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Infestation Density of Eucalyptus Gall Wasp, *Leptocybe invasa* Fisher and La Salle (Hymenoptera: Eulophidae) on Five Commercially Grown *Eucalyptus* Species in Tanzania

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This study explores infestation density of Leptocybe invasa *on five commercially grown* Eucalyptus *species in Coastal, Plateaux, and Southern Highlands agroecological zones of Tanzania. Infestation density between agroecological zones,* Eucalyptus *species, age classes and tree crown parts, relationship between stand altitudes and the magnitude of infestation, damage index, species age, and abundance of* L. invasa *on different* Eucalyptus *species were examined. There were significant differences in infestation between zones and* Eucalyptus *species.* Eucalyptus tereticornis *was more affected, followed by* E. camaldulensis*, and* E. saligna *was the least while* E. grandis *and* E. citriodora *were not affected. No significant differences in damage between different crown parts were observed. Trees with age of 1–3 yr were damaged more than those of age 4–6 yr. Pest infestation increased with an increase of* L. invasa *abundance but decreased with an increase of altitudes. Control efforts needs to focus on controlling the spread of the pest, using silvicultural methods and planting resistant* Eucalyptus *species.*

KEYWORDS incidence and severity, blue gum chalcid, Myrtaceae, agroecological zones, Tanzania

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INTRODUCTION

There are more than 800 species of *Eucalyptus* (Myrtaceae) belonging to two genera, *Eucalyptus* and *Corymbia* (Ohmart & Edwards, 1991; Ladiges, Udovicic, & Nelson, 2003). Eucalypts are the most valuable and widely planted hardwoods in the world and are estimated to be planted in more than 18 million hectares (ha) in about 90 countries (Food and Agriculture Organization of the United Nations [FAO], 2005). Eucalypts have been successful as exotics because of their capacity for fast growth and tolerance of harsh environments (Poore & Fries, 1989; Rockwood, Rudie, Ralph, Zhu, & Winandy, 2008). They are utilized for a diverse array of products including sawn timber, poles, fuelwood, pulp, fiberboard production, charcoal, essential oils, honey, and tannin as well as for shade, shelter, and soil reclamation (Eldridge, Davidson, Harwood, & van Wyk, 1993). In Tanzania, it is estimated that there are 4,665 ha of eucalypts in government plantations and an unknown area owned by the private sector and small-scale farmers (Ngaga, 2011) mainly for poles, pulp, fuelwood, timber, and fiberboard production. *Eucalyptus* species that are commonly planted in Tanzania are *E. saligna, E. grandis, E. camaldulensis, E. globules, E. viminalis, E. citriodora, E. regnas, E. microtheca, E. tereticornis, E. maidenii, E. maculata, E. botryoides, E. paniculata, E. resinifera, E. alba (urophylla)*, and *E. robusta* (Schabel, 1990; Nshubemuki, 1998). However, *E. saligna, E. grandis, E. camaldulensis, E. tereticornis*, and *E. citriodora* were widely planted in the study areas.

An outbreak of the gall-forming invasive wasp—*Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae), commonly called blue gum chalcid—is causing destruction in eucalyptus plantations throughout the world (Mendel, Protasov, Fisher, & La Sallae, 2004). The wasp lays eggs in the petiole and midrib of leaves and stems of young shoots that leads to gall formation. Gall formation by *L. invasa* damages growing shoot tips and leaves of eucalypts, resulting in quicker abscission of leaves and drying up of shoots. Severely affected eucalypts show gnarled appearance, stunted growth, lodging, die back, and sometimes tree death (Mendel et al., 2004; Nyeko, 2005; Protasov, Doganlar, La Salle, & Mendel, 2008; Kumari, Kulkarni, Vastrad, & Goud, 2010). The infestation is more severe on seedlings in the nursery and young (1–3 yr old) plantations than on older trees (Nyeko, 2005). Suitable hosts of the wasp include several *Eucalyptus* species and their hybrid clones (Mendel et al., 2004; FAO, 2009; Thu, Dell, & Burgess, 2009; Mutitu, Otieno, Nyeko, & Ngae, 2010). The wasp is native to Australia and was first reported in the Middle East in 2000 (Mutitu, 2003; Mendel et al., 2004; Thu, 2004). Currently, the wasp is reported in Africa, Asia, Pacific region, America, and Europe (Aytar, 2003; FAO, 2009).

The impact of climate change on the infestation and frequency of *L. invasa* outbreak is not clear, mostly because of lack of long-term data for analysis as it only about a decade since it was first reported. However, Menéndez (2007) reported that climate (temperature and precipitation in particular) have a very strong influence on the development, reproduction, and survival of insect pests; as a result it is highly likely that these organisms will be affected by any changes in climate. Since they are cold-blooded organisms, forest insects can respond rapidly to their climatic environment impacting directly on their development, survival, reproduction, and spread. With their short generation times, high mobility, and high reproductive rates it is also likely that they will respond more quickly to climate change than long-lived organisms, such as higher plants and mammals. Similarly, climate change, in particular increased temperature and level of atmospheric carbon dioxide as well as change in precipitation, results to stress trees due to insufficient good growing conditions (Moore & Allard, 2008). White (1984) postulated that plants stressed by nutrient deficiencies or growing on inferior sites, in general become good sources of food for invertebrate herbivores. Several studies have shown that aphid activity increases on stressed trees or growing on sites of poor quality (Mailu, Khamala, & Rose, 1978; Madoffe & Austarå, 1990; Petro, 2009) which are deficient in N-P-K, boron, and other trace elements which may result in increased aphid populations (Cowling & Bristow, 1979; Canon, 1985). The same case could be applied to *L. invasa*. This study, however, did not address the effect of climate change on infestation and frequency of *L. invasa* attack.

In Tanzania, *L. invasa* infestation was first recorded on young *E. camaldulensis, E. tereticornis*, and *E. grandis* in Tabora and Shinyanga in early 2005. Infestation was also reported in *E. grandis* clonal trial grown in Kibaha, Pwani Region and Mombo and Korogwe in Tanga Region (Petro, 2009). Since then, concern has been raised about the pest infestation on eucalypts in the country. Very little has been done to avert the threats posed by *L. invasa* in Tanzania. Considering the rapid global spread of this pest and the importance of *Eucalyptus* species to individual livelihoods and national economies in the tropics, research is required on various aspects of the pest and its hosts so that sustainable management strategies could be developed. Therefore, this study aimed at determining the infestation density of *L. invasa* on five commercially grown *Eucalyptus* species in three different agroecological zones of Tanzania. This information will be useful to forest managers, plant protectionists, conservationists, researchers, and individual tree growers in the country to find ways of managing the pest.

