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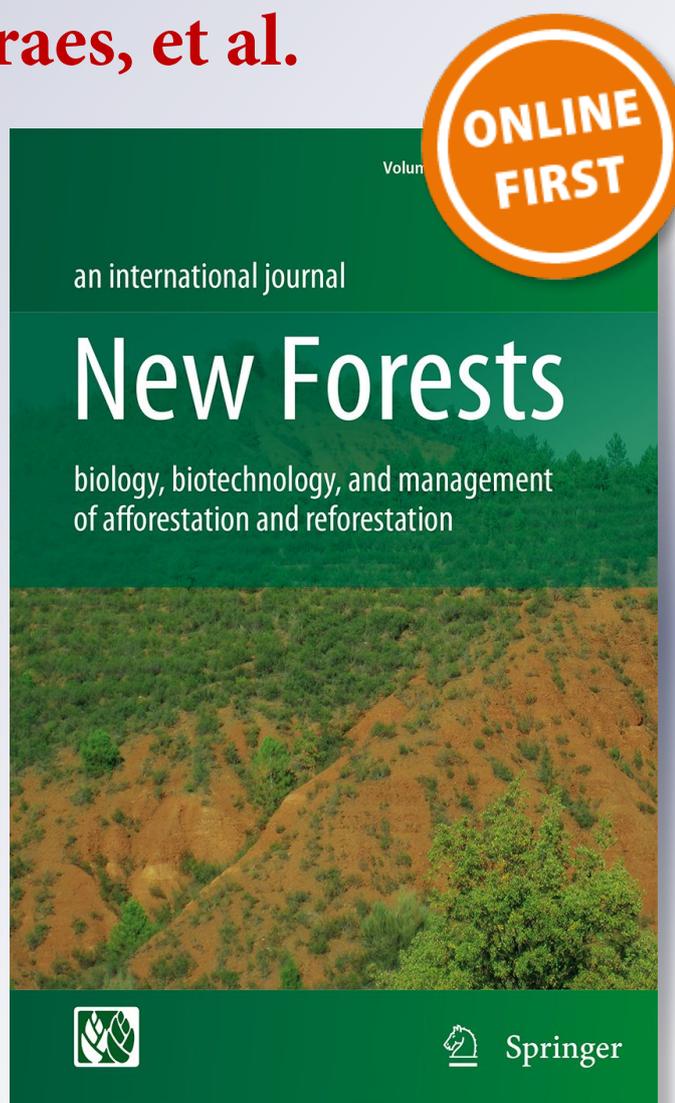
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Susceptibility of eucalypt taxa to a natural infestation by *Leptocybe invasa*

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Abstract

Recently, pest occurrence in forest plantations has been increasing influenced by genotypes and environmental conditions such as climate change, thus impacting production negatively. In 2008, the exotic pest *Leptocybe invasa* (Hym: Eulophidae), known as the blue gum chalcid, was introduced in Brazil causing damage to eucalypt plantations in many regions of the country. To this end, this study evaluated the susceptibility of *Eucalyptus camaldulensis* (one seedlot), *E. grandis* (four seedlots), *E. urophylla* (four seedlots), and the “*E. urograndis*” hybrid (*E. urophylla* × *E. grandis*) (three seedlots) exposed to a natural infestation by *L. invasa* in two seasons (winter and summer). The attack on seedlings was classified in terms of severity as healthy (no pest attack), oviposition (only oviposition signs) and gall formation. The results show a significant higher pest incidence in summer compared to winter. Further, *Eucalyptus urophylla* was the least attacked and 90% of the seedlings were healthy whereas *E. grandis* showed the highest number of seedlings with galls. The *E. urograndis* hybrid showed intermediate results between the two species. Differences in susceptibility were observed between seedlots within species. *Eucalyptus camaldulensis*, which was expected to have the highest incidence of galls, had a high oviposition incidence (60%) and low gall incidence (< 10%), probably due to its provenance. The susceptibility of the different eucalypt families varied significantly with respect to *L. invasa* infestation, and family heritability ranged from 0.27 to 0.68. The genetic control of *L. invasa* is possible through the selection of tolerant and resistant material, considering the species, provenance, and family.

