. Mass-trapping using lure-

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based traps is another control option that is currently being investigated (Verleur et al. 2017, unpublished manuscript).

A limitation to the implementation of any of the above-mentioned management approaches is the current lack of understanding of the basic life history traits of *C. tristis* on *E. nitens*. Only a few studies have been published that detail the life history of *C. tristis*, and these focused solely on populations in the Cape region on vineyards and quince trees, where there is a Mediterranean climate (Petty 1917; Höppner 1991). In quince trees, *C. tristis* requires approximately two years for full development from egg to adult (Petty 1917), while on vines the life cycle varies between one and three years (Höppner 1991). On both hosts, the majority of the life cycle is spent as larvae tunnelling within the wood and the adults are short lived and do not feed (Petty 1917; Höppner 1991). Petty (1917) described a pupal stage lasting approximately five to six months, while Höppner (1991) observed a fourteen-week pupal development period during winter and spring, as well as an eight-week pupal developmental period during early summer. No studies have yet investigated the life history of *C. tristis* in a temperate environment on *E. nitens*. As several studies have shown that temperature and other climatic factors, as well as host plant quality, have an influence on insect development (Philogene and McNeil 1984; Ratte 1984; Awmack and Leather 2002), it is possible that the phenology of *C. tristis* may be different in the Mpumalanga Highveld as compared to the Cape region.

Life history traits that would be relevant for the management of *C. tristis* include the seasonal development of the larvae within the tree host, the emergence period and the reproductive strategy. Knowledge on seasonal development and emergence period is important to inform management strategies, including when to implement control measures for the best results.

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In this study, the seasonal occurrence and development of *C. tristis* in a temperate climate on *E. nitens* was investigated. The development of the larval stage was monitored by felling and examining naturally infested trees. Lure-baited traps were used to investigate the adult flight period, including testing for a possibility of two or more annual flight periods. Data from this study were compared to previous studies on other hosts.

2.3 MATERIALS AND METHODS

2.3.1 Seasonal occurrence and development

Three sites were initially selected on the Mpumalanga Highveld for destructive sampling of *E. nitens* trees to investigate the seasonal occurrence and development of the immature stages of *C. tristis*. However, large-scale harvesting operations were being conducted in the area, owing to the pressure to harvest 6-8-year-old *E. nitens* as soon as possible due to damage caused by *C. tristis* infestations. The third site was thus felled during these ongoing operations and had to be replaced with another site in close proximity. This fourth site was also subsequently harvested and had to be replaced with a fifth site, and then again with a sixth site. The first site was also felled during this period and had to be replaced with a seventh site, and subsequently again with an eighth site. A total of eight different sites were thus used during the study (Table 1, Figure 1), however only a maximum of three sites were active study sites at a time (Table 1). The sites were spread over an area of approximately 110 km. Sites were selected based on similarity to each other with regard to age of the trees (six to eight years) and *C. tristis* infestation level (10–20% of the entire compartment). The age of the trees was considered suitable for sampling, as *C. tristis* infestations typically start when trees are around four years or older and re-infestation of the same trees in subsequent years is a common occurrence (Boreham 2010, unpublished manuscript).

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Five trees from each site were felled every two months over a 23-month period to investigate the seasonal occurrence and development of immature stages (larvae and pupae) of *C. tristis*. Infested trees were selected randomly, approximately 100 m from each other in a zig-zag pattern, where the direction of sampling changes 90° after every tree sampled/ 100 m. The following were recorded for each felled tree: the diameter of the tree at breast height (DBH) (standardised at 1.3 m above soil level); the diameter of the tree at each infestation point (DIP); the height of the tree at each infestation point (IPH); and the life stages present at each infestation point. From each infestation point on each felled tree (point of entry into the tree of a group of larvae) at least five larvae/pupae were collected where possible and preserved in sample bottles containing 70% ethanol. For each larva, the width across the narrowest part of the head capsule was measured as an indicator of development. Measurements of all collected larvae were made using a Zeiss stereo microscope and the AxioVision 4.9.1 (Carl Zeiss) image analysis software package.

2.3.2 Emergence period

Nine yellow cross-vane bucket funnel traps baited with a 95:2.5:2.5 volumetric blend of Z9-14:OAc, Z9-14:OH, and 14Ac, a synthetic sex pheromone of *C. tristis* developed by Bouwer et al. (2015), was installed in a six-year old *E. nitens* site (30.626S°, 26.363°E) on the Mpumalanga Highveld to monitor for additional adult flight periods outside the known flight period starting in late September. Traps were installed at a height of 4 m on trees and placed 50 m apart in a square grid pattern. Traps were monitored once a month for the presence of adult male moths between January and September 2017 to establish whether additional flight periods, other than the known flight period from September to December, were present for *C. tristis*. The pheromone blend was replaced once every six weeks.

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2.3.3 Data Analysis

The seasonal occurrence of the immature and mature stages of *C. tristis* infesting *E. nitens* from 2016-2018 was plotted on a circle calendar, and compared to the seasonal occurrence of *C. tristis* infesting vines (Höppner 1991) and quince trees (Petty 1917) using the same format.

Head capsule width measurements were separated into measurements taken from larvae feeding beneath the bark and larvae feeding within the wood, and the mean head capsule width for each infestation point was calculated. Mean head capsule measurements for both groups of data were then plotted separately against sampling period using boxplots showing the mean, maximum and minimum head capsule widths as well as the standard error of the mean.

Both groups of data were tested separately for normality and homogeneity using the Shapiro-Wilk test of normality and the Fligner-Killeen test of homogeneity. An ANOVA was used to test whether significant differences were present for mean head capsule measurement between sampling periods for larvae feeding beneath the bark. A non-parametric Kruskal-Wallis test was used to test whether significant differences were present for mean head capsule measurement between sampling periods for larvae feeding within the wood. Dunn's post hoc test was used to determine where significant differences were present for larvae feeding within the wood.

Mean head capsule measurement for larvae beneath the bark and larvae within the wood was also plotted separately against DIP and IPH per month and the R^2 values were calculated to examine the strength of the relationship between tree size and larval size.

2.4 RESULTS

2.3.4 Seasonal occurrence and development

A total of 123 trees with 471 infestation points were sampled from all the sites to evaluate the seasonal occurrence and development of the immature stages of *C. tristis*. Larvae feeding beneath the bark were observed during the months of January to May, August, September and November (Figure 2). An important observation was the presence of these larvae during August and September, as this had not been recorded in previous literature. The larvae observed in August had an average head capsule size of 0.85 mm (Figure 3a), suggesting these larvae were still very young. Larvae feeding within the wood were present throughout the year (Figure 2). Some larvae feeding within the wood during August and September had average head capsule widths exceeding 5 mm (Figure 3b), suggesting that these larvae were ready to pupate. Larvae that had just begun spinning cocoons were observed in August, and by the end of September all larvae had pupated. Pupation started in May and cocoons were present until November (Figure 2). The adult flight season started in September and continued until December (Figure 2). Egg clusters were not observed in this study.

A total of 2,079 larvae were collected from felled *E. nitens* trees (Table 2). Larvae beneath the bark were collected from the months of January, March, April, May, June, August, September and November. Head capsule widths for larvae beneath the bark ranged from 0.5 mm to 2.9 mm over the 23-month sampling period. There was a general increase in head capsule width of the larvae beneath the bark from March to November; however, this was not significant ($F_{7,12} = 0.649$, $p > 0.05$) (Figure 3a). Head capsule measurements for larvae within the wood varied from 0.6 mm to 5.5 mm over the 23-month sampling period. There was a significant decrease in head capsule width towards the winter months of May, June and August for larvae within the wood ($F_{9,387} = < 0.001$, $p < 0.05$), whereafter the average head capsule

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widths generally increased from September to January (Figure 3b). The large variation in size within the same sampling period suggested the presence of more than one generation of larvae within the same period.

Larvae were collected at infestation points on trees ranging in diameter (DIP) from 3 cm to 23 cm and at heights (IPH) from 0.1 m to 15.4 m. There was a weak correlation (R^2 values ranged between 0.00 to 0.1, with one exception) between diameter at the infestation point and head capsule width of larvae (Figure 4). This pattern was the same for each of the sampling periods, and for both larvae under the bark and larvae in the wood. Similarly, there was a weak correlation (R^2 values ranged between 0.00 – 0.09 with one exception) between height at the infestation point and head capsule width of larvae (Figure 5). This pattern was the same for each of the sampling periods, and for both larvae under the bark and larvae in the wood.

2.3.5 Emergence period

No adult moths were collected from the nine baited pheromone traps during the entire monitoring period from January to September 2017.

2.5 DISCUSSION

In this study, the seasonal phenology of *C. tristis* in the Mpumalanga Highveld on *E. nitens* was investigated. The seasonal phenology of *C. tristis* was generally similar to that recorded in previous studies in other areas of the country (Petty 1917; Höppner 1991), with the exception that larvae under the bark were observed in August and September. There was a large variation in larval size throughout the sampling periods, indicating the presence of overlapping generations. *Coryphodema tristis* showed no preference for tree size (diameter or height) within the age-class of trees (6-8 years) sampled. Neither the region within which the

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sampling occurred (Mpumalanga Highveld), nor the new host (*E. nitens*) has a major impact on the development of *C. tristis*, and this has significant relevance in the management of the pest.

The general phenology of the populations of *C. tristis* in the Western Cape and the Mpumalanga Highveld are not distinctly different from each other. Pupae and adults of both populations are consistently present from May to November and from September to December respectively (Petty 1917; Höppner 1991). The monitoring of the adult flight season in this study was, however, limited with regard to the number of traps used and the area sampled. A second adult flight period could thus not completely be ruled out. The larvae boring within the wood are generally present throughout the year in both populations, while the larvae feeding beneath the bark show a more restricted presence throughout the year. This, despite the difference in climate between the Western Cape and Mpumalanga. For example, the annual average temperature in Stellenbosch was 17.6°C and 17.5°C in 1988 and 1989 when Höppner (1991) conducted their studies on Chenin blanc vines, but 14.5°C and 14.0°C in Lothair (Mpumalanga Highveld) in 2016 and 2017 during this study period (NASA Langley Research Center Atmospheric Science Data Center 2015; C W Price & Co 2018). This 3°C difference might be expected to result in a difference in phenology between the two regions as ambient temperature has been shown to be a primary driver of insect development (see Ratte 1984, Hagstrum and Milliken 1988 and Mirhosseini et al. 2017). In addition, in a laboratory study Höppner (1991) showed that *C. tristis* larvae raised at 15°C required approximately 17.6 months for development to the pupal stage, while larvae raised at 18°C required approximately 12.9 months.