METHODS

Study Areas

The study was conducted in three districts located in three agroecological zones of Tanzania (Table 1). Eucalypt stands which were established between 2006 and 2011 were selected for this study because of the fact

TABLE 1 Characteristics of the Three Agroecological Zones of Study Sites

Agro-ecological zone*	District sampled	Mean annual rainfall (mm) and rainy season	Mean annual temperature (°C)	Mean annual relative humidity (%)	No. stands sampled	Altitude (masl) range of stands sampled
Coastal	Kibaha	750–1,200 October–December and March–June	26–28	54–65	6	60–134
Southern Highlands	Mufindi	800–1,400 November–April	21–23	52–62	5	1,246–1,540
Plateaux	Urambo	800–1,000 November–April	23–24	61–64	3	1,078–1,101

*Classification according to De Pauw (1984).

that *L. invasa* infestation is most severe on young trees. Fourteen eucalypt stands were examined for infestation density of *L. invasa* (Table 1). The stands consisted of five *Eucalyptus* species (*E. camaldulensis, E. tereticornis, E. grandis, E. saligna*, and *E. citriodora*).

Sampling

Three out of seven agroecological zones of Tanzania were purposefully selected whereby one district from each of the selected agroecological zones was selected. The choice of study and the site was based on dominance of *Eucalyptus* species. Eucalypt trees were grouped into two age classes—i.e., young (1–3 yr) and middle age (4–6 yr). Fourteen eucalypt stands with a total of 1,536 trees were sampled for assessment of infestation density. Each selected stand was divided into one, two, or three blocks of roughly equal size depending on the size of the stand. In each block, plots with 60 trees each were randomly established on which the assessment was made. In stands of mixed *Eucalyptus* species, species with at least 30 trees were assessed. In cases where the total number of trees per species was less than 60, but at least 30 trees available, all trees of that species within the stand were assessed. Six trees were randomly selected from each of sampled plots for counting the number of *L. invasa* galls. In each of the selected trees, two shoots of 20 cm in length were cut, using a pair of scissors randomly from each of the tree crown parts (lower, middle, and upper).

Data Collection

Assessment of *L. invasa* infestation was performed using two approaches: (a) visual scoring of all trees in every plot for incidence and severity of *L.*

invasa induced galls; and (b) counting the number of *L. invasa* induced galls per 20 cm shoot length. The incidence of *L. invasa* infestation on trees was based on the absence or presence of galls induced by the pest. The gall severity was assessed visually on the whole crown foliage whereby the following subjective scales were used: (1) none (trees with no visible gall); (2) minor (trees with galls in <25% of total shoots); (3) moderate (trees with galls in 25–50% of total shoots; and (4) severe (trees with galls in >50% of total shoots. The numbers of *L. invasa* galls were counted on the cut shoots in the field. The altitude of each stand was recorded by using a global positioning system (GPS). In addition, mean annual temperature and relative humidity data were obtained from nearby weather stations.

Data Analysis

Microsoft Office Excel (Microsoft Corp., Redmond, WA, USA) was used to compute the total number of trees infested (incidence) and the number of trees in each severity class of *L. invasa* infestation per plot. Analysis of variance (ANOVA) in Minitab 16 (Minitab Inc., State College, PA, USA) statistical package was used to test the significance of the variation of the *L. invasa* infestation between agroecological zones, *Eucalyptus* species, age classes, tree crown parts, and stand altitudes. For each *Eucalyptus* species, the percentage infestation incidence (percentage of trees infested by *L. invasa*) per plot was calculated in Microsoft Office Excel and analyzed using ANOVA. The average severity (AS) per plot was calculated as described by Sharma and Sankaran (1988):

$$AS = \frac{(1 \times a) + (2 \times b) + (3 \times c) + (4 \times d)}{N},$$

where 1, 2, 3, and 4 are severity categories; a, b, c, and d are the number of trees examined in each severity category; and N is the total number of trees assessed per plot. The AS was then analyzed using ANOVA. *Leptocybe invasa* damage index in each plot was calculated as the product of the average severity and incidence (proportional of infested trees) per plot. Simple linear regression analysis was used to determine the relationship between stand altitude and the magnitude of infestation, damage index, species age, and abundance (number of galls per 20 cm shoot length) of *L. invasa* on different *Eucalyptus* species. *Leptocybe invasa* damage index per stand was subjected to regression analysis in order to explore the relationship between stand altitude, gall wasp abundance, and the magnitude of *L. invasa* infestation.

RESULTS

Infestation Density of *L. invasa* in Different Agroecological Zones

Leptocybe invasa infestation density (incidence and severity) on *Eucalyptus* species was observed in all three agroecological zones studied although at different intensities. A total of 1,536 trees was recorded from all studied zones whereby 39% each of the total trees were recorded from the Coastal and Southern Highlands and 22% from the Plateaux zones. There was a significant variation in the incidence of *L. invasa* infestation among agroecological zones on *E. camaldulensis* ($F_{2,9}$ = 25.62, p = .000) and *E. saligna* ($F_{1,4}$ = 17.21, p = .014), and significant variation in the severity of *L. invasa* infestation among agroecological zones on *E. camaldulensis* ($F_{2,9}$ = 17.10, p = .001) and *E. saligna* ($F_{1,4}$ = 29.22, p = .006; Table 2). The Plateaux zone had the highest incidence and severity of pest infestation on *E. camaldulensis* followed by the Coastal zone. The infestation density of *L. invasa* in the Southern Highlands was significantly lower on *E. camaldulensis* with an average incidence and severity of 55% and 1.8, respectively (Table 2). *Eucalyptus saligna* had significantly higher incidence and severity of *L. invasa* infestation in the Coastal than Southern Highlands zone. In the Coastal and Plateaux agroecological zones where *E. citriodora* was recorded, the incidence of *L. invasa* was found to be 0%. The proportion of trees which were severely affected (i.e., trees with more than 50% of total leaves having galls) was high in the Coastal zone followed by the Plateaux zone and the Southern Highlands zone was the least.

