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Variations in *Leptocybe invasa* (Hymenoptera: Eulophidae) population intensity and infestation on eucalyptus germplasms in Uganda and Kenya

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Leptocybe invasa, an invasive gall-inducing wasp of Australian origin, recently emerged as a serious eucalyptus pest of global importance. We examined the spatial and temporal variations in *L. invasa* adult populations and evaluated eucalyptus gemplasms for infestations by the wasp in Uganda and Kenya. There were significant differences in *L. invasa* abundance, gall incidence, severity and damage index between sites. Adults occurred throughout the year, indicating overlapping generations since the adults are known to live <7 d. There was no obvious peak in *L. invasa* population abundance although a general decline was observed in dry months. Out of 35 eucalyptus germplasms evaluated for *L. invasa* infestations, only *Eucalyptus henryi* and the clonal hybrids GC 578 and GC581 were resistant to the pest. Most germplasms were ranked as tolerant or moderately susceptible to wasp attack. Highly susceptible germplasms included *Eucalyptus camaldulensis*, GC540 and GC784 in Tororo, Uganda, and MAU1, GC14, GC15 and GC10 in Busia, Kenya. Implications of the year-round occurence of *L. invasa* adult populations and gall infestations, and the potential for host resistance in managing the pest, are discussed.

Keywords: East Africa; eucalyptus; gall; host resistance; invasive species; *Leptocybe invasa*; pest

1. Introduction

The invasive eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae), recently spread to several eucalyptus nurseries and plantations in Africa, Asia, the Middle East, the Mediterranean basin and South America (Mendel et al. 2004; Branco et al. 2006; Protasov et al. 2007, 2008; Kim et al. 2008; Nyeko et al. 2009). *Leptocybe invasa* inflicts severe damage to eucalyptus trees by inducing galls on the midribs and petioles of young leaves, and on the tender bark of twigs. Severely infested trees have a gnarled appearance and show stunted growth, lodging, and twig dieback; the trees sometimes die (Mendel et al. 2004; Nyeko 2005). The severe infestations and rapid worldwide spread of this native Australian wasp pose a serious threats to eucalyptus plantation and timber enterprises. For example, planting of *Eucalyptus camaldulensis* Dehnh was curtailed in Israel because of extensive attacks by this wasp (Mendel et al. 2004).

Eucalyptus trees are a major component of the plantation forestry in East Africa. Farmers in the region value eucalyptus highly, especially as a source of construction materials, fuelwood and income (Nyeko et al. 2007a). *Leptocybe invasa* infestations on eucalyptus in east Africa were first reported in 2002 from Uganda and Kenya (Nyeko 2005; Mutitu 2003). The results of single-visit surveys conducted in Kenya and Uganda (see e.g. Mutitu 2003; Nyeko 2005; Nyeko et al. 2007a, 2007b; Mutitu et al. 2007; Nyeko et al. 2009) indicate that *L. invasa* infestation on eucalyptus is: (i) more severe on nursery seedlings and young (1–3 years old) plantations than on older trees (ii) higher in hotter and drier agroecological zones than in cooler and wetter zones, (iii) negatively correlated with altitude, (iv) variable among eucalyptus germplasms, and (v) causes serious concern among eucalyptus farmers who are in dire need of effective and sustainable control measures.

However, there is no recommendation for sustainable control of the pest in the region. Equally lacking is published information showing regular and prolonged monitoring of *L. invasa* populations and infestations on eucalyptus germplasms under different management situations and seasons in East Africa. Such information is necessary for identifying the conditions that influence the population build-up of the pest, and it is extremely useful in developing preventive measures against pest outbreaks (Rao et al. 2000). The aims of this study were to: (i) determine the spatial and temporal variations in *L. invasa* adult population and gall infestation (incidence, severity and damage) and (ii) compare *L. invasa* infestations on different eucalyptus germplasms.