Keywords Exotic pest · Environmental conditions · Blue gum chalcid · Heritability

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Introduction

There are many eucalypt species and animal species endemic to Australia and nearby islands that are well known and admired worldwide, whereas others are not so well known and have the potential to become major pests outside their natural habitats. Several eucalypt species have been planted around the world and, therefore, separated from their characteristic insects and pathogens, leading to an ecological imbalance (Crous et al. 2017). These worldwide commercial plantations are developing in areas without insects and pathogens that would normally evolve together, which partially explains the high productivity of different crops outside their original region. However, in the event an insect, or fungus, is introduced to its host on a large scale, high infestations may occur if environmental conditions favor pest development. This phenomenon has been occurring worldwide with eucalypt that was introduced into new environments, constituting a growing threat to eucalypt productivity (Wingfield et al. 2001, 2008).

Leptocybe invasa (Hymenoptera: Eulophidae) was first detected in Israel in 2000 and has, nowadays, spread to all continents, America, Asia, Africa, Europe, and Oceania (New Zealand), causing great losses to eucalypt plantations in Brazil and other countries (Mendel et al. 2004). In Brazil, this pest was first detected on a *Eucalyptus camaldulensis* and *E. grandis* hybrid, in Bahia (northeast region), and on *E. grandis* in São Paulo (southeast region), in Costa et al. (2008). The blue gum chalcid (*L. invasa*) is one of the most important eucalypt pests worldwide while other important pests are bronze bug (*Thaumastocoris peregrinus*), eucalypt gall wasp (*Ophelimus maskelli*), red gum lerp psyllid (*Glycaspis brimblecombei*) and eucalypt weevil (*Gonipterus spp.* complex) (Protasov et al. 2007; Wilcken et al. 2010; Paine et al. 2011; Valente et al. 2018).

Leptocybe invasa is native to a eucalypt host species in Australia that has already been described (Mendel et al. 2004; Thua et al. 2009; Silva et al. 2015). However, since there are some tolerant taxa among and within eucalypt species, it becomes important to know and keep the diversity of the eucalypt species to mitigate the attack of new pests.

Commercial eucalypt plantations are of great economic importance to tropical and subtropical regions around the world eucalypts plantation covering roughly a 20,000,000 ha. However, only nine species, all belonging to the *Symphyomyrtus* subgenus, and their hybrids, out of hundreds that exist are planted on a large scale worldwide (> 90% of eucalypt plantations) (Potts and Dungey 2004; Harwood 2011). In Brazil, *Eucalyptus grandis*, *E. urophylla*, and their hybrids are the most widespread taxa (Assis et al. 2015).

The *Eucalyptus grandis* species is not only important to Brazil but also to the tropical and subtropical areas of Argentina, South Africa, and Uruguay, among others. There are two contiguous occurrences in Australia, the Southern (25–32° S latitude range) and the Northern (16°–18° S latitude range) occurring in New South Wales and Queensland, respectively, with some small disjunction populations in between (Boland et al. 2006; Silva et al. 2019a).

Eucalyptus urophylla is native to the islands in eastern Indonesia (07°–10° S latitude range and 122°–127° S longitude range) and an important species to tropical regions that, however, does not occur naturally in Australia. Furthermore, this species performance is strongly related to the altitude of the provenance area, showing higher growth rates in Flores island (low altitude) compare to Timor (high altitude). However, Timor plants show better tolerance to leaf disease, which is important in humid and warm environments such as Am Koppen climate (Payn et al. 2008; Flores et al. 2016; Silva et al. 2018a, 2019b).

Eucalyptus camaldulensis is another important species of riparian forest that is widespread throughout the entire latitude range of Australia, whose performance is also affected by the provenance area (Silva et al. 2018a). The species is important due to drought tolerance, however it is highly susceptible to pests (Boland et al. 2006; Nyeko et al. 2010).

It has been stated that breeding programs focusing only on increasing productivity can be an agent for decreasing genetic variability (Silva et al. 2018b). Therefore, the demand for high productivity germplasm can decrease biotic stress tolerance, if the selection process does not consider stress tolerance.

This work evaluated seedling susceptibility and the genetic parameters of different eucalypt species, provenances, and family to natural infestation by *L. invasa* in winter and summer.