Infestation Density of *L. invasa* on Different *Eucalyptus* Species

Of the total 1,536 trees examined, results showed that *E. camaldulensis* formed the major part (47%), followed by *E. saligna* (23%), *E. tereticornis* (16%), *E. grandis* (8%), and *E. citriodora* (6%; Table 3). Distinct differences were observed in the incidence and severity of *L. invasa* between *Eucalyptus* species within zones. The incidence of *L. invasa* was significantly higher on *E. camaldulensis* than on all other *Eucalyptus* species in both the Coastal ($F_{3,7}$ = 238.13, p = .000) and the Southern Highlands ($F_{2,7}$ = 15.87, p = .0025) agroecological zones. In the Plateaux zone, the incidence of *L. invasa* on *E. camaldulensis* was 100%. *Eucalyptus camaldulensis* had significantly higher average severity in the Southern Highlands ($F_{2,7}$ = 9.35, p = .011) and the Plateaux ($F_{1,4}$ = 756, p = .000) than other species. In the Coastal zone, average severity was significantly higher in *E. tereticornis* ($F_{3,7}$ = 33.56, p = .000) than other species with most of the trees (more than 46% of total trees sampled) having galls in more than 50% of total shoots (Severity Class 4; Table 3). *Eucalyptus citriodora* (Coast and Plateaux) and *E. grandis* (Southern Highlands) were not affected. In the Coastal zone, *E. citriodora* was also found unaffected in the mixed farm with *E. camaldulensis* which was severely affected.

TABLE 2 Infestation Density (Incidence and Severity) of *Leptocybe invasa* in Three Agroecological Zones in Tanzania

Eucalyptus species and agroecological zones	Total samples	Incidence (%)	Average severity	Severity class (% of total sample)			
				1	2	3	4
Eucalyptus camaldulensis							
Coastal	180	97.2[a]	2.9[a]	2.8	30	32.8	34.4
Southern Highlands	240	55[b]	1.8[b]	45	35.4	10.4	9.2
Plateaux	300	100[a]	3.1[a]	0	19.7	50.7	29.7
Eucalyptus saligna							
Coastal	120	46.7[b]	1.9[b]	53.3	22.5	10	14.2
Southern Highlands	240	13.3[c]	1.2[c]	86.7	9.6	2.5	1.3
*Eucalyptus citriodora**							
Coastal	60	0	1.0	100	0	0	0
Plateaux	36	0	1.0	100	0	0	0
*Eucalyptus tereticornis**							
Coastal	240	95.8	3.1	4.2	24.2	25	46.7
*Eucalyptus grandis**							
Southern Highlands	120	0	1.0	100	0	0	0

*Statistical test not performed because of insufficient number of stands. For each incidence and average severity, values followed by the same letter within a column are not significantly different at 5% probability level.

TABLE 3 Variation in the Incidence and Severity of *Leptocybe invasa* Infestation in Different *Eucalyptus* Species in Three Agroecological Zones of Tanzania

Eucalyptus species and agroecological zones	Total samples	Incidence (%)	Average severity	Severity class (% of total sample)			
				1	2	3	4
Coastal							
Eucalyptus camaldulensis	180	97.2[a]	2.9[a]	2.8	30	32.8	34.4
Eucalyptus saligna	120	46.7[b]	1.9[b]	53.3	22.5	10	14.2
Eucalyptus citriodora	60	0.0[d]	1.0[b]	100	0.0	0.0	0.0
Eucalyptus tereticornis	240	95.8[a]	3.1[a]	4.2	24.2	25	46.7
p-value		.000	.000				
Southern Highlands							
Eucalyptus camaldulensis	240	55[b]	1.8[b]	45	35.4	10.4	9.2
Eucalyptus saligna	240	13.3[c]	1.2[c]	86.7	9.6	2.5	1.3
Eucalyptus grandis	120	0.0[c]	1.0[c]	100	0.0	0.0	0.0
p-value		.0025	.011				
Plateaux							
Eucalyptus camaldulensis	300	100*	3.1[a]	0.0	19.7	50.7	29.7
Eucalyptus citriodora	36	0.0*	1.0[d]	100	0.0	0.0	0.0
p-value			.000				

For each incidence and average severity, values followed by the same letter within a column are not significantly different at 5% probability level.

Overall mean results for the three agroecological zones showed that *E. tereticornis* (recorded only in the Coastal zone) had the highest mean incidence, severity, and damage index followed by *E. camaldulensis* and *E. saligna* was the least (Table 4).

Infestation Density of *L. invasa* in Different Tree Crown Parts

The infestation of *L. invasa* in different parts of the tree crowns differed between agroecological zones, species, and crown parts within the species. The total mean numbers of gall wasps per crown was high in *E. camaldulensis* recorded in the Coastal agroecological zone and lowest in *E. saligna* recorded in the Southern Highlands (Table 5). The lower crown parts for both *E. camaldulensis* and *E. tereticornis* in the Coast had higher total mean number of galls, followed by middle crown parts while the upper parts had the lowest total mean number of galls implying that the lower crown parts were more affected/damaged than the middle crown parts and the upper being least infested/damaged. *Eucalyptus camaldulensis* in the Plateaux agroecological zone had a higher number of galls on the upper crown, followed by the middle parts and the lower parts showing the least. *Eucalyptus saligna* and *E. camaldulensis* in the Coastal and Southern Highlands, respectively, were more affected in the middle crown parts than other parts. In spite of the differences observed in infestations, the infestation between crown parts was not significantly different for all species. There was no evidence of preference in infestation/damage for any particular level of the tree canopy.

There were no significant variations in mean number of galls per 20 cm shoot length between species in the Coastal zone ($F_{2,51} = 1.83$, $p = .171$) and in the Southern Highlands ($F_{1,46} = 3.63$, $p = .063$; Figure 1). The number of galls per shoot was higher in the Coastal zone for all species, followed by the Plateaux and then the Southern Highlands. *Eucalyptus camaldulensis* had a higher number of galls per shoot followed by *E. tereticornis* and *E. saligna* being the least while *E. citriodora* and *E. grandis* had no galls on their shoots.