The similarity in the phenology between Western Cape and Mpumalanga populations of *C. tristis* is also unexpected because of the different hosts involved. Host quality has been shown to affect insect developmental time (Scriber and Slansky 1981), where xylem-based

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diets which are low in nitrogen content result in longer life cycles for wood-boring insects (see Moore and Navon 1966; Solomon 1988). The nitrogen content of wood in the scions of Chenin blanc/99 Richter vines varies seasonally between 0.36% and 0.67% of the total dry mass (Conradie 1990), while the average nitrogen content of the wood and bark of *E. nitens* is reported to be 0.19% and 0.53% respectively (Madgwick et al. 1981). Nitrogen is crucial for metabolic processes, cellular structures, genetic coding and overall growth, and is thus expected to be one of the factors influencing insect development (Mattson 1980). Other nutritional and structural elements are also expected to vary between the various hosts on which *C. tristis* occurs.

Given that Stellenbosch is the warmer region, and vine scion trunks are more nutritious than a *E. nitens* xylem diet with respect to some nutrients (e.g. nitrogen), one would expect a shorter life cycle in this region compared to the Mpumalanga region, which would ultimately influence the seasonal occurrence and voltinism. While Höppner (1991) reported a life cycle lasting between one and three years in the Western Cape, the seasonal occurrence largely corresponds with the seasonal occurrence in the Mpumalanga Highveld. It may be that the annual average of 3°C difference in temperature between the two regions, as well as the difference in nitrogen content of the respective diets, is not significant enough to cause a deviation in phenology between the two regions. It could also indicate that environmental cues related to, for example, photoperiod or rainfall, or endogenous cues related to circadian rhythm may play a role in the development of *C. tristis* irrespective of environmental cues (see Miyazaki et al. 2009). Furthermore, it is possible that the microclimate inside the wood varies less than the general climate for the region and contributes to the similarity in phenology.

While the phenology of *C. tristis* in the Western Cape largely corresponds with that found in the Mpumalanga Highveld, some differences were observed regarding the seasonal occurrence of larvae. For example, very small, apparently young larvae were observed in

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Mpumalanga in August 2016 feeding beneath the bark (average head capsule size approximately 0.85 mm). As adults are only present from September until late December and eggs require an incubation period of at least 29 days at 20°C (Höppner 1991), the very last neonate larvae should be present late January or early February. If larvae feed beneath the bark for three to four months before they start boring into the wood (Höppner 1991), the last under-bark larvae should therefore be present in June, and not in late August.

One explanation for the occurrence of young larvae in August is that larvae may undergo diapause. An endogenous, circannual rhythm was shown to be present for *Cossus insularis* (Lepidoptera: Cossidae) (Nakanishi et al. 2017), where larval development is arrested by “gates” or endogenous cues. The “gate” concept as described for fruit flies, *Drosophila pseudoobscura* (Pittendrigh 1966), and the varied carpet beetle, *Anthrenus verbasci* (Nisimura and Numata 2003; Miyazaki et al. 2005, 2009), involves the presence of endogenous cues which prompts further development from larvae to pupae, or from one larval stage (feeding beneath the bark) to another (boring within the wood). If larvae are not sufficiently developed when the first cues are received, or the first gate is “opened”, they will either remain active or enter diapause until the second gate opens. Larval diapause has been shown to be present in the Cossidae, for example *C. insularis* (Nakanishi et al. 2017) and *Paropta paradoxus* (Plaut 1973). It is possible that *C. tristis* shares this trait. Larval development may be delayed for several reasons, including variation in growth rate between larvae, low ambient temperatures (especially during winter months), insufficient nutrition and the long egg-laying period (September to December). Larvae hatching in late summer could undergo diapause and become active only after winter. Based on these factors, it is possible that larvae feeding beneath the bark are also present throughout the year, instead of being restricted to certain months of the year, as had been previously thought.

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Another difference between the findings of this study and those of Höppner (1991) was the presence of larger, pre-pupal larvae in August 2016 and September 2017, along with larvae that were starting to pupate. Pupation has previously been observed to start in May (Petthey 1917; Höppner 1991). Nakanishi et al. (2017) reported two pupation peaks for *C. insularis* and explained that these peaks were a result of their endogenous, circannual rhythm. *Cossus insularis* larvae would hatch and develop until the first gate opened, whereafter they would enter diapause until the second gate opened. Some larvae would then pupate, while a second group would enter diapause again and pupate only when the third gate opened. Höppner (1991) also described two pupal stages for *C. tristis*. It was suggested that there was a group of larvae that would start pupation in May and eclose approximately fourteen weeks later in September, while a second group would pupate in early summer (middle October) and eclose eight weeks later in December. The second group's accelerated development was attributed to higher ambient temperatures. It is therefore possible that pupation in *C. tristis* populations on the Mpumalanga Highveld in *E. nitens* plantations is also subject to an endogenous circannual rhythm, with a second group of mature larvae pupating once a developmental gate opened in August.

No correlation was found between the tree diameter (DIP) and height (IPH) of each infestation point and larval size (head capsule width) in 6-8-year-old trees. While larval size showed little variation within each infestation point, it frequently differed substantially between infestation points on the same tree, likely because more than one generation of larvae were present within an infested tree. Larval diapause and environmental conditions that may either accelerate or delay development may also play a role in the significant variation of larval sizes within a tree. According to Höppner's (1991) observations, females will lay a complement of eggs as soon as they emerge, as they are too heavy to fly off immediately to be mated. Thereafter, they will mate and lay the remainder of their egg complement irrespective of tree

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size. This shows that *C. tristis* females do not prefer to lay their eggs on certain trees, namely stressed or stunted trees as opposed to healthy trees, and larvae do not restrict themselves to certain parts of a tree (i.e. top, middle or bottom). Tree diameter and height within 6-8-year-old trees can therefore not be used as a proxy for infestation, and management strategies should focus on strategies that encompass whole stands, as opposed to strategies targeting individual trees.

This study has provided the first data on the development of *C. tristis* on *E. nitens*. The results of this study indicated that neither region (despite the differences in climate), host species, tree size nor position of infestation on the tree influences larval development or phenology. Clearly *C. tristis* is a robust, polyphagous insect that can deal with variation in host nutrition and environmental conditions. These findings will aid management strategies with regard to more accurate timing of the implementation of management strategies against the various life stages of *C. tristis*, especially when locating, developing and deploying biological control agents for future management.

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2.6 TABLES AND FIGURES

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Table 1. Sampling dates and sites for the felling of *E. nitens* plantations from May 2016 to March 2018.

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	May-16	Aug-16	Oct-16	Dec-16	Apr-17	Jun-17	Sep-17	Nov-17	Jan-18	Mar-18
Lothair (1)	●	●	●	●	●	●	○			
Lothair (2)								●	○	
Lothair (3)									●	●
Carolina (1)	●	●	●	●	●	●	●	●	○	
Machadodorp (1)	●	●	●	○						
Machadodorp (2)					●	○				
Amsterdam (1)						●	●	○		
Amsterdam (2)									●	●

Note: ● indicates when a compartment was sampled; ○ indicates when a compartment was felled.

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Table 2. Number of trees/ infestation points/ larvae sampled from May 2016 to March 2018 per sampling site in *E. nitens* plantations on the Mpumalanga Highveld.

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Date	Lot (1)	Lot (2)	Lot (3)	Car†	Mac (1)	Mac (2)	Ams (1)	Ams (2)	Total
May 2016	5/38/178			5/24/120	5/14/65				15/76/363
Aug 2016	5/14/43			5/18/80	5/23/112				15/55/235
Oct 2016	5/23/80			5/18/71	5/12/60				15/53/211
Dec 2016	5/27/95			5/22/68	○				10/49/250
Apr 2017	5/18/77			5/25/100		3/12/53			13/55/230
Jun 2017	5/19/79			5/31/137		○	5/15/70		15/65/286
Sep 2017	○			5/14/139			5/31/49		10/45/188
Nov 2017		5/11/34		5/20/95			○		10/31/129
Jan 2018		○	5/13/50	○				5/13/53	10/26/103
Mar 2018			5/6/30					5/10/53	10/16/84
									123/471/2079