Materials and methods

Few seeds per container from each seedlot were sown in 25 containers. In the initial phase (30 days after), the plants were thinned and only one seedling was left per container. We evaluated more than 4800 seedlings of 204 families, 18–25 repetitions (some families had low seed germination), from open pollination of 12 seedlots from Brazilian populations of *Eucalyptus camaldulensis*, *E. grandis*, *E. urophylla* and “*E. urograndis*” hybrids from the *E. urophylla* and *E. grandis* cross (Table 1).

The seedlings were grown in 55 cm³ polypropylene containers, filled with the organic substrate consisting of rice husk, coconut fiber, pine bark, and vermiculite. Three times a week, soil was fertilized with 5 mm of a solution containing 450 g calcium nitrate, 300 g ammonium nitrate, 250 g monoammonium phosphate, 300 g potassium nitrate, 250 g magnesium sulfate, 250 g ammonium sulfate, 2.5 g Tenso iron, 0.85 g manganese sulfate; 0.75 g boric acid; 0.325 g zinc sulfate; 0.1 g copper sulfate, and 0.005 g sodium molybdate in 1000 L of water. The irrigations were performed four times daily, regardless of climate conditions.

Table 1 Studied eucalypt taxa, seedlots, and families

Seedlot	Species	SITE	provenance	Number of families
–	<i>E. camaldulensis</i>	Selvíria (MS)	Notts Crossing and Katherine River	20
11d 84	<i>E. grandis</i>	Anhembi (SP)	Coffs Harbour (NSW)	18
22b 58	<i>E. grandis</i>	Itatinga (SP)	Atherton (QLD)	20
13a 19	<i>E. grandis</i>	Itatinga (SP)	Coffs Harbour (NSW)	10
13b 20	<i>E. grandis</i>	Itatinga (SP)	Atherton (QLD)	8
08d 65	<i>E. urophylla</i>	Anhembi (SP)	Flores	19
08f 67	<i>E. urophylla</i>	Anhembi (SP)	Wukoh, Ilegele, Londangwuang, Egon, Ara Detung, Saler, Lewotobi, Iimandiri	19
08i 70	<i>E. urophylla</i>	Anhembi (SP)	Flores	20
10b 71	<i>E. urophylla</i>	Anhembi (SP)	Adonara, Lomblem, Alor and Pantar	20
01f 129	<i>E. urograndis</i> ^a	Anhembi (SP)	–	20
15b 153	<i>E. urograndis</i>	Anhembi (SP)	–	20
06 74	<i>E. urograndis</i>	Itatinga (SP)	–	10
Total	4	3	–	204

^a*E. urophylla* × *E. grandis* hybrid

The evaluations were performed when the seedlings were approximately 120 days old in nursery conditions in Piracicaba/SP (22° 43' S and 47° 38' W, 547 m alt.), Cwa—Köppen classification. The severity of pest infestation was evaluated in July (winter $T_{jul} = 17.1$ °C; $Rainfall_{jul} = 0.0$ mm) and December (summer $T_{dec} = 24.3$ °C; $Rainfall = 152.2$ mm) in 2017 (Fig. 1). No inoculation was needed since the infestation occurred naturally as a result of the high occurrence of the pest in the site. Therefore, we evaluated a natural infestation by *Leptocybe invasa*.

The seedlings, whether attacked or not by *L. invasa*, were classified according to their symptoms as, category 1—healthy: no pest attack; category 2—oviposition: only oviposition signs; and category 3—galled: observed gall formation (Fig. 2).

The severity of the pest attack was treated as an ordinal characteristic (category 1–3, as shown above) while a generalized linear mixed model (GLMM) was adjusted for the individual species in the data analysis. The GLMM approach was used to infer quantitative genetic parameters more realistically since it allows to deal with non-additivity and non-normal distribution of the data (Mc Cullagh and Nelder 1989; Bolker et al. 2009; Villemereuil et al. 2016). The analysis contemplates a multinomial distribution with a probit binding function and allows either generalizing or flexibilizing a nonlinear model to be analyzed with the same structure to estimate and predict a classical linear model (Nelder and Wedderburn 1972; Villemereuil 2018). Therefore, the model was adjusted considering the following linear predictor:

$$\eta = X_S + Z_{f(ss)} + Z_{ss} + Z_{Sf(ss)}$$

$\eta = g(\mu) = \Phi^{-1}\mu$: is the link function (probit) connecting the expected value μ of the observed phenotype Y (category 1–3) to the latent scale (standard normal function).