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2. Materials and methods

2.1. Leptocybe invasa *abundance and infestation at different sites in Uganda*

Our study was conducted in four stands of *Eucalyptus grandis* W. Hill ex Maiden in Tororo district, eastern Uganda from April 2006 to June 2007. Tororo district was selected for the study not only because of severe *L. invasa* infestations observed in the district (Nyeko et al. 2009), but also because of the availablity of land for experimental evaluation of eucalyptus germplasms (see section 2.2). The rainfall pattern in Tororo district is bimodal with the first precipitation during March to June and the second rainy season from August to November. The dry season is most pronounced during December to February. The mean annual rainfall in the district ranges from 900 to 1300 mm, and the mean monthly minimum and maximum temperatures are 18 and 32°C, respectively.

The characteristics (location, size, year of establishment, altitude and silvicultural practices) of the eucalyptus stands selected for this study varied. Stand 1 was located in Kasoli village, stand 2 in Mudodo, stand 3 in Nyangole and stand 4 in Iyokango. The sizes of stands 1, 2, 3 and 4 were 10, 5, 50 and 15 ha, respectively. Stand 4 was at the highest altitude (1205 m) followed by stand 2 (1193 m), stand 1 (1182 m) and stand 3 (1180 m). Stands 1 and 3 were established in 2005 and had not been harvested. Stand 2 was established in 1988. The trees were last harvested (clear-felled) in 2005, and 6–8 coppices (re-growths from stumps) per stump were maintained. Site 4 was established in the 1960s. The trees were last harvested in 2005, and 3–4 coppices per stump were maintained. The weed control methods used were slashing (stands 1 and 3) and hand-hoeing (stands 2 and 4). However, stand 1 was bushy during most of the study because of the very low weeding frequency (twice yearly). Intercropping was practiced only in stand 2 where maize, millet and cassava were grown during the study. There was waterlogging in some parts of stand 3 during wet season, although channels were used to drain the water.

Each eucalyptus stand was divided into 3 blocks (2 blocks at either end and 1 in the middle). A plot of 10 × 10 tree lines was established at the centre of each block, and two trees were randomly selected from each of the 10 tree lines. This resulted into a total of 20 and 60 trees selected per plot and stand respectively. In stands of coppices (stands 2 and 4), one coppice per stump was randomly selected and considered as one tree. Every selected tree was marked for determining spatial and temporal variations in *L. invasa* adult population and gall infestation. *Leptocybe invasa* was sampled monthly using the branch beating method, which is inexpensive but may produce low arthropod yields (Majer et al. 1996). Sticky plates that could produce higher wasp catches (Protasov et al. 2007) were not available for this study. Sampling was done in the fourth week of every month. On every sampling occasion, the leader shoot (in first 4 months of sampling when the trees were less than 1 m tall) or a branch of every selected tree at heights ranging from 0.5 to 1.5 m above-ground (in later months of the study) were held and shaken or beaten sharply over a white beating tray (0.7 × 0.3 m, length × width). Any *L. invasa* adult observed on the tray was collected using an aspirator. A standard branch length of about 0.5 m from the tip was used throughout the study. Samples of *L. invasa* adults were kept in labelled vials containing 70% alcohol and counted within a week of sampling.

The 20 trees selected in each plot were also scored for the incidence and severity of *L. invasa* infestation (galls) from April to December 2006 and in June 2007. *Leptocybe invasa* galls on each sample tree were recorded as absent or present. Severity of infestation was scored visually according to the following scales; 0: no *L. invasa* induced gall observed on any leaf or twig, 1: < 25 of all leaves and twigs bearing *L. invasa* induced galls, 2: 25–50% of all leaves and twig-bearing galls, and 3: > 50% of all leaves and twigs bearing galls.

2.2. Leptocybe invasa *infestation on different eucalyptus germplasms*

2.2.1. *Uganda evaluation*

This evaluation was established in September 2006 at the District Agricultural Training and Information Centre (DATIC) at 1140 masl in Tororo district, eastern Uganda. The rainfall and temperature patterns at Tororo DATIC are as described in section 2.1. The soil is sandy loam. Nine eucalyptus clones imported from South Africa and six species (all Ugandan provenances) were evaluated (Table 1). Trees for the evaluation were produced at two nurseries belonging to the Uganda National Forest Resources Research Institute (NaFORRI) at Kifu Mukono district (for clones) and Mbale tree nursery (for other germplasms).