Note: ○ indicates when a compartment was felled

Lot: Lothair

Car: Carolina

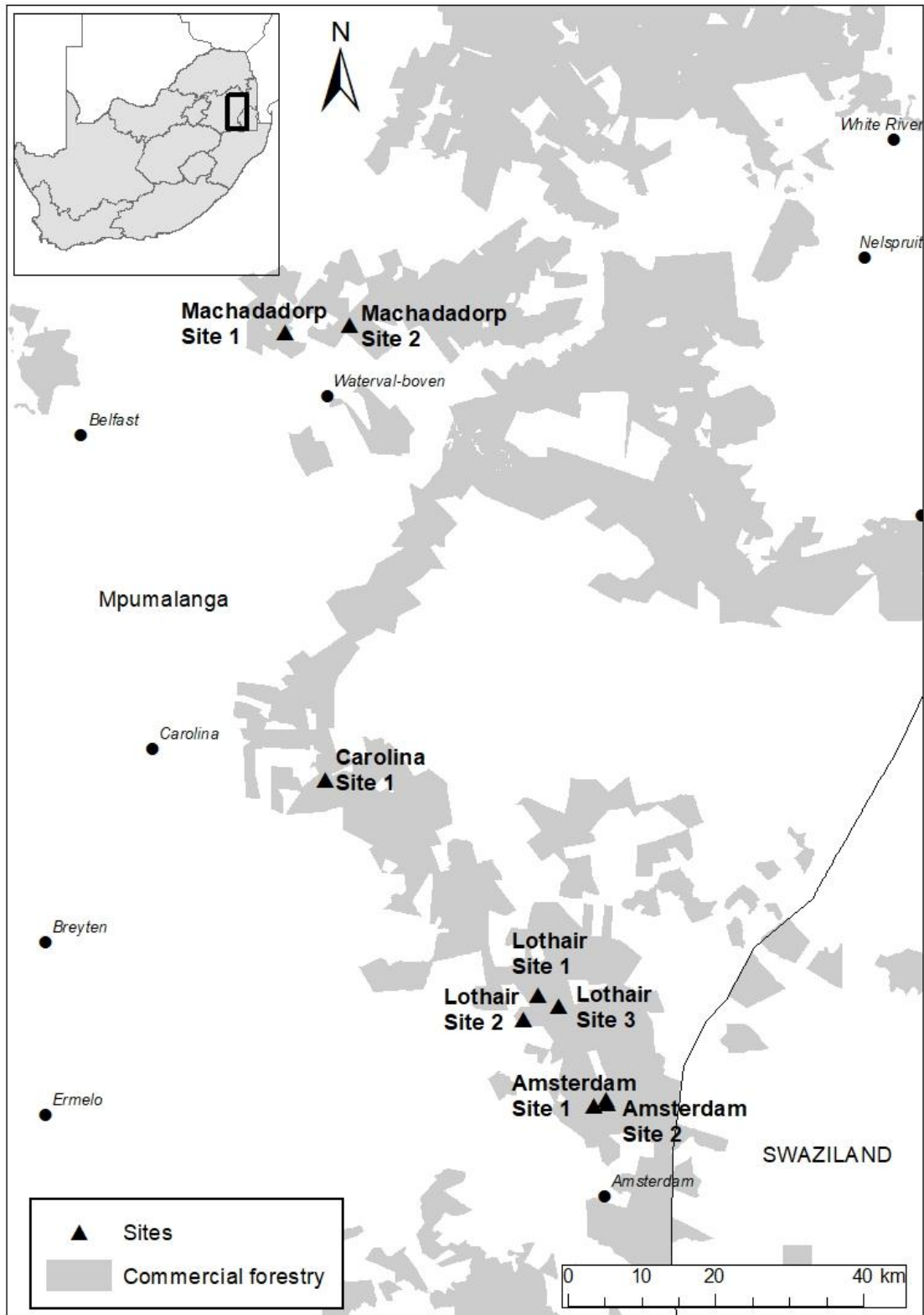
Mac: Machododorp

Ams: Amsterdam

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Figure 1. Sample sites on the Mpumalanga Highveld where destructive felling of *E. nitens* was conducted to investigate the seasonal occurrence and development of *C. tristis*.

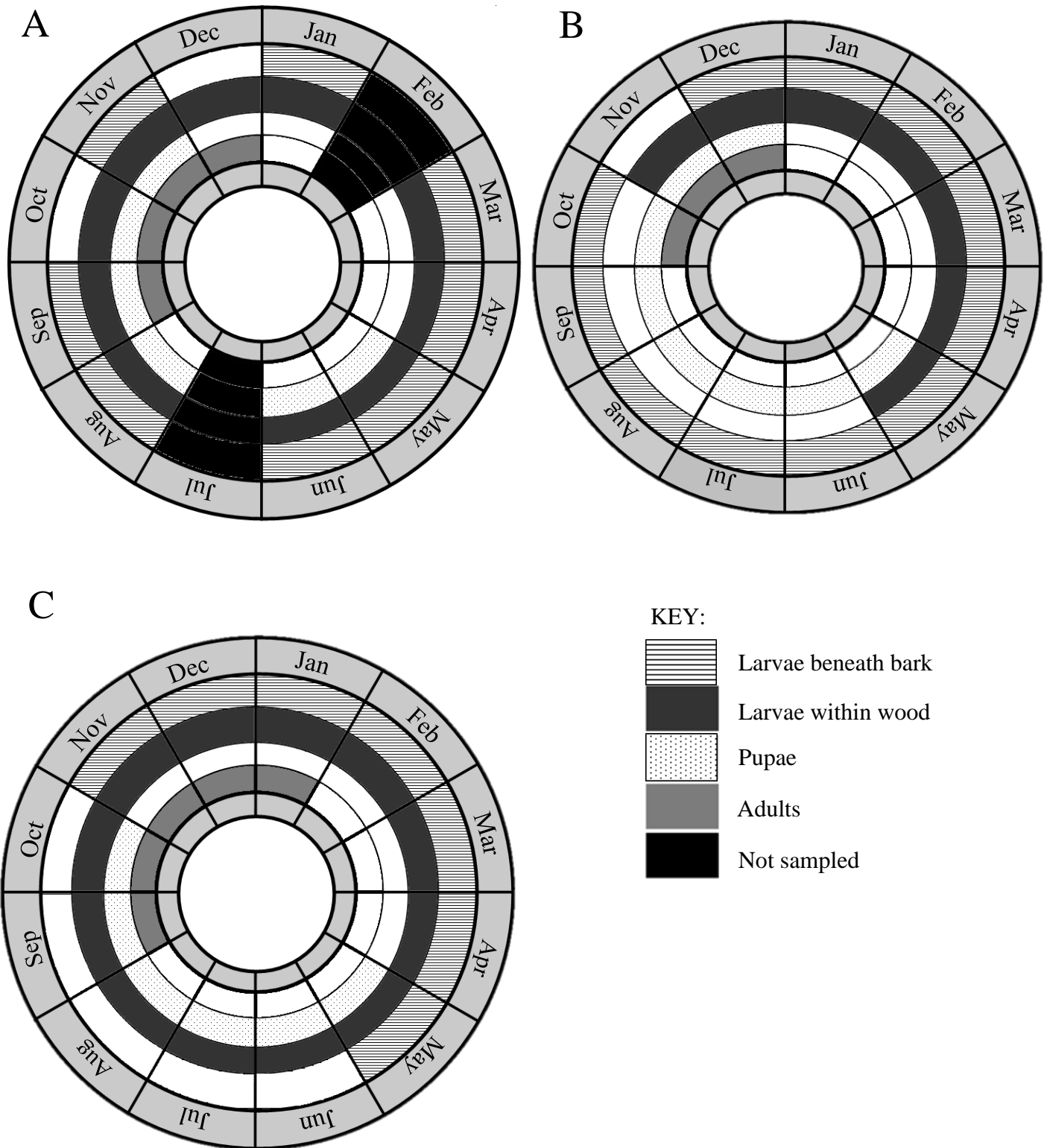
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Figure 2. Seasonal occurrence of the immature and mature stages of *C. tristis* (Lepidoptera: Cossidae) infesting A) *E. nitens* in the Mpumalanga Highveld during 2016-2018 (current study); B) quince trees in the Western Cape during 1917 (Petthey 1917); C) vines in the Western Cape during 1988-1989 (Höppner 1991).

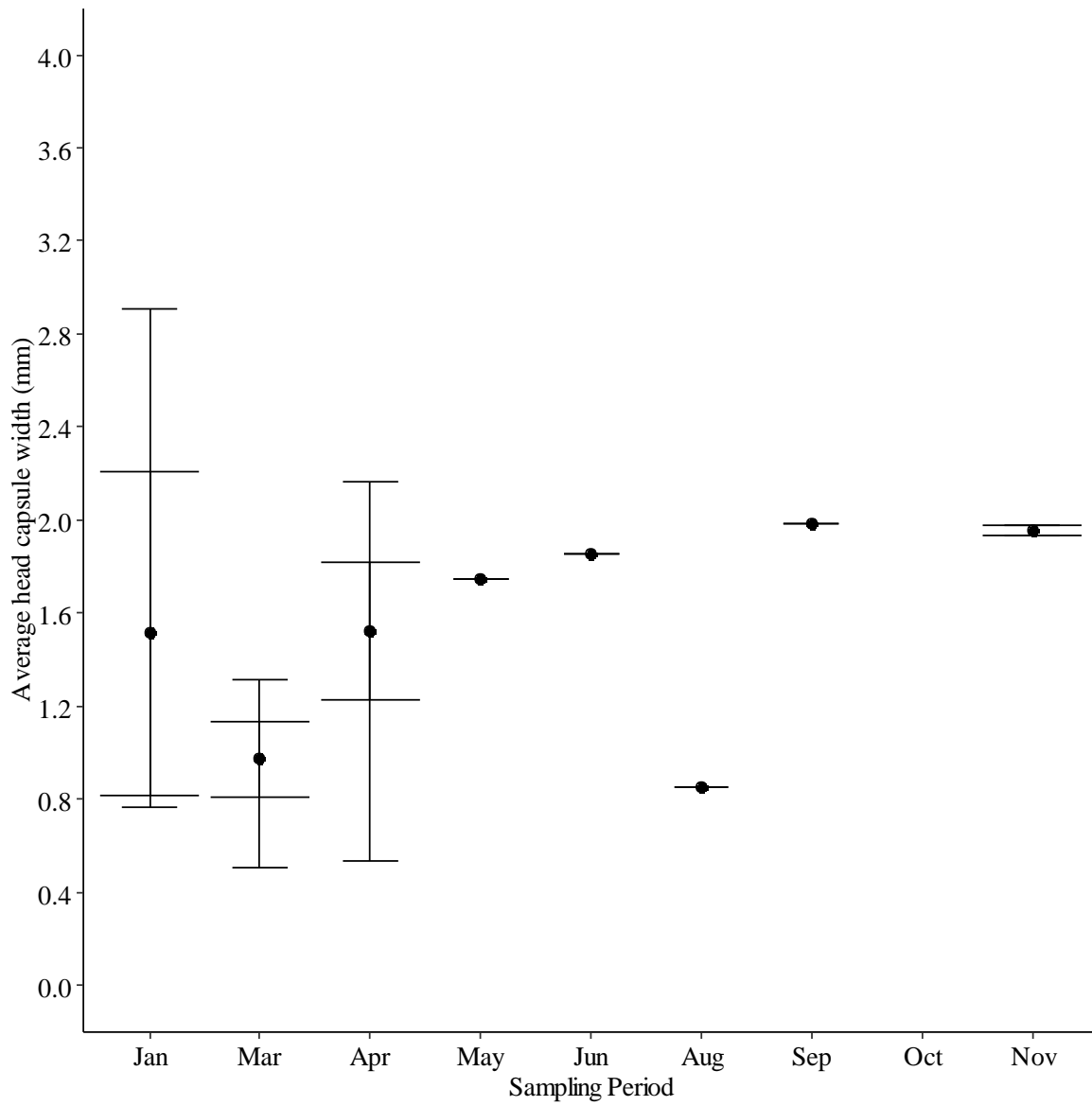
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Figure 3a. Box plot showing mean head capsule widths of *C. tristis* larvae feeding underneath the bark collected from *E. nitens* trees measured over time as an indicator of seasonal development. The mean head capsule width for each month is indicated by a black circle, the maximum and minimum head capsule width for each month is indicated by the shorter horizontal bars and the standard error for each month is indicated by the longer horizontal bars.