Where the vectors are: S : season (summer or winter) and repetition effects, considered as fixed; $f(ss)$: genetic family effect inside the seedlot, considered as random; ss : seedlot effect, considered as random; $Sf(ss)$: interaction between Season and Family within the seedlot, considered as random; Z and X : incidence matrices of random and fixed effects, respectively.

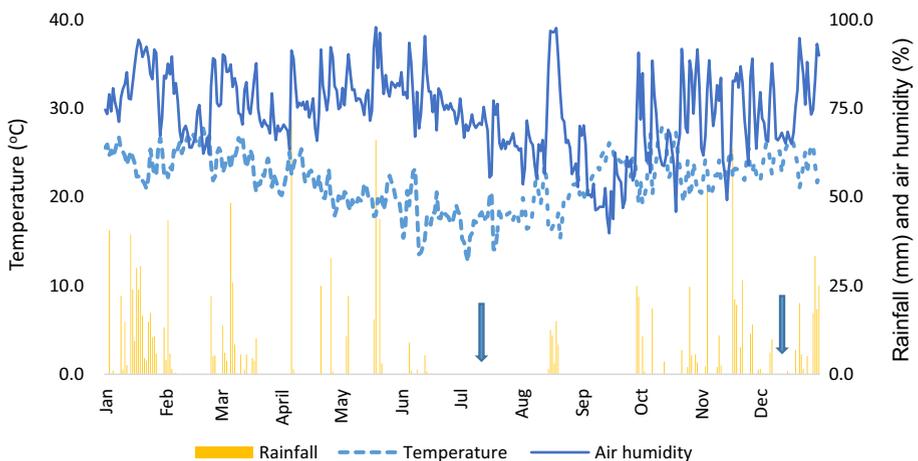


Fig. 1 Rainfall, temperature, and humidity in 2017. The arrows indicate the time of assessments



Fig. 2 Seedling classification (left to right): 1—healthy: no pest attack; 2—oviposition: only oviposition signs; and 3—gall formation

A parallel analysis was performed to test the significance of the difference between species for infestation by *L. invasa*. The same model used for each species (described above) was adjusted in a joint analysis containing all species, therefore, considering the fixed effect of species in vector S . There is no error term in η as there is in traditional linear models. Instead, the equivalent of residual variance in GLMM depends on the distribution function (Nakagawa and Schielzeth 2010; Villemereuil 2018). We use the probit link function to associate η with Y under the assumption of residue $e \sim N(0, 1)$ (Gianola and Foulley 1983; Harville and Mee 1984).

Given the estimates of variance components, broad-sense heritability at the family level (h_f^2) and mean family level (h_{mf}^2), as well as the coefficient of determination or heritability of the seedlot (c_{ss}^2), were obtained for each species, as follows:

$$h_f^2 = \frac{\sigma_{f(ss)}^2}{\sigma_{f(ss)}^2 + \sigma_p^2 + \sigma_{Sf(ss)}^2 + \sigma_\epsilon^2}$$

$$h_{mf}^2 = \frac{\sigma_{f(ss)}^2}{\sigma_{f(ss)}^2 + \frac{\sigma_{ss}^2}{ss} + \frac{\sigma_{Sf(ss)}^2}{S} + \frac{\sigma_\epsilon^2}{k}}$$

$$c_{ss}^2 = \frac{\sigma_{ss}^2}{\sigma_{f(ss)}^2 + \sigma_{ss}^2 + \sigma_{Sf(ss)}^2 + \sigma_\epsilon^2}$$

where $\sigma_{f(ss)}^2$: genetic variance of family within seedlot; σ_{ss}^2 : variance of seedlot; $\sigma_{Sf(ss)}^2$: variance of season \times family interaction within seedlot; σ_ϵ^2 : residual variance (error); ss and S : number of seedlots and seasons, respectively; k : harmonic mean number of replicates (considering only live plants) per family.

The residual variance implicit in the underlying scale was set at 1 for the probit link function as described by Gilmour et al. (2015). The significance of the fixed effects was tested with the Wald F test and the likelihood ratio test was used to test the significance of the random effects. GLMMs were adjusted using the ASReml 4.1 program (Gilmour et al. 2015).