A randomised complete block design with three replicates was used. Blocks were established parallel to each other, and adjacent blocks were separated by 2 m. Each block was a replicate, and consisted of nine plots among which the germplasms were allocated randomly. A total of 12 seedlings was planted in each plot at a spacing of 2 × 2 m. Two guard rows, comprising *Eucalyptus grandis* seedlings spaced at 2 × 2 m, were established at the periphery of the experimental site. The site was initially ploughed using a tractor, and subsequent weeding was done by hand-hoeing. Data were collected at 1, 3 and 9 months after planting (MAP) on the incidence and severity of *L. invasa*-induced galls on all seedlings in every plot as described in section 2.1. In addition, the height of every surviving tree was determined at 9 MAP using a tape measure.

Table 1. Eucalyptus Germplasm evaluated for *Leptocybe invasa* infestations in Uganda and Kenya.

	Eucalyptus germplasms	
Germplasm category	Uganda	Kenya
Species	*Eucalyptus grandis* W. Hill ex Maiden, *E. saligna* Smith., *E. camaldulensis* Dehnh., *E. tereticornis* Smith., *E. robusta* Smith., Unidentified species 1.	*Eucalyptus grandis*, *E. saligna*, *E. camaldulensis*, *E. dunii* Maiden, *E. urophylla* S.T. Blake., *E. henryi* S.T. Blake, *E. tereticornis*.
Hybrid clones	GC540, GC550, GC578, GC784, GC796, GU7, GU8, GU607, GU609	GC3, GC10, GC12, GC14, GC15, GC16, GC522, GC581, GC584, GC642, GC785, GC796
Improved hybrids	–	MAU1, MAU12, MAU16, MAG18, KMUG14.

Note: GC, *E. grandis* x *E. camaldulensis*; GU, *E. grandis* x *E. urophylla*.

2.2.2. Kenya evaluation

This evaluation was established at Dindi Farm, Matayos division in Busia district at 1196 m. Busia district has a bimodal pattern of rainfall with heavy rains occurring from March to May and light rains from October to December. The mean annual rainfall is ca. 1400 mm. The soils are nitisol (deep, friable clay). The mean annual temperature ranges from 15–25°C. This site was selected because it is situated in the region of the initial *L. invasa* invasion in Kenya (Mutitu 2003); hence the pest population was expected to be high enough for natural infestations of the test germplasms.

A total of 24 eucalyptus germplasm lines (or cultivars) comprising seven eucalyptus species, five improved eucalyptus hybrids and 12 eucalyptus hybrid clones, were examined for *L. invasa* infestations (Table 1). All the germplasms were obtained from Karura Tree Biotechnology Project nursery, Kenya. They were evaluated in two replicate blocks. Only two replicates were used because there was inadequate land area for the study at the site. Each block consisted of 24 plots where the germplasms were allocated randomly. A total of 12 seedlings were planted in each plot at a spacing of 2.5 × 2.5 m. The seedlings were planted out in May 2006 when they were 4 months old, and were watered for the first 3 months to enhance their survival and establishment. Weeds were managed by spot-hoeing around the tree base and by slashing. Seedlings were protected against termite attack by applying Fipronil (Regent 3G) at the rate of 33 g per tree at the time of planting.

The germplasms were evaluated for *L. invasa* infestations using two approaches. The first involved visual scoring of all seedlings in every plot for the incidence and severity of *L. invasa*-induced galls as described in section 2.1. This was done eight times from July 2006 to April 2008. The second approach involved counting the number of *L. invasa*-induced galls per 20 cm branch length. This was done five times from July 2006 to August 2007 in order that we could examine the relationship between visual scoring of *L. invasa* infestations and gall intensity. Four trees were selected randomly in every plot to determine gall intensity (number of galls per 20 cm branch length). From each tree, two branches were selected randomly from the top five branches. The leader shoot was taken as the first branch. Because *L. invasa* mostly attacks young meristematic tissues (Mendel et al. 2004), the number of *L. invasa* galls was counted on a 20-cm length of the branch tip.