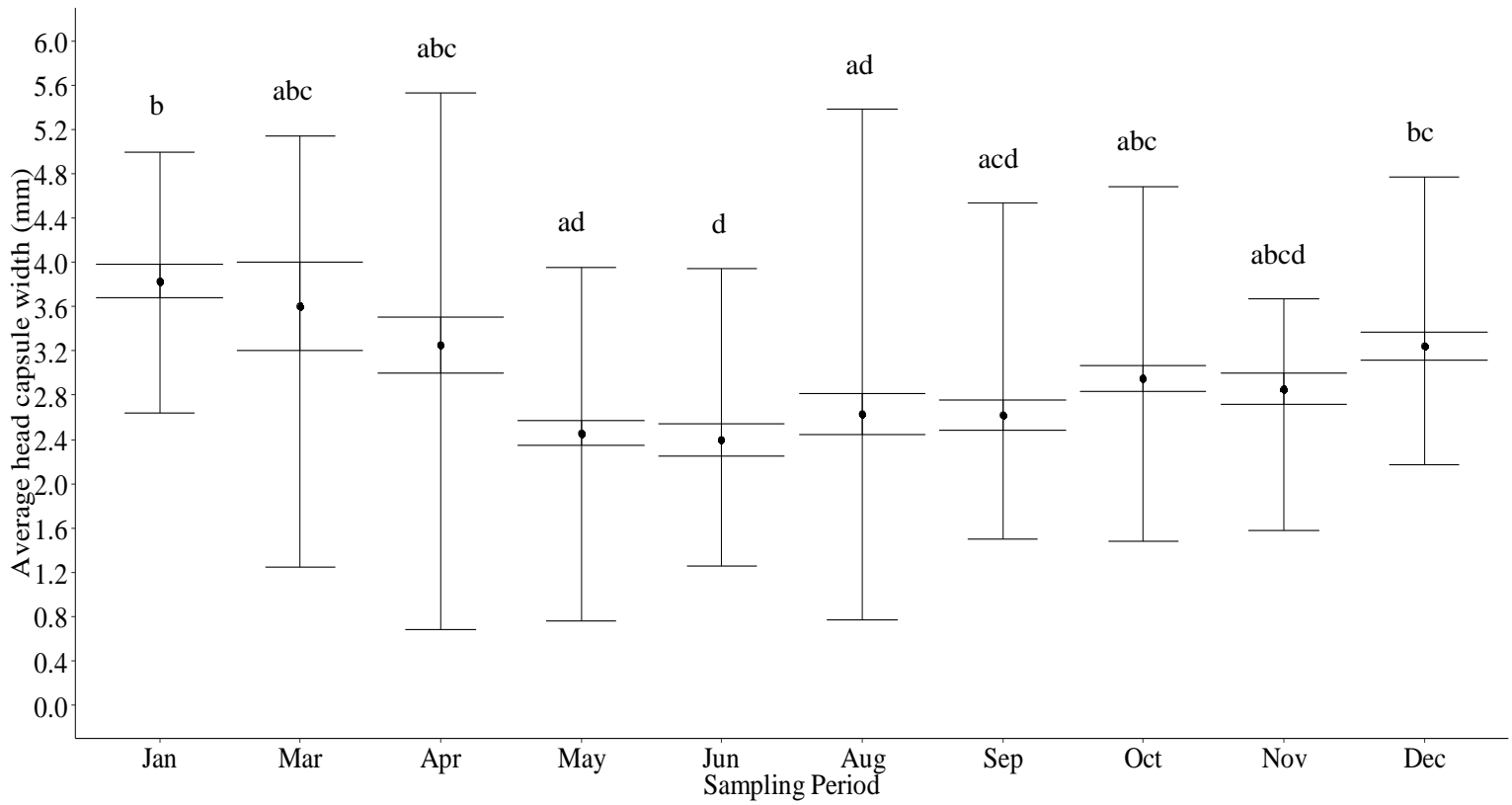
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Figure 3b. Box plot showing mean head capsule widths of *C. tristis* larvae feeding within the wood collected from *E. nitens* trees measured over time as an indicator of seasonal development. The mean head capsule width for each month is indicated by a black circle, the maximum and minimum head capsule width for each month is indicated by the shorter horizontal bars and the standard error for each month is indicated by the longer horizontal bars. Alphabetical letters indicate significant differences between months.

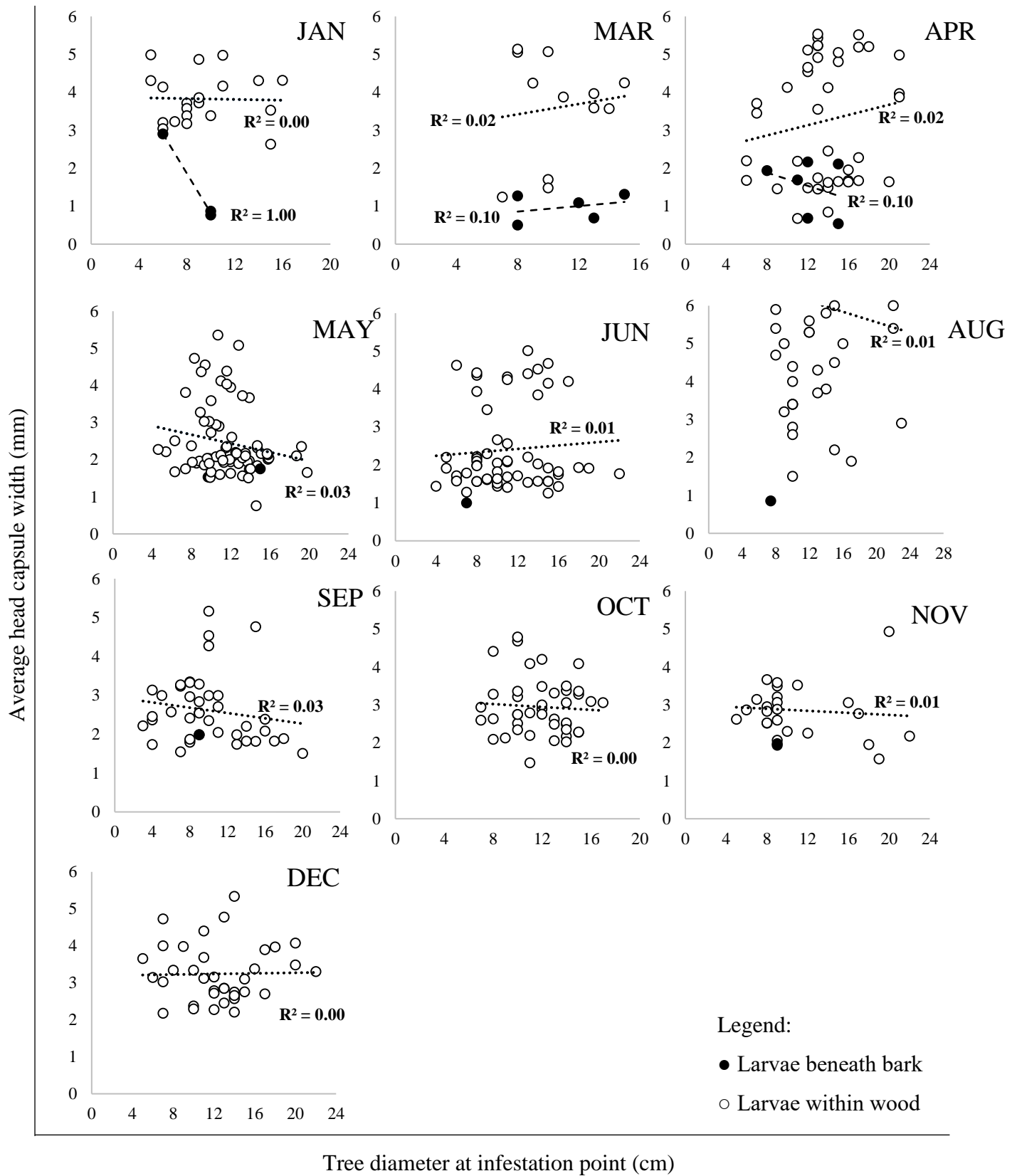
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Figure 4. Mean head capsule size of *C. tristis* larvae collected from felled *E. nitens* trees correlated against tree diameter at each infestation point from January to December.