TABLE 4 The Mean Incidence, Severity, and Damage Index of *Leptocybe invasa* Infestations of Five *Eucalyptus* Species in Three Agroecological Zones in Tanzania

Eucalyptus species	Incidence	Severity	Damage index
E. tereticornis	0.96^{a}	3.10^{b}	3.02^{b}
E. camaldulensis	0.84^{a}	2.65^{b}	2.37^{b}
E. saligna	0.24^{d}	1.41^{a}	0.40^{a}
E. citriodora	0.00^{d}	1.00^{a}	0.00^{a}
E. grandis	0.00^{d}	1.00^{a}	0.00^{a}
$F_{4,22}$ value	25.90	16.52	15.57
p-value	.000	.000	.000

Values followed by the same letter within a column are not significantly different at 5% probability level.

TABLE 5 Means and Standard Errors of *Leptocybe invasa* per 20 cm Shoot Length for Three Parts of Tree Crown in Three Agroecological Zones in Tanzania

	Agroecological zones					
	Coastal			Southern Highlands		Plateaux
Tree crown part	*E. camaldulensis*	*E. saligna*	*E. tereticornis*	*E. camaldulensis*	*E. saligna*	*E. camaldulensis*
Upper	43.94 ± 12.18	14.33 ± 7.34	31.21 ± 7.86	4.88 ± 2.00	0.96 ± 0.42	20.67 ± 4.28
Middle	45.67 ± 9.78	26.92 ± 1248	32.63 ± 4.46	10.83 ± 4.27	1.96 ± 0.72	17.23 ± 3.16
Lower	46.44 ± 9.58	23.42 ± 12.19	35.21 ± 5.81	9.67 ± 3.76	4.04 ± 1.29	14.80 ± 2.67
F-value	$F_{2,51} = 0.015$	$F_{2,33} = 0.353$	$F_{2,69} = 0.107$	$F_{2,69} = 0.823$	$F_{2,69} = 3.117$	$F_{2,87} = 0.737$
p-value	.9855	.7049	.8987	.4435	.0506	.4815

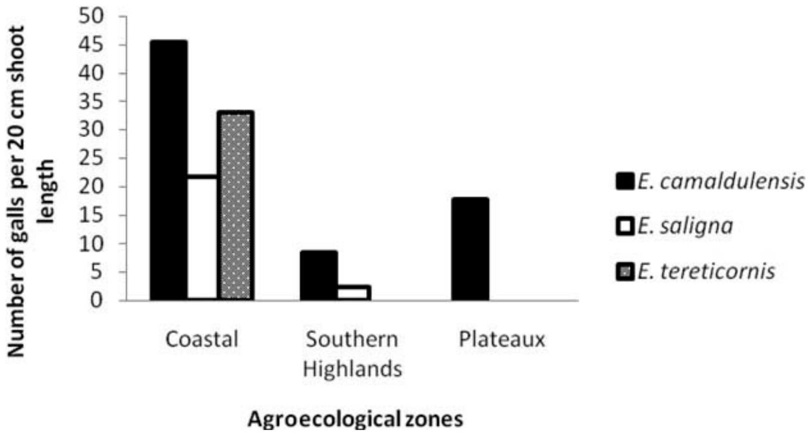

FIGURE 1 Mean number of gall wasps per 20 cm shoot length of eucalypts in three agroecological zones of Tanzania.

Variation of Gall Wasp Abundance and Infestation Between Tree Age Classes

Only *E. saligna* and *E. tereticornis* were recorded in the two age groups—i.e., young (1–3 yr) and middle (4–6 yr) while *E. camaldulensis* was recorded only on the young age group. The mean gall wasp abundance per 20 cm shoot was found to be 15.41 and 2.06 for *E. saligna* and 35.5 and 30.53 for *E. tereticornis* for the young and middle age classes, respectively. However, there were no significant differences observed in mean gall wasp abundances between young and middle age classes in both *E. saligna* ($F_{1,34} = 3.71$, $p = .063$) and *E. tereticornis* ($F_{1,22} = 0.21$, $p = .654$).

Relationship Between *Leptocybe invasa* Damage and Stand Altitude

Stand altitude of sampled eucalypts stands in all three zones ranged from 60 masl in the Coastal zone to 1,540 masl in the Southern Highlands (Table 1). In the Coastal zone, a nonsignificant negative relationship was observed between stand altitude and *L. invasa* damage index on *E. tereticornis* ($F_{1,2} = 0.34$, $p = .619$). No relationship was shown between stand altitude and *L. invasa* damage index on *E. saligna* and *E. camaldulensis* as their damages were recorded on the same stands with the same altitudes (Figure 2a). In the Southern Highlands zone, the weak and nonsignificant negative relationships were observed in both *E. camaldulensis* ($F_{1,2} = 0.23$, $p = .677$) and *E. saligna* ($F_{1,2} = 0.27$, $p = .656$; Figure 2b). Conversely, in the Plateaux zone where only *E. camaldulensis* was recorded, a nonsignificant positive relationship was observed ($F_{1,3} = 0.29$, $p = .064$; Figure 2c).