2.3. Data analysis

Variation in the population of *L. invasa* over time at each stand (or site) was determined by ANOVA using SPSS version 10. ANOVA was also used to determine the mean *L. invasa* infestations (incidence, severity and damage index) at the different sites. The least significant difference (LSD) test was used, *a posteriori*, to separate mean values. Sites were compared pairwise in the patterns of *L. invasa* population by the *Z*-sample Kolmogorov–Smirnov test using SPSS. The mean severity and incidence (proportion of infested seedlings) of *L. invasa* infestations per plot was calculated using Pivot Table in Microsoft Excel. The damage index in each plot was calculated as the product of the mean severity and incidence (proportion of infested trees) per plot. A two-sample Kolmogorov–Smirnov was used to compare sites in terms of the patterns of *L. invasa* infestations. The relationship between *L. invasa* adult population intensity and gall infestation (incidence, severity and damage index) at each site was determined using simple linear regression.

ANOVA was used to analyse the variation in *L. invasa* infestations (incidence, severity and damage index) among eucalyptus germplasms, and it was also used to compare the height of the trees of each germplasm. The relationship between germplasm height and the severity of *L. invasa* infestations was determined for each germplasm using linear regression in SPSS. Linear regression was also used to determine the relationship between *L. invasa* damage index and gall intensity (number of galls per 20 cm branch length). Germplasms were ranked as resistant,

tolerant, moderately susceptible and highly susceptible to *L. invasa* infestation based on mean damage index (Uganda evaluation) and gall intensity (Kenya evaluation).

3. Results

3.1. Leptocybe invasa *abundance and infestations at diferent sites in Uganda*

The mean number of *L. invasa* adults captured per branch was significantly lower at site 1 (3.5 ± 1.25) than at site 2 (4.4 ± 1.34), site 3 (4.2 ± 1.42) and site 4 (4.4 ± 1.11) ($F = 9.5$; $P < 0.001$). Adult *L. invasa* occurred at all sites throughout the study period, but varied significantly in abundance over time. Pairwise comparison of sites showed statistically similar temporal patterns of *L. invasa* abundance between all site combinations (site 1 vs. site 2: Kolmogorov–Smirnov $Z = 1.278$, $P = 0.076$; site 1 vs. site 3: $Z = 0.730$, $P = 0.660$, site 2 vs. site 3: $Z = 0.913$, $P = 0.375$; site 2 vs. site 4: $Z = 0.913$, $P = 0.375$; site 3 vs. site 4: $Z = 1.095$, $P = 0.181$), except site 1 vs. site 4 (Kolmogorov–Smirnov $Z = 1.461$, $P = 0.028$). Although population peaks were not very obvious, relatively higher wasp numbers were observed in April and December of 2006 and also in June 2007 (Figure 1). Wasp numbers generally declined during April–August 2006 and December–January 2007, which were mostly dry periods.

Significant differences were observed between sites in terms of average *L. invasa* infestation incidence, severity and damage index (Table 2). The incidence of the infestation was generally high at all sites (77–89%). Site 3 had the highest damage index while site 4 had the lowest. There was no distinct peak of *L. invasa* infestation incidence, severity or damage index at any of the sites (Figure 2). There were significant differences in *L. invasa* infestation between sites (Table 3). *Leptocybe invasa* infestation severity and damage index at site 3 were significantly different from those at any of the other sites. However, infestation incidences at site 3 and site 1 were statistically non-significant (Table 3). The proportion of highly infested trees (> 50% of total leaves having galls) was high (20–70%) throughout the study, especially in sites 2 and 3. Some trees that had minor infestations (< 25% of total leaves having galls) shed all infested leaves (especially during November and December 2006), and were scored as healthy trees. There was no significant relationship between *L. invasa* population and damage incidence, severity or damage index at any of the sites.

3.2. Leptocybe invasa *infestation on different eucalyptus germplasms*

3.2.1 Uganda evaluation

Eucalyptus germplasms varied significantly in *L. invasa* infestation incidence, severity and damage index (Table 4). GC578 was not infested throughout the study. Germplasms GC550, GC796, GU609 and *E. tereticornis* had very low infestation levels; both of these germplasms were ranked as tolerant (Table 4). In contrast, *E. camaldulensis*, GC540 and GC784 showed

Table 2. The mean incidence (proportion of 60 trees), severity and damage index of *Leptocybe invasa* infestations on *Eucalyptus grandis* at four sites in Tororo district, Uganda.