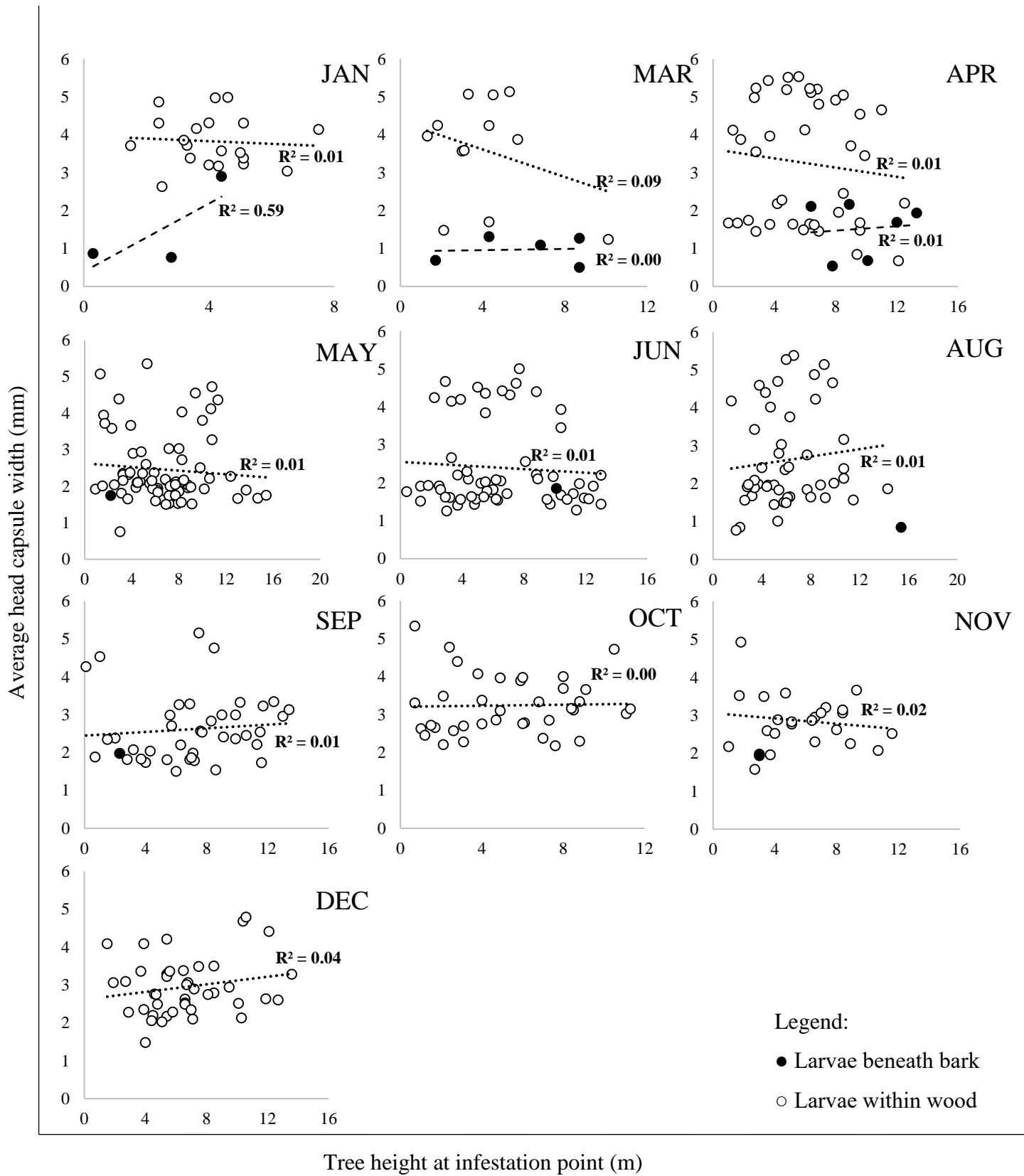
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Figure 5. Mean head capsule size of *C. tristis* larvae collected from felled *E. nitens* trees correlated against tree height at each infestation point from January to December.

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CHAPTER 3

**Optimising trap density for the mass trapping of
Coryphodema tristis Drury, a native wood-boring
moth on commercial *Eucalyptus nitens* plantations**

CHAPTER 3: OPTIMISING TRAP DENSITY FOR THE MASS TRAPPING OF *CORYPHODEMA TRISTIS* DRURY, A NATIVE WOOD-BORING MOTH ON COMMERCIAL *EUCALYPTUS NITENS* PLANTATIONS

3.1 ABSTRACT

Coryphodema tristis (Drury, 1782) (Lepidoptera: Cossidae) is a native wood-boring moth that was first reported infesting *Eucalyptus nitens* plantations on the Mpumalanga Highveld in 2004. It has since had a significant economic impact on the forestry industry. Early management efforts included the felling of over-aged *E. nitens* stands and avoiding off-site plantings. Recently, a sex pheromone for *C. tristis* was developed that has the potential to be used in control strategies. In this study, we investigated the optimal trap density for mass trapping of *C. tristis* in *E. nitens* stands using this pheromone in lure-based traps. Two trap spacing trials were implemented at the same site on the Mpumalanga Highveld in 2016 and 2017 to investigate six different trap spacing treatments. During 2016, the trap spacing treatments considered spacing of 10 m, 20 m and 40 m between traps (100 traps/ha, 25 traps/ha and 6.25 traps/ ha, respectively). In 2017, the trap spacing treatments considered spacing of 30 m, 50 m and 60 m between traps (11.1 traps/ha, 4 traps/ha and 2.78 traps/ ha, respectively). Significant differences existed between mean annual moth captures for 2016 and 2017, with more moths captured in 2017. No significant differences existed in mean moth captures per trap between the three trap spacing treatments in either 2016 or 2017. Total estimated captures per hectare was the highest for the higher trap spacing treatments in each year (10 m and 30 m for 2016 and 2017, respectively), compared to the lower trap spacing treatments. Results from this study suggest that trapping programmes at a smaller scale (i.e. for monitoring) could consider lower trap densities without sacrificing on the number of moth captures per trap, while saving on the cost of the trapping programme. Larger scale trapping programmes will need to strike a balance between trap density, impact of the programme and cost of implementation.

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3.2 INTRODUCTION

Intensively managed plantation forestry is an important contributor to the South African economy, accounting for approximately 0.7% of the total GDP (Department of Agriculture Forestry and Fisheries 2016b). *Eucalyptus* is one of three major species planted in South Africa, comprising approximately 43% of the total planted area. This makes *Eucalyptus* one of the most important commodities in the country (Forestry Economics Services 2017). *Eucalyptus* as a plantation genus has become increasingly popular over the last few decades due to its favourable pulping and paper properties and its relatively short rotation length compared to other plantation species (Swain and Gardner 2003). However, *Eucalyptus* plantations in South Africa and the world are increasingly under threat from insect pests and pathogens of these trees (Wingfield et al. 2008, 2015).

Insect pests of *Eucalyptus* in South Africa consist of both native and non-native insects (Roux et al. 2012). Non-native insects feeding on *Eucalyptus* have often been accidentally introduced by trade or travel either directly or indirectly from their native range in Australasia (Wingfield et al. 2008). A number of these introduced insects have become important pests of *Eucalyptus* around the world, and the rate of introduction of these pests has increased over time. Hurley et al. (2016) stated that the rate that new insect pests of *Eucalyptus* have been reported outside their native range has increased from an average of once every 6.3 years from 1873 to 1986 to once every 1.4 years from 1986 to 2014. Some of the most serious non-native insect pests of *Eucalyptus* in South Africa include *Gonipterus* sp. 2 (first reported in 1916) (Mally 1924), *Thaumastocoris peregrinus* (first reported in 2003) (Jacobs and Naser 2005) and *Leptocybe invasa* (first reported in 2007) (Wingfield et al. 2008).

Native insects also become important pests of *Eucalyptus* planted as exotics. These include several native Lepidoptera and Coleoptera that have had significant economic impacts

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on *Eucalyptus* plantations around the world, such as *Thyriniteina arnobia* (Lepidoptera: Geometridae), *Sarsina violascens* (Lepidoptera: Noctuidae) and *Costalimaita ferruginea* (Coleoptera: Chrysomelidae) in Brazil; *Chilecomadia valdiviana* (Lepidoptera: Cossidae) in Chile; and *Mnesampela private* (Lepidoptera: Geometridae), *Paropsisterna agricola* and *P. bimaculata* (Coleoptera: Chrysomelidae) in Tasmania (Paine et al. 2011). Several theories have been developed to explain the invasion of native insects in exotic plantations. For example, phylogenetic relatedness of native trees and exotic plantations may play a role in these invasions, especially concerning polyphagous insects (Goßner et al. 2009; Branco et al. 2015). The inability of female insects to discriminate hosts may be another factor leading to the successful invasion of native insects to exotic plantations (Larsson and Ekbohm 1995). Finally, the enemy-free space present in an exotic plantation environment may facilitate these host expansion events (Jeffries and Lawton 1984; Singer et al. 2004).

Coryphodema tristis is a polyphagous wood-boring moth native to South Africa that has undergone several host expansions over the last hundred years. Native host families include Combretaceae, Malvaceae, Myoporaceae, Myrtaceae, Rosaceae, Scrophulariaceae, Ulmaceae and Vitaceae (Gebeyehu et al. 2005). Its first report as a pest was on quince in 1917 in the Cape region (Petty 1917) and later on vineyards in the same region (Höppner 1991). In 2004, *C. tristis* was reported for the first time on *Eucalyptus nitens* in commercial plantations in Mpumalanga province (Gebeyehu et al. 2005; Boreham 2006). Within ten years *C. tristis* has caused extensive losses in these *E. nitens* plantations, sparking concern over the continued viability of this *Eucalyptus* species (Boreham 2006). *Eucalyptus nitens* is a particularly valued species, as it is one of four cold-tolerant species capable of survival in areas with low mean annual temperatures and is also tolerant to heavy snowfall and frost (Swain and Gardner 2003). Extensive losses of *E. nitens* from *C. tristis* infestations have led to its replacement in some areas by species such as *E. macarthurii* and *E. benthamii* (J. Crous, pers comm.).

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however, do not exhibit the same snow tolerance as *E. nitens* (Swain and Gardner 2003), nor are their pulping and paper properties as favourable (J. Crous, pers comm.).