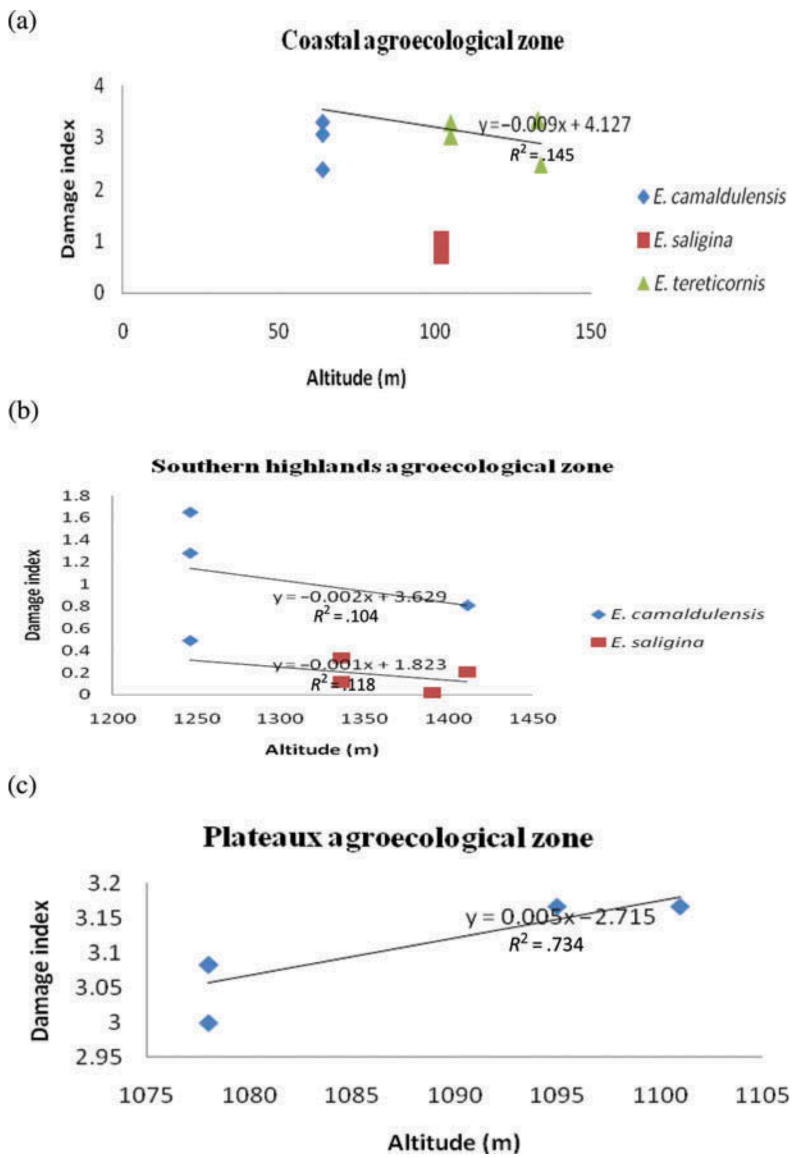

FIGURE 2 Relationship between altitude and *Leptocybe invasa* damage on *Eucalyptus* species in three agroecological zones in Tanzania.

Relationship Between Eucalyptus Species Age and Infestation

The relationships between *Eucalyptus* species age and *L. invasa* infestation (severity and incidence) or damage index were detemined on *E. camaldulensis, E. saligna*, and *E. tereticornis* which were recorded in both young and middle age classes. *Eucalyptus grandis* and *E. citriodora* were not included as they were not affected by the pest. In the Coastal zone, the negative insignificant ($F_{1,2} = 1.37$, $p = .363$) relationship was observed in *E. tereticornis*. *Eucalyptus camaldulensis* and *E. saligna* did not show any relationship as they were recorded in the stands with the same age (3 yr; Figure 3a). In the Plateaux zone where only *E. camaldulensis* was recorded, the insignificant and negative relationship between damage index and age was observed ($F_{1,3} = 9.60$, $p = .053$, $R^2 = 76.1\%$; Figure 3b). In the Southern Highlands zone, an insignificant and negative relationship ($F_{1,2} = 4.11$, $p = .180$) was recorded on *E. saligna* while a positive relationship was recorded on *E. camaldulensi* ($F_{1,2} = 0.23$, $p = 0.677$; Figure 3c).

Relationship Between *L. invasa* Abundance and Infestation

The relationship between *L. invasa* abundance (number of galls per 20 cm shoot length) and infestation (incidence and severity) was determined only on *E. camaldulensis, E. saligna*, and *E. tereticornis*. In the Coastal zone, there was a strong positive significant relationship between *L. invasa* abundance and damage index in *E. camaldulensis* ($F_{1,2} = 746.18$, $p = .025$) and *E. tereticornis* ($F_{1,2} = 34.70$, $p = .028$) with $R^2 = 99.8$ and 94.5%, respectively (Figure 4a). In the Southern Highlands, an insignificant relationship was recorded in *E. camaldulensis* ($F_{1,2} = 1.63$, $p = .330$) and *E. saligna* ($F_{1,2} = 0.34$, $p = .618$; Figure 4b). A nonsignificant relationship was also observed in *E. camaldulensis* ($F_{1,3} = 0.08$, $p = .795$) recorded in the Plateaux zone (Figure 4c).

DISCUSSION

Infestation Density of *Leptocybe invasa* in Different Agroecological Zones

The study revealed significant variation in infestation density of *L. invasa* between agroecological zones. This variation between zones is probably due to the differences in climatic variables existing between the studied zones. For example, the range of annual mean temperature for 12 yr (2000–2011) for the three agroecological zones differed. The annual mean temperature for the Coastal, Plateaux, and Southern Highlands ranged from 26 to 28°C, 23 to 24°C, and 21 to 23°C, respectively (Table 1). The results showed that there was a close relationship between temperature and *L. invasa* infestation. Optimal temperature is essential for the production and growth of new leaves of *Eucalyptus* species and metabolic activities within the wasp body (Mendel et al., 2004). The Southern Highlands zone where infestation was relatively low is a low temperature zone, which probably affected the development, survival, and abundance of the insect. A rise in temperature, within a favorable range, will speed up the metabolism of an insect and consequently