Location	Incidence	Severity	Damage index
Site 1	0.81^{ab}	1.65^{ac}	1.37^{ac}
Site 2	0.79^{a}	1.77^{a}	1.46^{a}
Site 3	0.89^{b}	2.21^{b}	1.96^{b}
Site 4	0.77^{a}	1.47^{c}	1.16^{c}

Note: Means followed by the same supercript within a column are not significantly different at $P < 0.05$.

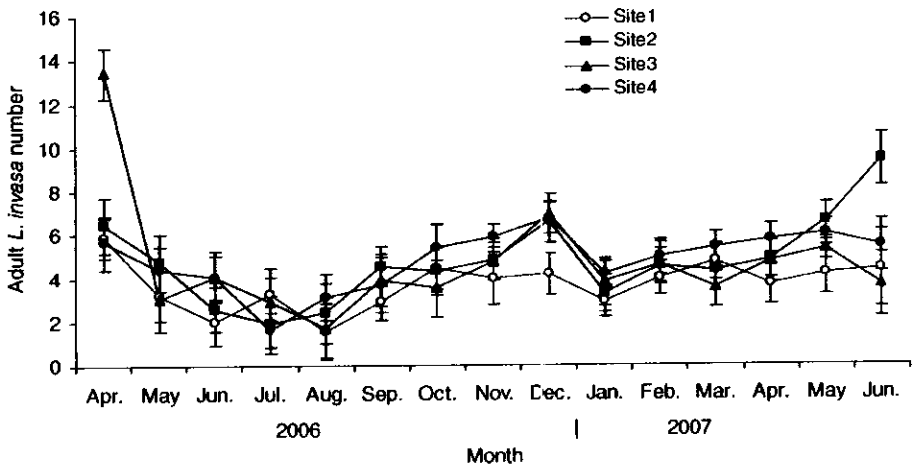

Figure 1. Abundance of *L. invasa* adults at four sites in Tororo district, Uganda during 2006 and 2007. Error bars are ±SE.

high susceptibility to insect attack. By 9 months after planting, GC784 had the highest mean incidence (100%), severity (3.0) and damage index (3.0) followed by *E. camaldulensis* and GC540. Tree height at 9 months after planting varied significantly among germplasms. On average, GC784 was the tallest despite the high *L. invasa* infestation observed on this germplasm (Table 4). There was no significant relationship between the severity of *L. invasa* and height of all germplasms, except *E. camaldulensis* ($R^2 = -0.45$, $P = 0.03$).