Effective management of *C. tristis* has been challenging as biological control has been unsuccessful to date, since natural enemies of *C. tristis* have not been reported in the new environment (*E. nitens* plantations) and efforts to find natural enemies on native hosts have, to date, been unsuccessful. Some progress was made to introduce cultural (silvicultural) management, with Boreham's (2006) observations that infestations were significantly worse on over-aged trees and off-site plantings, resulting in the recommendation of felling over-aged plantations and avoiding off-site plantings. However, infestations were later recorded on younger trees and on more productive sites, limiting the use of these tactics (J. Crous, pers comm.).

The use of insecticides to manage *C. tristis* has limitations. Since the larvae of *C. tristis* spend a considerable part of their life cycle boring within the wood and the adult moths do not feed, the application of foliar and contact insecticides is not feasible. The application of systemic insecticides through trunk injections or soil drenches may prove useful (Poland et al. 2006; Goulson 2013; Liebhold et al. 2016). However, these insecticides have many broad-spectrum non-target effects, such as the contamination of ground and surface water, and can remain in the environment for a considerable amount of time, leading to accumulation of these insecticides in the food chain (Pimentel 1995; Goulson 2013). In addition, systemic insecticides are transported throughout the tree, where they pose health risks to other insects in the environment, especially those insects depending on nectar and pollen (Goulson 2013). Finally, the translocation of systemic insecticides throughout the tree is unpredictable due to variability in sap flow which is influenced by season and rainfall, and this, in combination with the often asynchronous development of the larvae of wood-borers, may result in many larvae escaping treatment (Hajek and Bauer 2007).

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The most promising development to manage *C. tristis* has been the use of behavioural control through mass trapping. Insect pheromones are often used in lure-based traps to monitor insect populations, but can also be used in control methods such as mass trapping and mating disruption (El-Sayed et al. 2006). However, the application of lure-based traps in a mass trapping programme requires development and optimisation of the pheromone blend, and an understanding of optimal trap density (El-Sayed et al. 2006). Following the successful development of a synthetic sex pheromone for *C. tristis* (Bouwer et al. 2015) and its later optimisation for commercial use in management strategies (Bouwer et al. 2017), a local forestry company deployed 5,802 bucket funnel traps baited with the synthetic sex pheromone across roughly 1,600 ha of *E. nitens* plantations (Verleur et al. 2017, unpublished manuscript). Results from this mass trapping programme were positive, with 22,423 male moths captured over a four-month trapping period (Verleur et al. 2017, unpublished manuscript), but optimisation of trap density is required to increase the efficacy and feasibility of future efforts.

In this study, we aimed to optimise the use of mass trapping of *C. tristis* in *E. nitens* stands using lure-based traps. We compared trap catches between six different trap spacing treatments. Data from these trials were used to determine optimal trap density for the trapping of *C. tristis*, considering the average number of adults captured per trap, the total estimated captures per hectare and potential cost-effectiveness.

3.3 MATERIALS AND METHODS

3.3.1 Experimental Site

Two trials were implemented on the same site in Rooihooigte plantation near Carolina on the Mpumalanga Highveld, South Africa (26°08'39"S 30°23'23"E), but in consecutive years (2016 and 2017) to investigate optimal trap density for the mass trapping of *C. tristis* (Figure

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1). The site was planted to *E. nitens* and was selected based on age of trees and the presence of *C. tristis* infestation. The selected site was planted in December 2008 and was thus approximately 7.8 years old at the start of the trial in 2016. The age of the trees was suitable for the trial, as *C. tristis* infestations start as early as when trees are around four years old, and re-infestation of the same trees in subsequent years has been observed (Boreham 2010, unpublished manuscript). The site was 41.60 ha with 18% of the trees infested by *C. tristis*, according to enumeration data supplied by the forestry company.

3.3.2 Trial design and experimental procedure

Trapping of *C. tristis* took place during the flight season from October to November in 2016 and 2017. Cross-vane bucket funnel traps were used (Figure 2 A), as these had proved successful in trapping *C. tristis* in previous trials (Bouwer et al. 2015). Traps were baited with the sex pheromone lure, consisting of a 95:2.5:2.5 volumetric blend of Z9-14:OAc, Z9-14:OH, and 14:OAc loaded into pheromone permeation devices (Bouwer et al. 2015) (Figure 2 B, C). The release rate of the pheromone varies with temperature, but generally has a release rate of 9 ng/h at 20°C to 570 ng/h at 32°C for the major component (Z9-14:OAc) (Bouwer et al. 2015). Traps were hung at a height of approximately 3–4 m (Figure 2 D) to prevent traps from being stolen or interfered with by animal activity.

A total of six different trap spacing treatments were investigated over the two-year period (Figure 3). The three trap spacing treatments tested in 2016 considered spacing of 10 m, 20 m and 40 m between traps (100 traps/ha, 25 traps/ha and 6.25 traps/ha respectively). The three trap spacing treatments tested in 2017 considered spacing of 30 m, 50 m and 60 m between traps (11.1 traps/ha, 4 traps/ha and 2.78 traps/ha respectively). Twelve traps were used for each trap spacing treatment in a block of 3 x 4 traps. The trap spacing blocks were separated by 50 m. The group of three trap spacing treatment blocks was repeated four times in the stand

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with a distance of 100 m between each replication. There were thus 48 traps per trap spacing treatment, with a total of 288 traps for all the treatments over the two-year period. Traps were serviced once a month over a period of two months. The total number of moths per trap was counted, recorded and removed at each service period. Only male moths were counted, as the lure is based on the female sex pheromone and any captures of female moths was considered incidental. Pheromone baits were not replaced during the course of the trial due to the sufficient longevity of the pheromone attractant (M. Bouwer, pers. comm.).

3.3.3 Data Analysis

Data were analysed for normality using Shapiro's test, as well as for homogeneity of variance using the Fligner-Killeen test. Negative results were obtained for both instances. A non-parametric test, Kruskal-Wallis, was subsequently used to compare mean male moth trap captures per trap between positions (edge versus inner traps), year (2016 and 2017) and trap spacing treatments. The area (ha) for each trap spacing block was determined based on the length and breadth of the trap spacing treatment block and used to calculate the total estimated captures per hectare (Equation 1). Data from all four repetitions and both collection periods in the year were included in all the statistical analyses. Significant differences between means were compared using Dunn's test. All statistical analyses were done in R (R Core Team 2017).

Equation (1) calculates the total estimated male moth captures per hectare:

$$\text{Total estimated captures per hectare} = 1 / \frac{L \times B}{10000} \times T \times \bar{n}_x \quad \text{Equation (1)}$$

where,

L= length of treatment block

T= total number of traps in treatment block (12)

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B= breadth of treatment block

\bar{n}_x = mean number of moth captures for treatment
block x

3.4 RESULTS

A total of 3,982 moths were collected during the two-year study, with 1,076 moths collected from the three trap spacing treatments in 2016 and 2,906 collected from the three trap spacing treatments in 2017. No significant differences existed between the edge traps and inner traps for the 30 m ($\chi^2(1) = 0.28$; $p = 0.59$), 40 m ($\chi^2(1) = 0.39$; $p = 0.53$), 50 m ($\chi^2(1) = 0.01$; $p = 0.74$), and 60 m ($\chi^2(1) = 1.12$; $p = 0.29$) trap spacing treatments, while significant differences existed between the edge traps and inner traps for the 10 m ($\chi^2(1) = 6.50$; $p < 0.05$) and 20 m ($\chi^2(1) = 10.64$; $p < 0.05$) trap spacing treatments. Since only two of the six trap spacing treatments showed significant differences between edge traps and inner traps, the edge effect present in these trials was considered negligible. Data from all 12 traps for each trap spacing block were therefore used in all subsequent analyses, as opposed to only the inner traps.

Significant differences existed in annual moth captures ($\chi^2(1) = 108.92$; $p < 0.001$), where the trap spacing treatments in 2017 ($\bar{x} = 10.09 \pm 14.96$; $n = 2,906$) captured more moths than the trap spacing treatments in 2016 ($\bar{x} = 3.74 \pm 8.98$; $n = 1,076$). Further analyses were subsequently analysed per year, since the year had a significant influence on moth captures. Considering the total moth captures, the 30 m treatment captured the most moths ($n = 1,026$; $s.e = 1.395$), followed by the 50 m ($n = 951$; $s.e. = 1.019$), 60 m ($n = 929$; $s.e. = 2.012$), 10 m ($n = 427$; $s.e. = 1.376$), 40 m ($n = 382$; $s.e. = 0.633$) and the 20 m treatments ($n = 267$; $s.e. = 0.477$) (Figure 4).

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In 2016, there was no significant difference in moth captures per trap between the trap spacing treatments ($\chi^2(2) = 2.92$; $p = 0.23$), with a mean rank of 146.21, 133.79 and 153.50 for the 10 m, 20 m, 40 m trap spacing treatments, respectively. Mean moth capture per trap in 2016 was the highest for the 10 m ($\bar{x} = 4.45 \pm 13.48$), followed by the 40 m ($\bar{x} = 3.98 \pm 6.21$) and 20 m ($\bar{x} = 2.78 \pm 4.67$) trap spacing treatments (Figure 5 A). Total estimated captures per hectare in 2016 was the highest for the 10 m ($n = 889.58$), followed by the 20 m ($n = 139.06$) and 40 m ($n = 49.74$) trap spacing treatments (Figure 5 B).

In 2017, there was no significant difference in moth captures per trap between the trap spacing treatments ($\chi^2(2) = 6.08$; $p = 0.05$), with a mean rank of 153.68, 152.38 and 127.44 for the 30 m, 50 m and 60 m trap spacing treatments, respectively. Mean moth captures per trap in 2017 was the highest for the 30 m ($\bar{x} = 10.69 \pm 13.67$), followed by the 50 m ($\bar{x} = 9.91 \pm 9.99$) and 60 m ($\bar{x} = 9.68 \pm 19.72$) trap spacing treatments (Figure 5 C). Total estimated captures per hectare in 2017 was the highest for the 30 m ($n = 237.50$), followed by the 50 m ($n = 79.25$) and 60 m ($n = 53.76$) trap spacing treatments (Figure 5 D).