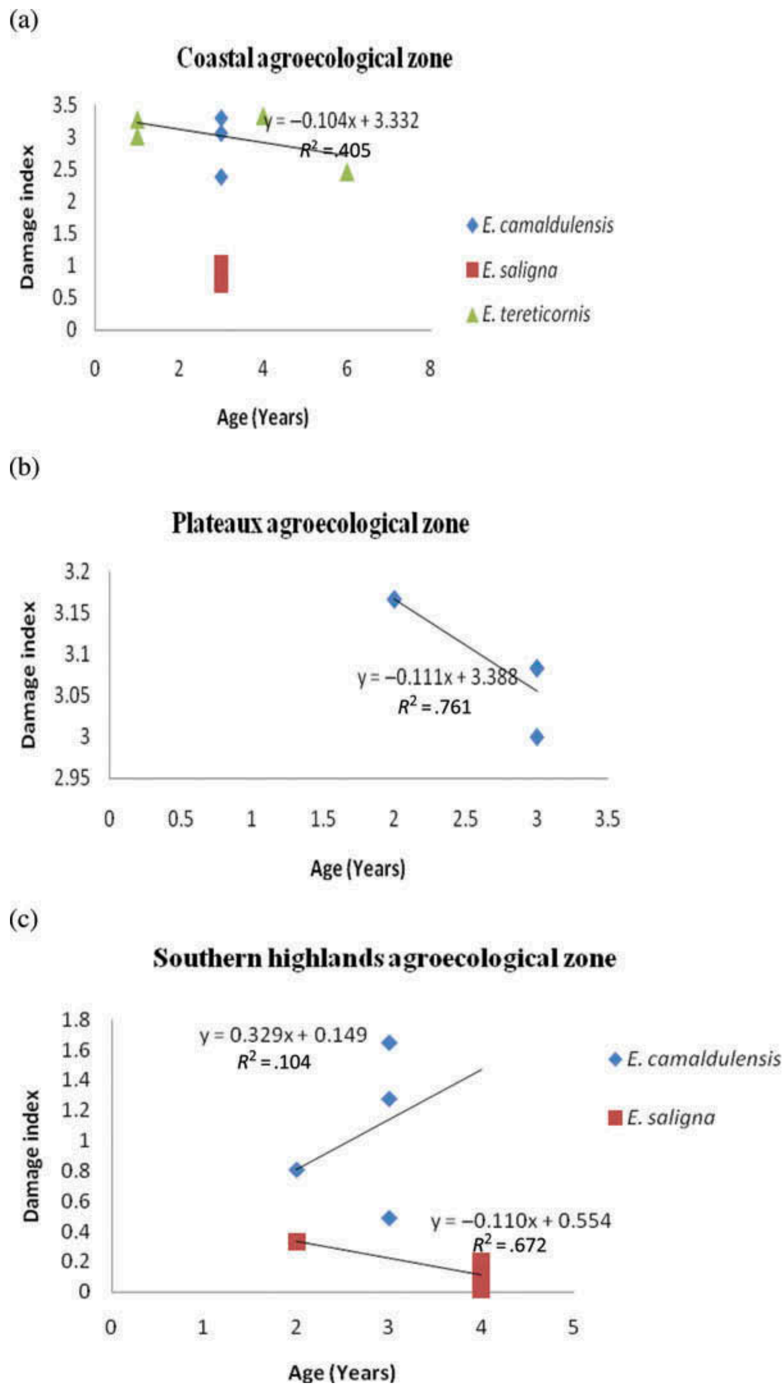

FIGURE 3 Relationship between species age and *Leptocybe invasa* infestation (damage index) on *Eucalyptus* species in three agroecological zones in Tanzania.

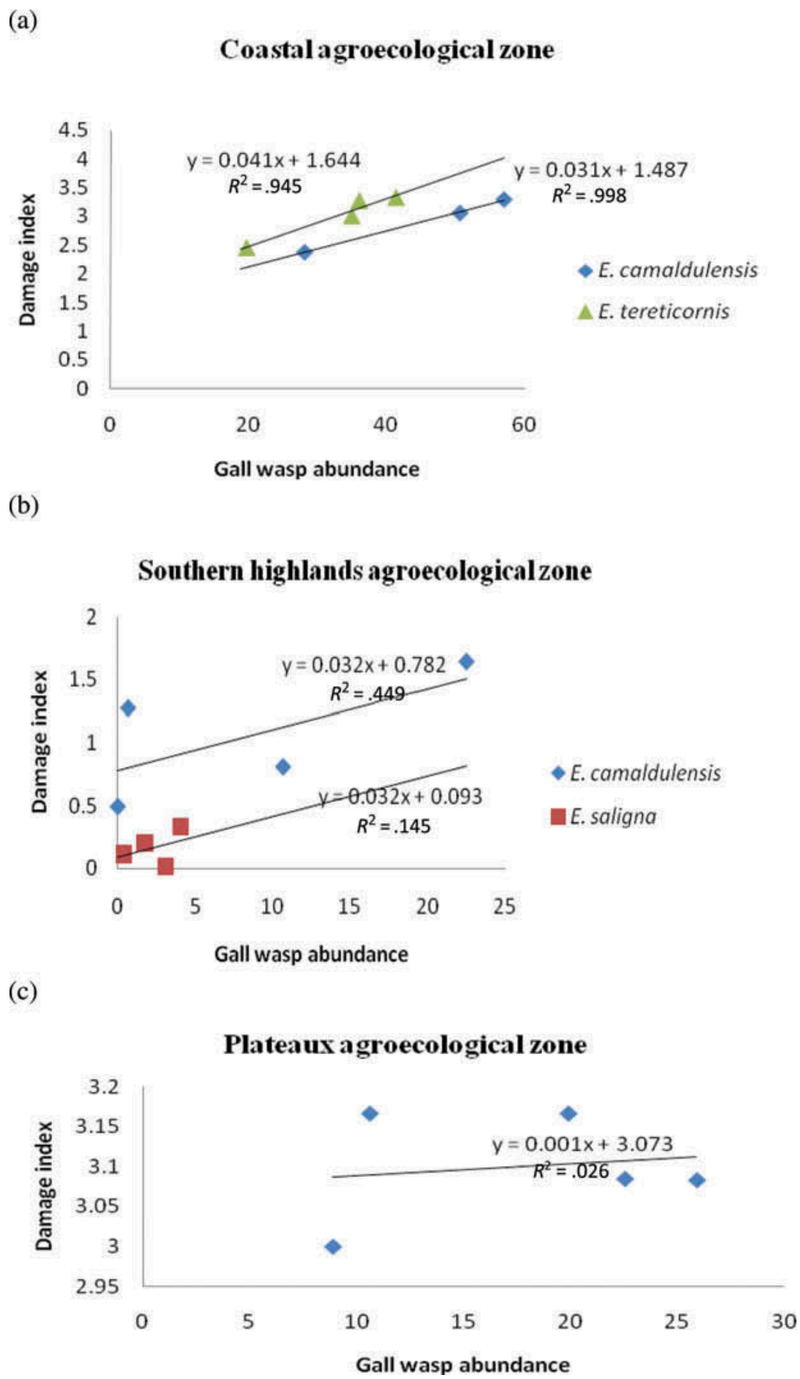

FIGURE 4 Relationship between *Leptocybe invasa* abundance and infestation (damage index) on *Eucalyptus* species in three agroecological zones in Tanzania.

increase its rate of development (Gullan & Cranston, 2005). Similarly, Leahy, Oliver, and Leather (2007) reported elevated feeding at increased temperatures among forestry pests which is likely due to the higher metabolic rates experienced at those temperatures as well as the effect of temperature and volatiles released from the wood, which might stimulate feeding.