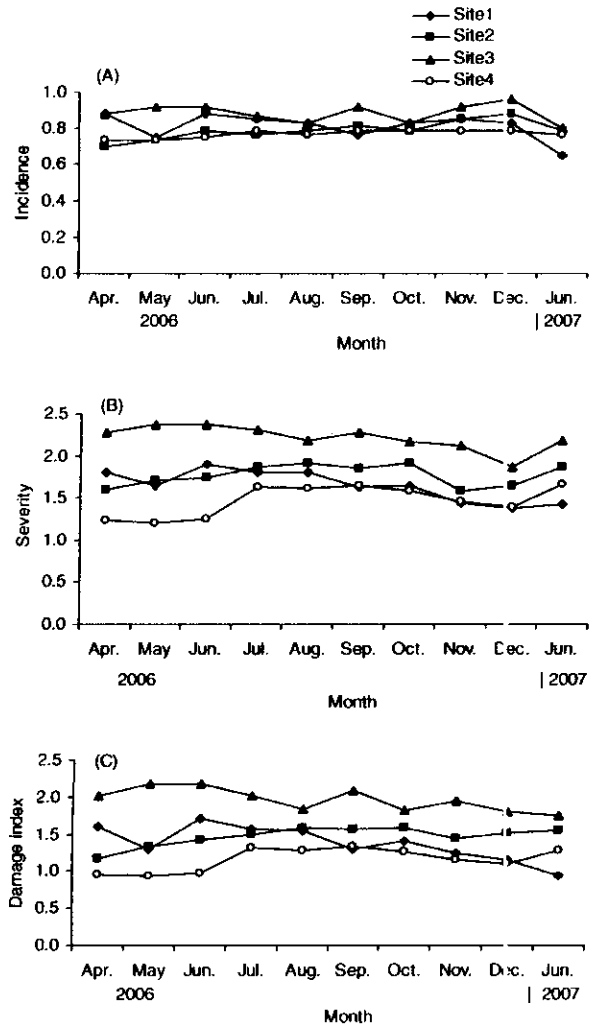

Figure 2. *Leptocybe invasa* gall incidence (proportion of 60 trees), severity and damage index at four sites in Tororo district, Uganda during 2006 and 2007.

3.2.2. *Kenya evaluation*

Highly significant variations were observed in the level of *L. invasa* infestation over the study period (Figure 3). There were no *L. invasa*-induced galls on all eucalyptus germplasms at 2 months after planting (Figure 3). Peak *L. invasa* infestation was at 15 months after planting. Germplasms differed significantly in the level of *L. invasa* infestation (Table 5). Only *Eucalyptus henryi* and GC581 were uninfested throughout the study. In contrast, germplasms GC10, GC14, GC15 and MAU1 showed very high infestation levels, and were categorised as highly susceptible. The remainder of the germplasms bore low to moderate *L. invasa* infestations (Table 5). There was a very strong positive relationship between *L. invasa* gall intensity (number of galls per 20 cm branch length) and damage index ($R^2 = 0.851$, $P < 0.001$). Thus the rapid visual scoring method can be reliably used to estimate *L. invasa* infestations instead of the labour-intensive gall intensity method.

4. Discussion

4.1. Leptocybe invasa *population and infestation dynamics*

Our study has revealed significant differences in *L. invasa* adult population and gall infestation levels between sites. *Leptocybe invasa* infestation intensity may also vary enormously among neighbouring trees of the same species or provenance (Nyeko P. unpublished observation) possibly due to genetic differences between individual trees. Because our study sites were located in the same agro-ecological zone, the observed

Table 3. Relationships between sites in the patterns of *L. invasa* infestation incidence, severity and damage index on *Eucalyptus grandis* at four sites in Tororo district, Uganda.

	Kolmogorov–Smirnov statistics					
	Incidence		Severity		Damage index	
Relationship	*Z*	*P*	*Z*	*P*	*Z*	*P*
Site 1 vs. Site 2	1.118	0.164	0.894	0.400	0.671	0.759
Site 1 vs. Site 3	1.118	0.164	2.012	0.001	2.012	0.001
Site 1 vs. Site 4	1.565	0.015	0.894	0.400	1.118	0.164
Site 2 vs. Site 3	1.565	0.015	2.012	0.001	2.236	<0.001
Site 2 vs. Site 4	0.671	0.759	1.565	0.015	1.789	0.003
Site 3 vs. Site 4	2.236	<0.001	2.236	<0.001	2.236	<0.001

Table 4. Mean height of and *Leptocybe invasa* gall infestations on different eucalyptus germplasms in Tororo district, Uganda.

Eucalyptus Germplasm	Height (m)[1]	*L. invasa* infestation			
		Incidence	Severity	Damage index	Ranking
GC578	1.28	0.00	0.00	0.00	R
GC550	1.77	0.05	0.05	0.01	T
E. tereticornis	1.73	0.06	0.07	0.01	T
GC796	1.50	0.10	0.12	0.04	T
GU609	1.16	0.13	0.13	0.05	T
GU8	1.39	0.13	0.13	0.11	MS
GU607	1.10	0.15	0.32	0.16	MS
GU7	1.53	0.20	0.20	0.17	MS
E. saligna	1.46	0.27	0.37	0.19	MS
E. sp.1	1.42	0.32	0.38	0.21	MS
E. grandis	1.41	0.25	0.48	0.34	MS
E. robusta	0.84	0.30	0.42	0.35	MS
E. camaldulensis	1.23	0.53	0.95	0.75	HS
GC540	2.04	0.65	1.23	1.02	HS
GC784	2.86	0.72	1.50	1.47	HS
SE	0.202	0.064	0.103	0.099	
F value	6.2	9.3	14.4	12.5	
P value	<0.001	<0.001	<0.001	<0.001	

Note: [1]Height measured at 9 months after planting. R, resistant (damage index = 0); T, tolerant (damage index >0 < 0.1); MS, moderately susceptible (damage index >0.1 < 0.5); HS, highly susceptible (damage index >0.5). SE, *F* and *P* values are for pooled germplasm means.