Results

The results showed significant differences among the studied species and the two evaluated periods (winter and summer), as well as season \times species interaction (supplementary material—Tables S1 and S2). Pest incidence and severity were significantly higher in the summer compared to winter and even *E. grandis* seedlings, a susceptible species, did not present high numbers of infected plants in the winter. Furthermore, *Eucalyptus urophylla* was the least attacked, with 90% healthy seedlings, *E. grandis* had the highest number of seedlings with galls, and the *E. urograndis* hybrid had intermediate susceptibility. Differences in susceptibility were observed for seedlots/provenances of *E. grandis* and *E. urophylla*, but not for *E. urograndis* species. Surprisingly, *E. camaldulensis*, which was expected to behave similarly to the most susceptible material, presented only high oviposition incidence (60%) and low gall incidence ($< 10\%$), even in the summer (Fig. 3).

The families showed significant differences in the susceptibility to *L. invasa*, where family heritability (h_f^2) ranged from 0.27 to 0.68 (Table 2). Furthermore, the gain expected from selection to control pest incidence and severity ranged from moderate to high since mean family heritability ranged between 0.68 and 0.87 for *E. camaldulensis* and *E. urograndis*, respectively.

Discussion

Environmental conditions play a significant role in the susceptibility to infestation by *L. invasa*, with pest incidence higher in the summer (higher temperatures) compared to winter due to the changing insect biology. *Leptocybe invasa* life cycle varies according to the world region, a cycle of 136 days has been reported in Israel while a shorter cycle of 80 days was observed in the Botucatu region (Cfa-Koppen classification), in Brazil, close to the 91 days reported in South Africa. However, still longer than the life cycle of 45 days observed in Thailand (Mendel et al. 2004; Sangtongpraow et al. 2011; Dittrich-Schroder et al. 2014). The periods more prone to the *L. invasa* infestation are rather different from other exotic eucalypt pests already introduced in Brazil since the most affected areas were the shoots and new eucalypt leaves while late spring and summer are the critical times of the year. Therefore, because the environmental conditions affect damage intensity (severity), some local and temporal effects are expected due to the varying climatic conditions observed over the years, so it is suggested to undertake further studies over monitoring periods of 2 years or longer instead of the two seasons of this study.

The eucalypt taxa showed different susceptibility to infestation by *L. invasa*. Silva et al. (2015) observed that half of 28 taxa (species and provenances) were susceptible to gall formation in Brazil. These authors reported that 70% of the species were susceptible, with the species of the *Eucalyptus* than *Corymbia* genera being the most susceptible and within the *Eucalyptus* genus, the *Exsertaria* and *Latoangulatae* sections were the