3.5 DISCUSSION

In this study, we investigated six different trap spacings to determine the optimal trap density for the mass trapping of *C. tristis*. An edge effect was present for only two of the six trap spacing treatments, and while there were no significant differences in the mean number of moths captured per trap between trap spacing treatments, the total estimated captures per hectare was the highest for the higher trap spacing treatments. Our results indicate that trap spacing and density is not a major factor to consider with a small trapping area (i.e. monitoring trials or infestations restricted to only a few sites). However, trap spacing and density become

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important financial factors to consider when implementing a trapping programme on a larger scale (i.e. mass trapping programmes or widespread infestations on several sites).

The total number of male moths captured was significantly higher during the 2017 trapping season, compared to the 2016 trapping season. This may have been due to the harvesting of two older, heavily infested *E. nitens* compartments adjacent to the study site during October and November 2017. These two compartments, along with the study site, were the only *E. nitens* compartments in the vicinity. Adult moths emerging from the harvested compartments could therefore be expected to infest trees in the study site, since the pupae already developing within the wood will continue to develop regardless of whether trees are live or harvested. The presence of pheromone baited traps might even have aided in directing the moths to the study site, resulting in the high number of male moths captures observed during 2017. Another explanation is that the emerging population in 2017 may have been greater than that in 2016. The host expansion of *C. tristis* into *E. nitens* plantations may have happened more than once in consecutive years, resulting in successive invasions, with the presence of a one or more-year lag in adult emergence between populations.

The number of male moths captured differed significantly between edge traps and inner traps for the 10 m and 20 m trap spacing treatments, but not for the other four trap spacing treatments (30 m, 40 m, 50 m and 60 m spacing). The results from this study are possibly due to differences in the distance of the traps from the edge of the compartment between the six trap spacing treatments investigated: all 12 traps for each block of the low trap spacing treatments (10 m and 20 m) were within 60 m of the compartment edge, where the edge effects of insect invasions have generally been found to be more pronounced (El-Sayed et al. 2006). Traps from the other four trap spacing treatments were spaced further into the compartment, up to 180 m for the 60 m trap spacing treatment, and thus may have been influenced less by any possible edge effects present.

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The mean number of adult males captured per trap did not differ significantly between trap spacing treatments for both trapping seasons, even though the lowest trap spacing treatments for both years (10 m and 30 m trap spacing treatments for 2016 and 2017 respectively) captured the highest mean number of adults per trap. The higher trap spacing (lower density) treatments were expected to capture significantly more moths per trap compared to the lower trap spacing (higher density) treatments, since interference could occur between trap active areas where the trap density is higher, thus reducing the amount of moths captured per trap (Wall and Perry 1978; El-Sayed et al. 2006). In addition, the area covered by the lower trap spacing treatments would be smaller compared to the higher trap spacing treatments, resulting in less area covered to attract moths from infested trees. Other studies generally found that trap density treatments in the vicinity of 10 traps per hectare (≈ 30 m spacing) performed the best. Twelve traps per hectare (≈ 28 m spacing) were recommended for the control of *S. myopaeformis* (Lepidoptera: Sesiidae) (Trematerra 1993), while 10 traps per hectare were recommended for the control of *Cossus cossus* (Lepidoptera: Cossidae) (Faccioli et al. 1993) and 5–10 traps per hectare (≈ 45 –30 m spacing) were recommended for the control of *Zeuzera pyrina* (Lepidoptera: Cossidae) and *C. cossus* (Pasqualini and Natale 1999).

Several factors that influence the trap catch have been identified in the literature, but one of the most important factors to consider is inter-trap interference. According to Wall and Perry (1978), inter-trap interference occurs when the effective attraction radius (EAR) of the pheromone blend (defined as the radius of a passive trap that would capture the same amount of insects as trap baited with a sex pheromone (Byers et al. 1989) is larger than the spacing between traps. Information available on quantitative estimates for the EAR is scarce; however, the EAR for some Lepidoptera has been estimated to be between 200–400 m (Schlyter 1992). Wall and Perry (1987) estimated a range of attraction for the pea moth (*Cydia nigricana*, Lepidoptera: Tortricidae) of at least 200 m, whereas Kishaba et al. (1970) estimated an

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attraction range of up to 400 m for *Trichoplusia ni* (Lepidoptera: Noctuidae) and Karandinos (Karandinos 1974) recovered male *Synanthedon pictipes* (Lepidoptera: Sesiidae) from up to 800 m. Greater distances of up to 1.6 km have been recorded for some giant saturniid moths (*Callosamia promethea* and *Hyalophora cecropia*) (Lepidoptera: Saturniidae) (Rau and Rau 1929) and 1.2 km for *Lasiocampa quercus* subsp. *callunae* (Lepidoptera: Lasiocampidae) (Kettlewell 1961).

Presently, the EAR for the sex pheromone blend of *C. tristis* is unknown, but it might be hundreds of metres, as opposed to tens of metres, considering that most of the Lepidoptera for which EAR have been estimated range from several hundred metres to a kilometre or more. It is possible that inter-trap interference occurred between all the different trap density treatment blocks and may explain why no significant differences were observed between the treatments. It is also possible that, at the higher trap density treatments, “false trail following” occurred due to the potency of the pheromone blend in a relatively small space, leading to a diminished amount of captures as males are unable to pinpoint the source of the attraction (Yamanaka et al. 2001). Further studies should investigate the EAR of *C. tristis* by testing moth catches at large distances between traps. Understanding the EAR for *C. tristis* would allow more optimal spacing of traps with no inter-trap interference and thus higher moth catches per trap.

The results from this study indicated that trap density was not an important factor influencing the number of *C. tristis* moths caught per trap, at least within the trap densities tested in this study (between 10 m and 60 m spacing). As there were no significant differences in moth captures per trap between the trap density treatments, the higher trap density treatments would catch substantially more moths per hectare, as these treatments would include more traps per hectare. This was shown to be theoretically true from our total estimated captures per

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hectare, where the higher trap density treatments in each year (10 m in 2016 and 30 m in 2017) captured more moths than the lower trap density treatments.

The relevance of trap density will be related to the specific objective of the trapping and costs of implementation. With a set number of traps available, the total moths caught would not be significantly different whether the traps were placed at low or high density. Using a high trap density over a smaller area would be a preferred strategy to catch high numbers of moths in a small area, for example a specific compartment with a high infestation. This approach may also be more cost-effective than spreading the traps over a large area, due to less time and thus cost to set up and monitor the traps in a smaller area. Using a low trap density would be a preferred approach when infestations are widespread and thus a greater area needs to be covered by the traps.

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3.6 TABLES AND FIGURES

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Figure 1. Sample site on the Mpumalanga Highveld where two trap spacing trials were implemented during 2016 and 2017 within a stand of *E. nitens* infested with *C. tristis*.

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Figure 2. Cross-vane bucket funnel traps baited with conspecific sex pheromones of *C. tristis*:

A) cross-vane bucket funnel trap showing the position of the lure holder; B) lure holders used in the cross-vane bucket funnel traps; C) pheromone permeation device, showing the glass connector into which the pheromone is loaded; D) cross-vane bucket funnel trap mounted on a tree at a height of approximately 4 m, using a shelf bracket and cable ties.

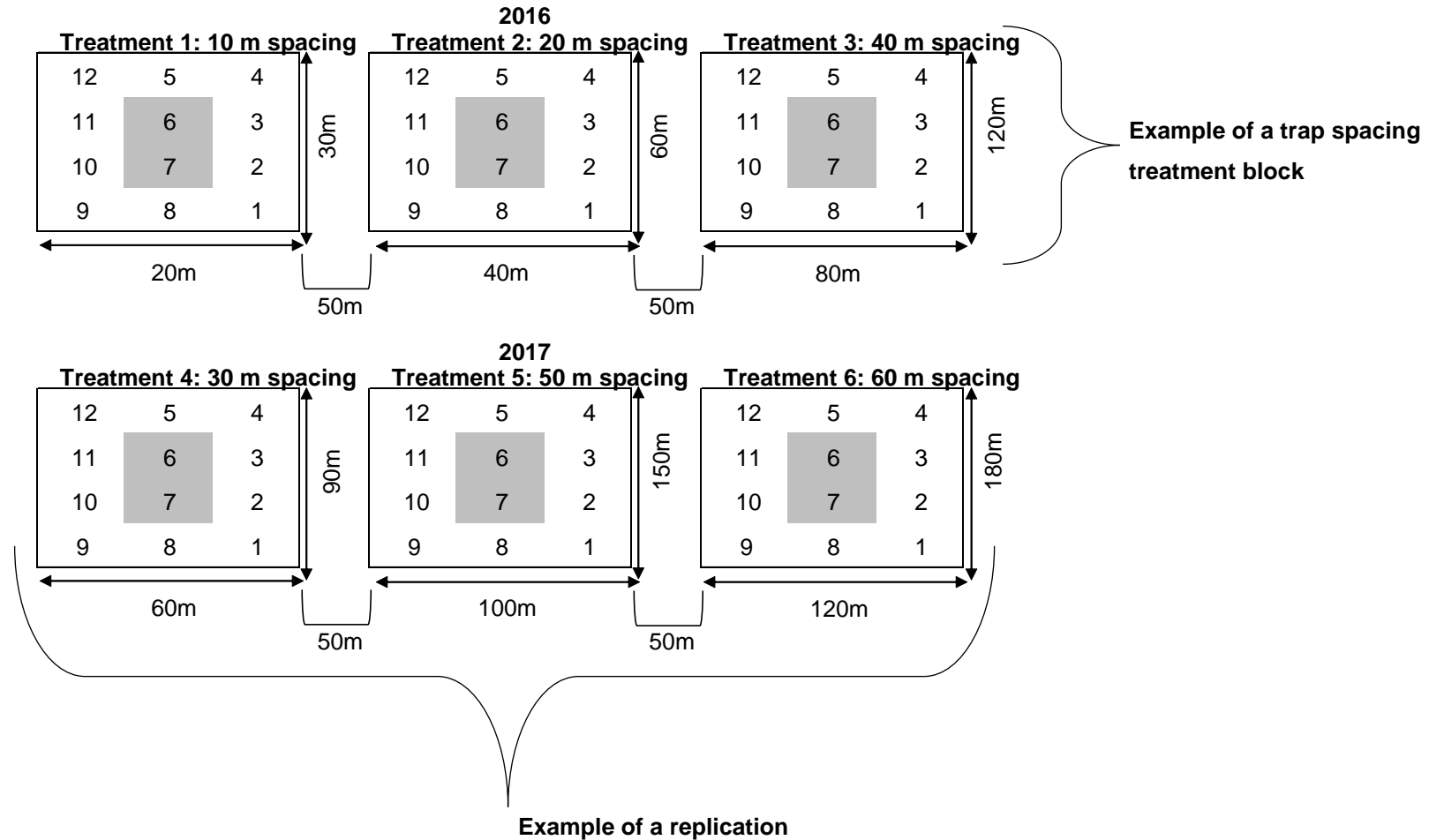
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Figure 3. Layout of trials implemented during 2016 and 2017, showing one replication each. Three trap spacing treatment blocks were compared in 2016 and three different trap spacing treatment blocks were compared in 2017. There were 12 traps per treatment block. Distances between treatment blocks and the width and breadth of each treatment block are indicated. Greyed trap positions indicate inner traps, and the other trap positions indicate edge traps.