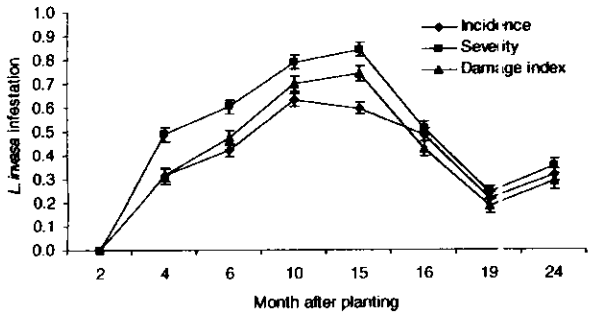

Figure 3. *Leptocybe invasa* gall infestation incidence, severity and damage index in Busia, Kenya during 2006 and 2007. Data are pooled germplasm means.

site-to-site vaiations in *L. invasa* adult abundance and gall infestations may be attributed to differences in microclimatic variables, silvicultural practices and crop type (coppices i.e. regrowth from tree stumps vs. first crop i.e. trees raised from seedlings and not yet harvested) at the sites, which presumably caused differences in the quantity of new eucalyptus growth suitable for oviposition and development of *L. invasa*. Such variation in resource availability and carrying capacity are important determinants of fluctuations in the populations of insects (Dempster and Pollard 1981).

There is a paucity of literature on the relationship between the abundance of *L. invasa* and seasonal changes. Protasov et al. (2008) observed in Israel that adults of the gall wasp emerge from eucalyptus foliage throughout the year in the greenhouse under a temperature regime of 23–31°C and humidity ranging from 40 to 70%. However, field surveys by Mendel et al. (2004), also in Israel, indicated that the insect 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. In our study *L. invasa* adults occurred throughout the year although their mean life-span has been reported to be only 6.5 days (Mendel et al. 2004). The year-round existence of adult *L. invasa* may be attributed to the generally warm tropical climate in which eucalyptus produces new leaves throughout the year. Thus the wasp can thrive and produce overlapping generations capable of inflicting severe damage to eucalyptus irrespective of seasonal changes. However, the number of generations of *L. invasa* per year was not obvious in the present study. In Israel Mendel et al. (2004) observed that the development of *L. invasa* from oviposition to emergence in the field is about 4.5 months, and these authors estimated that the wasp may produce two or three overlapping generations annually.

The occurence of adult *L. invasa* throughout the year may have implications for control decisions. For example, it is apparently impossible to schedule planting or cutting mature eucalyptus trees for regeneration to avoid or minimise the galling of seedlings or coppices. In contrast, establishment of biological control agents may be facilitated by the year-round availability of suitable developmental stages of their host (*L. invasa*). Protasov et al. (2008) observed that a *Megastigmus* species which is a parasitoid of *L. invasa* could easily emerge from eucalyptus foliage throughout the year in the laboratory because there were

Table 5. Variation in mean *Leptocybe invasa* gal infestation incidence, severity, damage index and gall intensity on different eucalyptus germplasms in Busia, Kenya.