The results of this study concur with that of Protasov et al. (2008) in Israel where adults of the gall wasp emerged from eucalypt foliage throughout the year in the greenhouse at a temperature range of 23–31°C. However, field surveys in Israel by Mendel et al. (2004), indicated that the wasp oviposits only during the warm season when the average maximum temperature has risen above 20°C, and that wasps which inhabit galls in the winter may develop slowly or die depending on their developmental stages. Furthermore, Nyeko, Mutitu, and Day (2009) did not record any *L. invasa* infestation in Kabale District because of cool temperatures with mean annual temperatures of 10–23°C. The temperatures recorded in this study which ranged from 21°C in the Southern Highlands to 28°C in the Coastal region are within the range of temperatures recorded in Israel, hence ensuring good survival of *L. invasa* in the studied sites. In most areas of Tanzania, the prevailing climate is warm throughout the year which may provide optimum conditions for gall wasp development in its preferred host. On the other hand, the annual mean relative humidity recorded for 12 yr (2000–2011) in the studied agroecological zones ranged from 61 to 64, 54 to 65, and 52 to 62% for the Plateaux, Coastal, and Southern Highlands, respectively (Table 1). The Southern Highlands which was relatively less affected by *L. invasa*, showed the lowest mean annual relative humidity. Low relative humidity can affect the physiology and thus development, longevity, and oviposition of many insects (Gullan & Cranston, 2005). In Israel, the adults of the gall wasp emerged from eucalypt foliage in the greenhouse at a humidity ranging from 40 to 70% (Protasov et al., 2008).

Infestation Density of *L. invasa* on Different *Eucalyptus* Species

In this study considerable variation in the severity of attack among *Eucalyptus* species was recorded. *Eucalyptus camaldulensis* and *E. tereticornis* were most affected by *L. invasa* compared to other species recorded in this study. According to Nyeko, Mutitu, Otieno, Ngae, and Day (2010), *Eucalyptus* species showing a damage index (DI) = 0 are considered to be resistant, 0 > DI < 0.1 (tolerant), 0.1 > DI < 0.5 (moderately susceptible), and DI > 0.5 (highly susceptible). Therefore, *E. grandis* and *E. citriodora* (with DI = 0.00) can be classified as resistant, *E. saligna* (0.40) as moderately susceptible, and *E. camaldulensis* (2.37) and *E. tereticornis* (3.02) as highly susceptible. This variation in infestation may be environmental, but a large component is genetic controlled (Nadel & Slippers, 2011). Mutitu et al. (2010) and Dittrich-Schröder, Wingfield, Hurley, and Slippers (2012) identified preferred *Eucalyptus* species for oviposition by *L. invasa*. These included *E. camaldulensis, E. globulus, E. grandis, E. nitens, E. paniculata, E. saligna, E. daniae, E. nitens* × *E. grandis*, and *E. grandis* × *E. camaldulensis*. *Eucalyptus tereticornis* and *E. urophylla* were less preferred. Nyeko et al. (2010) reported that out of 24 *Eucalyptus* germplasms evaluated for *L. invasa* infestations in Busia, Kenya, *E. henryi* was resistant, *E. camaldulensis* and *E. urophylla* were tolerant while *E. tereticornis, E. grandis*, and *E. saligna* were moderately susceptible to the pest. *Leptocybe invasa* infestation differences in the same species in different sites may be attributed to differences in climatic variables, provenances, soil factors, silvicultural practices, and crop type (coppice against first crop; Nyeko et al., 2010). The resistance against *L. invasa* infestation shown by *E. grandis* in the Southern Highlands and *E. citriodora* in the Coastal and Plateaux zones is an indication that some *Eucalyptus* species in Tanzania could be used for planting in agroecological zones. The leaves of *E. citriodora* were found to be characterized by strong lemon scent. This characteristic scent probably acts as a repellent, hence contributing to resistance to *L. invasa* attack.

Infestation Density of *L. invasa* in Different Tree Crown Parts

There was no considerable variation of *L. invasa* infestation in different eucalypt tree crown parts probably due to the open structure of the eucalypt tree crowns. This type of crown structure receives light, moisture, and wind fairly equally in all parts, hence relatively equal distribution of gall wasps within the tree crown. Correspondingly, Chilima and Leather (2001) found that the pine woolly aphid (PWA) on 5-yr-old *Pinus kesiya* was generally settling and reproducing on the outer shoot-end sections of young *P. kesiya* trees and there was no evidence of preference for any particular levels of the tree canopy. Similarly, Madoffe (1989) and Petro (2009) reported that there was no evidence of preference of PWA damage to any particular levels of the tree canopy between tree crowns of *P. patula* and *P. elliotii* in Sao Hill, Tanzania.

The mean number of galls per measured shoot length was higher in the Coastal agroecological zone compared to other zones perhaps because of the high temperature recorded in this zone. An increase in temperature within the recommended range results in an increase in numbers of *L. invasa* (Mendel et al., 2004). *Eucalyptus camaldulensis* and *E. tereticornis* harbored more galls than other *Eucalyptus* species. The mean number of galls recorded in the Coastal agroecological zone in this study did not differ much with that recorded by Mendel et al. (2004) which showed that the leaves carried much higher densities (46.0 ± 14.3) of wasp per leaf although their results did not specify the length of the leaf. Kumari et al. (2010) in India reported similar densities of 36.99 galls/10 cm shoots in the nursery seedlings and coppices, 15.67 galls/10 cm shoot on older trees.