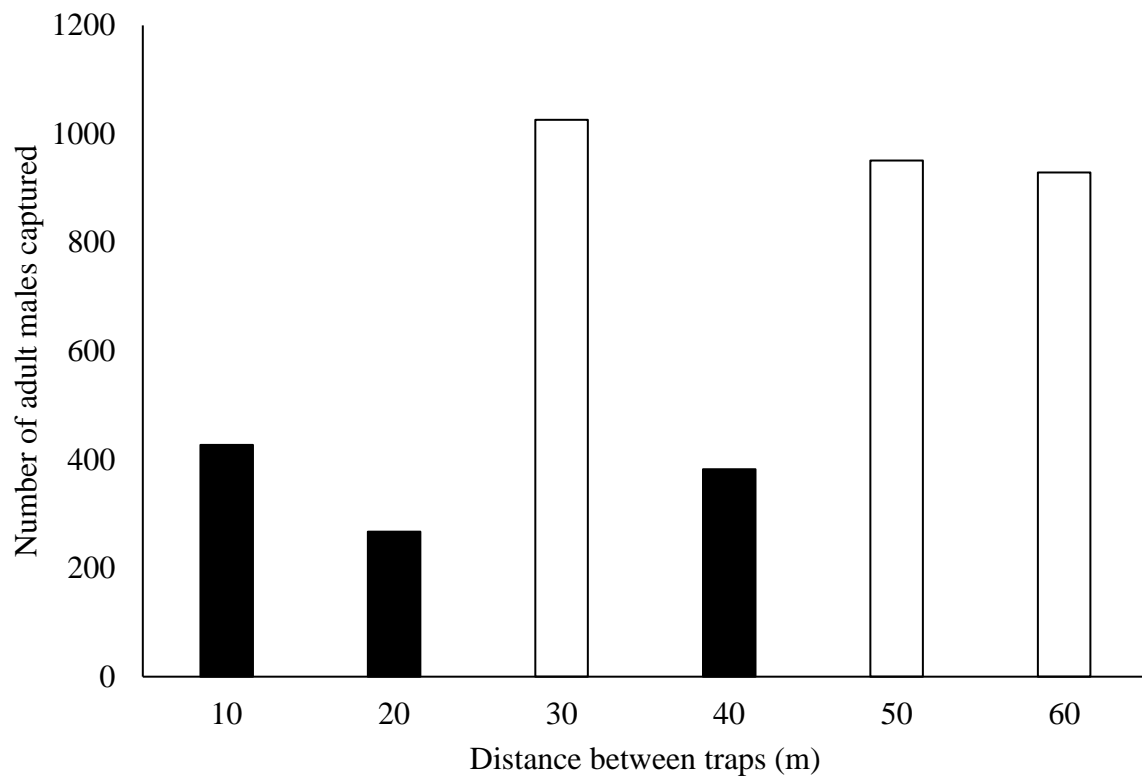
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Figure 4. Total number of *C. tristis* adult males captured for each trap spacing treatment. Black bars indicate moth captures in the 2016 trial and white bars indicate moth captures in the 2017 trial.

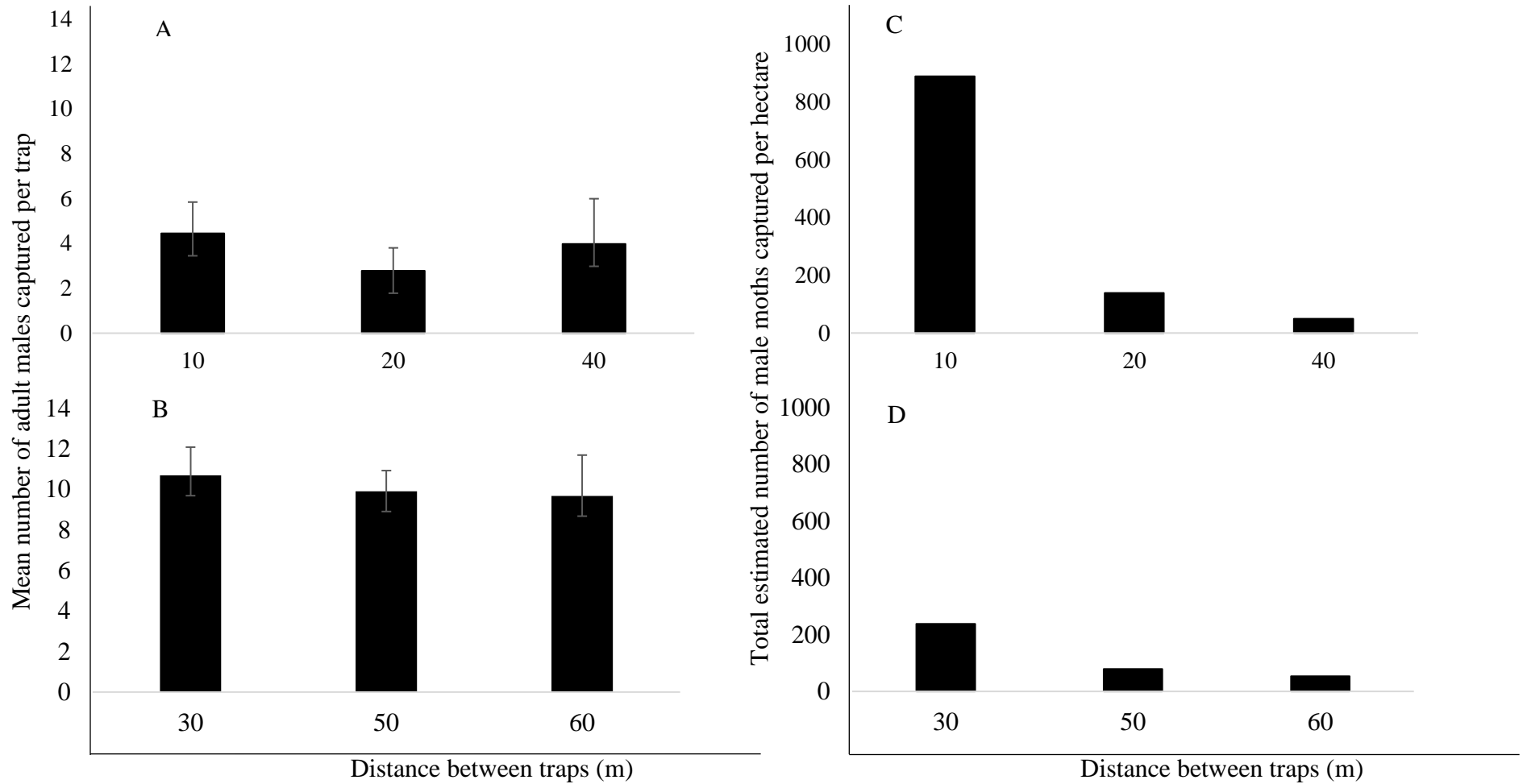
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Figure 5. Mean number of *C. tristis* adult males captured per trap for each trap spacing treatment during 2016 (A) and 2017 (B), and total estimated number of *C. tristis* adult males captured per hectare for each trap spacing treatment during 2016 (C) and 2017 (D). Standard error bars are indicated on figures 5 A and 5 B.

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CHAPTER 4

GENERAL DISCUSSION AND CONCLUSIONS

In this dissertation, the recent association of the cossid moth, *Coryphodema tristis*, on *Eucalyptus nitens* in the Mpumalanga Highveld of South Africa was investigated. Studies investigating the biology and ecology of the cossid moth have previously focused on its host associations with agricultural crops in the Western Cape. Little information is available on its new host association with *E. nitens*, especially regarding the seasonal development of the immature stages and the flight season(s) of the adult moths. Effective management of this wood-boring pest necessitated knowledge of its biological and ecological characteristics in its novel environment.

In the first research chapter the seasonal development and occurrence of *C. tristis* on *E. nitens* was investigated and compared the findings to previously published results from studies of the cossid moth on quince and grape vines in the Western Cape. Results showed that there were no major differences in the development and seasonal occurrence of *C. tristis* between the two regions and no additional flight seasons were detected for the adult moths. Further, tree size and position of the infestation on the tree did not influence larval development or phenology.

The second research chapter investigated the optimisation of the management of *C. tristis* using behavioural control tactics. Results indicate that the trap densities used in this study were not an important factor influencing the number of *C. tristis* males captured per trap. Rather, the relevance of trap density will depend on the specific objective/s of the trapping programme, as well as the costs of implementation.

This study showed the ability of *C. tristis* to deal with variation in host nutrition, specifically nitrogen content, and environmental differences without compromising on development. The results also indicate that higher trapping densities would be more effective to catch high numbers of moths in a smaller area, while lower trap densities would be more

effective where the area of infestation is widespread, and trapping would thus be required over a larger area. These findings have important implications for management of this insect pest in *E. nitens* plantations.

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