Eucalyptus Germplasm	Incidence	Severity	Damage index	Gall intensity	Rank[1]
E. henryi	0.00	0.00	0.00	0.00	R
GC581	0.00	0.00	0.00	0.00	R
MAG18	0.03	0.03	0.00	0.03	T
KMUG14	0.17	0.17	0.06	0.10	T
E. dunii	0.06	0.06	0.02	0.15	T
MAU12	0.36	0.36	0.27	0.38	T
E. urophylla	0.14	0.14	0.07	0.45	T
E. camaldulensis	0.13	0.14	0.08	0.50	T
GC785	0.23	0.23	0.12	0.50	T
GC3	0.21	0.21	0.13	0.76	T
GC642	0.10	0.11	0.04	1.44	MS
GC584	0.20	0.20	0.16	1.45	MS
GC167	0.34	0.34	0.26	1.50	MS
MAU16	0.46	0.46	0.38	4.55	MS
GC522	0.59	0.69	0.63	5.19	MS
GC796	0.41	0.49	0.33	10.81	MS
GC12	0.76	0.89	0.81	13.20	MS
E. tereticornis	0.55	0.66	0.48	17.38	MS
E. grandis	0.58	0.76	0.57	18.03	MS
E. saligna	0.46	0.65	0.43	21.13	MS
MAU1	0.76	1.07	0.98	32.35	HS
GC14	0.84	1.31	1.27	35.04	HS
GC15	0.70	1.08	0.88	38.88	HS
GC10	0.87	1.43	1.41	53.69	HS
SE	0.043	0.052	0.056	2.43	
F value	42.1	67.4	55.5	39.2	
P value	<0.001	<0.001	<0.001	<0.001	

Note: [1]Ranking for resistance is based on gall intensity as R, resistant (no gall); T, tolerant ($> 0 \leq 1$ gall/20 cm branch length); MS, moderately susceptible ($> 1 \leq 25$ galls/20 cm branch length); HS, highly susceptible (>25 galls/20 cm branch length). SE, *F* and *P* values are for pooled germplasm means.

overlapping generations of *L. invasa* larvae. Populations of such natural enemies may thus build up rapidly in tropical conditions where the host (*L. invasa*) does not overwinter.

4.2. Leptocybe invasa *infestation among eucalyptus germplasms*

There was considerable variation in *L. invasa* infestation among eucalyptus germplasms. Only *Eucalyptus henryi* and GC581 in Busia, and GC578 in Tororo showed complete resistance to *L. invasa*. This suggests there is a limited range of existing eucalyptus germplasms in east Africa that could be selected for complete resistance against *L. invasa*. The predominant eucalyptus species in east Africa (*E. grandis, E. camaldulensis, E. tereticornis* and *E. saligna*) belong to the sections *Exsertia* and *Latoangulata*, which are suitable hosts for the development of *L. invasa* (Mendel et al. 2004). Also worrying is the observation that *L. invasa* develops successfully on eucalyptus hybrids when the parents of the hybrid are suitable hosts for the wasp (Mendel et al. 2004). This implies that various hybrids of parents suitable for the wasp e.g. *E. grandis* x *E. urophylla* (GU) and, also *E. grandis* x *E. camaldulensis* (GC) hybrids being promoted in the tropics are suitable hosts to the gall wasp. However, the resistance exhibited by GC578 and GC581 in our study contradicts this notion, thereby emphasizing the need for a case-by-case evaluation. That way, germplasms identified as resistant or tolerant to *L. invasa* in an agro-ecological zone could be grown successfully in the area as they may overcome infestations by the pest (Nyeko et al. 2009). However it may be uneconomical to plant germplasms that are highly susceptible to *L. invasa* in areas where there is high likelihood of infestation occuring.

Little is known about the mechanisms governing host resistance to *L. invasa*. Variations in structural, chemical and nutritional properties may underlie the susceptibility of eucalyptus germplasms to galling (Ohmart and Edwards 1991). Identification of resistance traits would simplify germplasm screening techniques (Dent 1991). We did not examine whether *L. invasa* attacks resistant germplasms such as *E. henryi* and GC578 but fails to develop on them. Although it is relatively easy to score absence or presence of galls on an individual tree to determine its resistance to *L. invasa*, detailed assessments of host reaction or pest behaviour are required to develop a better understanding of what general mechanisms of resistance are at work (Yanchuk and Allard 2009). Considering the increasing invasions of gall-inducing wasps in eucalyptus plantations (see e.g. Mendel et al. 2004; Doğanlar and Mendel 2007; Protasov et al. 2007; Nyeko et al. 2009), tree-breeding programmes may have most utility in managing such pests if resources are directed towards

testing, developing and utilising cross-resistance (Andrew et al. 2007). Such efforts could be focused on eucalyptus genotypes that are already employed in tree improvement programmes, in order to minimise the use of substantial resources often required for the identification and development of silviculturally useful resistant genotypes.

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