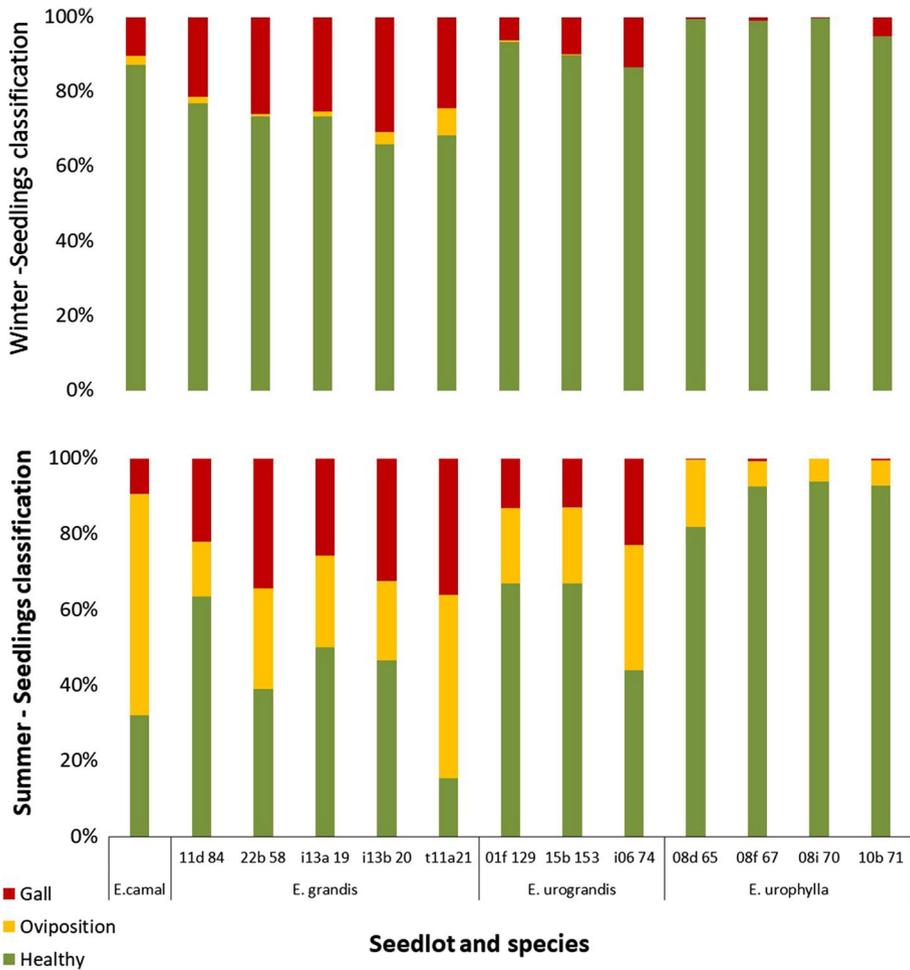


Fig. 3 Seedlings classification according to symptoms of an infestation by *L. invasa*, in the studied eucalypt taxa, during summer and winter. Healthy: no pest attack; oviposition: only oviposition signs; and gall: observed gall formation

most susceptible. This study evaluated in detail the most important species in Brazil, *E. urophylla* and *E. grandis* (Silva et al. 2019a, b) and their hybrids, belonging to *Latoangulatae* (Nicolle 2018). *Eucalyptus urophylla* was less susceptible than *E. grandis* while their hybrids had intermediate susceptibility. In South Africa, the most susceptible taxa were *E. nitens* × *E. grandis* hybrids followed by *E. grandis* × *E. camaldulensis* hybrid. However, even in hybrids from two susceptible species, not all trees had the same susceptibility levels due to the intraspecific variation of parental plants (Dittrich-Schröder et al. 2012). In this work, although the hybrids were not obtained from studied parent populations, they are representative of those species. In Brazil, *Leptocybe invasa* damaged few commercial plantations since the damage caused by the wasp is mitigated because *E. urophylla* (85% of plantations, pure or hybrid combinations) is used in most plantations (Assis et al. 2015). If the genetic base were *E. grandis* only, the damage

Table 2 Genetic parameter estimates [variance of seedlots (σ_{ss}^2), genetic variance of family in the seedlot ($\sigma_{f(ss)}^2$), variance of season \times seedlot interaction ($\sigma_{Sf(ss)}^2$), implicit residual variance in the underlying scale fixed 1 to the probit link function (σ_{ϵ}^2), family broad-sense heritability (h_f^2), coefficient of determination or seedlot heritability (c_{ss}^2) and family mean heritability (h_{mf}^2)] with the approximate standard error between brackets for *Eucalyptus* seedling species to the ordinal trait, *L. invasa* severity infestation

	<i>E. urophylla</i>	<i>E. grandis</i>	<i>E. camaldulensis</i> *	<i>Eurograndis</i>
σ_{ss}^2	1.96 (1.80)***	1.80 (1.96)***	NA	0.10 (0.48) ^{ns}
$\sigma_{f(ss)}^{2*}$	3.64 (0.74)***	5.73 (1.33)***	0.51 (0.27)***	5.29 (1.36)***
$\sigma_{Sf(ss)}^2$	0.49 (0.15)***	1.39 (0.32)***	0.40 (0.18)***	1.40 (0.35)***
σ_{ϵ}^2	1 (Fixed)	1 (Fixed)	1 (Fixed)	1 (Fixed)
h_f^2	0.51 (0.14)	0.58 (0.13)	0.27 (0.11)	0.68 (0.08)
c_{ss}^2	0.28 (0.19)	0.18 (0.16)	NA	0.01 (0.06)
h_{mf}^2	0.82 (0.09)	0.83 (0.07)	0.68 (0.16)	0.87 (0.05)

ns=not significant ($p > 0.05$); ***significant ($p < 0.001$); NA not applicable; σ_{ss}^2 was not calculated because the **E. camaldulensis* species refers to only one seedlot and, therefore, only the genetic variance between families (σ_f^2) was considered

would be greater as observed in the hybrid combinations in South Africa (Dittrich-Schröder et al. 2012).