Variation of *L. invasa* Infestation Densities Between Tree Age Classes

The gall wasp infestation densities between two age groups—i.e., young (1–3 yr) and middle (4–6 yr) did not differ significantly in both *E. saligna* and *E. tereticornis*. However, the trend in both species indicated that young trees were more preferred by gall wasps than middle age trees. This is because the wasp prefers to lay eggs on the soft and delicate midrib and petiole of the leaves and stems of young shoots (Mutitu, 2003; Mendel et al., 2004; Protasov et al., 2008). The results of this study agree with that of Nyeko (2005) and Mutitu et al. (2010) that *L. invasa* infestation is more severe on young (1–3 yr old) trees than on older trees. Similarly, Mendel et al. (2004) reported the same, that eucalypt seedlings in the nurseries, saplings in plantations, and coppiced shoots in plantations are more susceptible to *L. invasa* attack. In South Africa, *L. invasa* attacks trees of all ages, from nursery stock to mature trees, but the damage is most severe on younger plants (Dittrich-Schröder et al., 2012). Kumari et al. (2010) reported the same in India, that *L. invasa* was more severe in young trees than on 6-yr-old trees. This is similar with Madoffe (1989), whose results indicated that young pine trees were more vulnerable to PWA infestation than old trees. In contrary, Ruohomäki et al. (2000) found that *Epirrita autumnata* outbreaks took place mostly in mature birch trees because of low parasitism or high foliage quality and availability of more suitable oviposition sites in mature trees.

Relationship Between *Leptocybe invasa* Damage and Stand Altitude

The study indicated a negative relationship between altitude and *L. invasa* damage with the exception of *E. camaldulensis* in the Plateaux zone. The contradicting results recorded in the Plateaux zone could be due to an influence of higher relative humidity recorded in the zone. However, the damage index was observed to be high in all eucalypt stands located in low altitude (Coastal zone) and the damage decreases as the altitude increases. All species except *E. camaldulensis* in the Plateaux zone showed a weak coefficient of determination implying that there are other factors than altitude influencing *L. invasa* damage. The magnitude of *L. invasa* infestation like other insects depends on other factors like species, tree age, season, zone/site, soil, climate, genetic makeup, etc. (Petro, 2009). Nyeko et al. (2009) observed similar relationships between altitude and *L. invasa* damage on *E. grandis, E. camaldulensis*, and *E. saligna* in Uganda. Many factors can affect insect herbivore performance along an elevation gradient—including plant phenology, plant secondary compounds, leaf traits, abundance of natural enemies, and variation in abiotic conditions related to elevation (Hodkinson, 1997). Bird and Hodkinson (2005) demonstrated that altitudinal limits of *Craspedolepta nebulosa* and *C. subpunctata* are climatically determined and are not as a result of failure of the species to disperse to higher elevations. This may well apply to

L. invasa, as its infestation on eucalypts was higher in stands at low altitudes than in highlands.

Relationship Between *Eucalyptus* Species Age and Infestation

The study revealed that *Eucalyptus* species age influenced *L. invasa* infestation (damage index). An increase in species age resulted in a decrease in infestation, though statistically not significant. This is because the wasp prefers to insert its eggs into the midrib, petiole, and stems of young trees, young coppice as well as nursery seedlings. This is probably due to the fact that these parts are softer on young trees than on mature/old trees. It is also possible that young eucalypt trees have a low defense mechanism against pests. The same case was reported by Orcutt and Nilsen (2000) that young leaf and meristem tissue is most susceptible to herbivory during young stages of phenological development. Several defense reactions against herbivores have been reported in different plant species (Khattab & Khattab, 2005). In general, plant metabolites and macromolecules (e.g., peptides, proteins, enzymes, lignin, phenolic metabolites, cuticular waxes) serve as defense mechanisms against herbivores (Gutterman & Chauser-Volfson, 2000). Accumulation of secondary defense substances—such as tannins, their phenolic precursors, and lignin—are considered defense reactions against wounding or the presence of foreign organisms (Rohfritch, 1981). All secondary defense substances are considered to increase with tree age (Rohfritch, 1981). Results of this study are also supported by Kolb, Guerard, Hofstetter, and Wagner (2006) who reported that *Ips pini* were found to select young trees with thin bark. Attacks on stems with thin bark required less expenditure of energy by the insect than an attack on stems of mature trees with thick bark (Kolb et al., 2006). The relationship between *L. invasa* gall abundance (number of galls per 20 cm shoot length) and damage index implies that a rapid visual scoring method can be reliably used to estimate *L. invasa* infestation instead of counting the galls which is labor intensive (Mutitu et al., 2010; Nyeko et al., 2010). Similar results were observed by Petro (2009) where intensity of crown damage of *P. patula* and *P. elliotti* in Sao Hill forest plantation increased with an increase in mean number of adult PWA. Similarly, Madoffe, Ngoo, and Tarimo (2001) reported a higher damage level of growing *Leucaena leucocephala* (Lam) de Wit seedlings with an increase of leucaena psyllid (*Heteropsylla cubana*) Crawfords (Homoptera: Pyllidae) nymphs.

CONCLUSIONS AND RECOMMENDATIONS

The study has shown that *L. invasa* infestation is widely spread in all three studied agroecological zones. The infestation was more severe in the Coastal zone than the Plateaux and Southern Highlands. Incidence and severity of infestation differed significantly among *Eucalyptus* species. The trend showed that *E. tereticornis* was more affected followed by *E. camaldulensis* and *E. saligna*. *Eucalyptus grandis* and *E. citriodora* were not affected by *L. invasa*. There was no significant difference in damage between different crown parts. The young age group of trees (1–3 yr) was more damaged than the middle age group (4–6 yr). Pest infestation decreased with increasing altitudes except for *E. camaldulensis* recorded in the Plateaux zone. It was observed that the higher the infestation density/*L. invasa* abundance, the higher the damage.

A similar study should be conducted on all major hosts of *L. invasa* in Tanzanian agroecological zones to determine the susceptibility of *Euaclyptus* species for the areas. This study needs to be extended to include mature eucalypt trees to determine whether there is any variation in infestation compared to young trees. Control efforts need to focus on controlling the spread of the pest using silvicultural methods and planting resistant *Eucalyptus* species (e.g., *E. grandis* and *E. citriodora*). A coordinated program for the management of the pest, evaluation of the control strategies, and breeding of resistant varieties should be implemented urgently.

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