The tolerance to *L. invasa* observed in most of the commercial plantations in Brazil resulted from the fact that *E. urophylla* was introduced earlier to increase resistance to canker disease. Crous et al. (2017) and Silva et al. (2019a, b) reported that this species has other good traits whether pure or in hybrid combinations, but neither study reported on tolerance to *L. invasa*, which is another good trait of the species. This tolerance was partially observed in the *E. urophylla* \times *E. grandis* hybrids, the most planted hybrid combination in Brazil (Assis et al. 2015). It is possible to obtain tolerant material considering the variation between species, provenance and families, however apparently little segregation occurs so that the resulting tolerance is intermediate regarding the parental material.

Eucalyptus camaldulensis from the *Exsertaria* section was the other species studied (Nicolle 2018). Although showing a lower than expected susceptibility in this study, *E. camaldulensis* has been reported as one of the most susceptible hosts in Vietnam, Uganda, Kenya and Brazil (Thua et al. 2009; Nyeko et al. 2010; Silva et al. 2015). However, the studied seedlot had good tolerance and possibility to select tolerant individuals. Tolerance is probably a trait linked to the studied provenance (Notts Crossing and Katherine River), which was confirmed by a few field visits in Ghana, where the studied plants showed greater tolerance compared to species from other provenances planted side-by-side (Israel Vieira personal comments). This result may explain the species low heritability (h_f^2 ; Table 2), indicating less genetic variability from the evaluated families compared to other species. Additionally, it also indicates lower expected gain for the selection aiming at controlling pest incidence and damage severity since the families are genetically similar for this trait, showing lower mean family heritability (h_{fm}^2 ; Table 2) compared to the others.

Regions in Minas Gerais and Bahia (mainly As, Aw and Cwa by Koppen classification) where *E. camadulensis* is planted show *L. invasa* infestation in Brazil (Costa et al. 2008; Fernandes et al. 2014). Therefore, this provenance/local may be suitable (Notts Crossing and Katherine River) for pure or hybrid plantations in areas with gall

occurrence, where *E. camaldulensis* is commonly used to withstand drought or as a drought-tolerant source in hybrids.

The genetic control of pest incidence and severity in *E. urophylla* and *E. grandis* is little explained by seedlot provenance (c_p^2 of 0.28–0.18, respectively). On the other hand, seedlot had no effect on *E. urograndis* (c_p^2 0.01 and σ_p^2 not significant) (Table 2). However, at the family level, these species showed good genetic control for pest incidence and severity, and genetic variability among families explains more than 50% of the trait variation (h_f^2 0.51, 0.58 and 0.68 for *E. urophylla*, *E. grandis* and *E. urograndis*, respectively) (Table 2). In addition, the mean family heritability (h_{fm}^2) was of high magnitude, indicating that the selection of tolerant families could be used for pest management.

Our data from seedlings in the nursery are a good indicator of pest susceptibility; however, a slightly different susceptibility is expected in field infestation. Thua et al. (2009) studied 18 eucalypt species and observed *L. invasa* occurrence in 13 species of *Eucalyptus* and in one *Corymbia* species in the nursery. However, five species considered susceptible in nursery tests were not damaged in field conditions. Controlling environmental effects may improve genetic expression but it is necessary to consider many different aspects in the field, namely tree age, natural pest occurrence, such as “multiplication spots”, which increases pressure over the material, besides the genetic materials of nearby plots. Therefore, nursery selection for susceptible materials is important to aid researchers to understand their potential for field use. Care must be taken to not discard materials under controlled conditions.

Regarding the environmental effect on gall development, extrapolation of our results to different environments could be risky due to genotype and environment interaction. Therefore, studies under various environmental conditions could provide more accurate genetic parameters and check if genotype rankings remain consistent under a range of environments. Another possibility that needs to be further investigated is the change from juvenile to adult leaves, which occurs in the field for several eucalypt species and can change the susceptibility to pest attack.

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