The effect of three species of *Eucalyptus* on growth and fecundity of the *Eucalyptus* snout beetle (*Gonipterus scutellatus*)

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Summary

The *Eucalyptus* snout beetle, *Gonipterus scutellatus*, was first detected in NW Spain in 1991, in the area with the largest European eucalypt plantations. Feeding preferences in the field and the effect of three species of *Eucalyptus* on larval development, survival, and adult fertility were studied. It was estimated that individuals of *G. scutellatus* consume 1.2–1.7 g of fresh biomass in *Eucalyptus cinerea* and *E. globulus* during their development. Diet had a significant effect on larval survival and rate of development, the least suitable tree species being *E. obliqua*. Nevertheless, females fed with these eucalypt species or with an alternated diet containing all three eucalypts, did not produce significantly different numbers of larvae. In the field, *G. scutellatus* showed a marked preference for *E. globulus*, *E. longifolia*, *E. grandis* and *E. propinqua*, and completely avoided other species.

Introduction

Eucalypt plantations are widespread in temperate and tropical regions (Anonymous, 1997) because they grow at a high rate even on poor soils, making them highly productive. One of the reasons for the high productivity of eucalypt plantations in Europe is the absence of significant herbivore losses, especially by insects. Nevertheless in their country of origin, eucalypts are dramatically affected by herbivore insects (Morrow, 1977; Fox and Morrow, 1983), and in many parts of Australia, there is currently a generalized dieback phenomenon due to repetitive insect attacks (Lowman and Heatwole, 1992).

In Spain eucalypts are basically cultivated to produce paper. Two species are widespread: *E. globulus* Labill. (325 000 ha) and *E. camaldulensis* Dehnh. (175 000 ha; Montoya, 1995). In Galicia (NW Spain), monocultures of *E. globulus* are a basic resource in areas where agriculture is not profitable. There is a growing concern about

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the ecological effects of eucalypt plantations (Anonymous, 1997), mainly due to the losses of biodiversity because there are almost no herbivore insects feeding on *E. globulus* in the Iberian peninsula, which means that higher trophic levels are also scarce (Paiva, 1992). Productivity in these stands may reach a maximum of 60 m^3 ha^{-1} a^{-1}, but the mean productivity is 20 m^3 ha^{-1} a^{-1} (Calvo de Anta, 1992).

In theory, monocultures are intrinsically highly susceptible to insect outbreaks. Three Australian insect species have colonized NW Spain, but only the *Eucalyptus* snout beetle, *Gonipterus scutellatus* Gyllenhal, has produced significant damage. Outside Australia, *G. scutellatus* was first found in South Africa in 1916 (Tooke, 1955), but it is now widespread in Africa, America and Europe (Mansilla and Pérez Otero, 1996). Damage to eucalypts by *G. scutellatus* in South Africa is so intense that its presence is a factor limiting eucalypt planting in some localities (Lowman and Heatwole, 1992). Biological control of this species by means of the importation of *Anaphes nitens* (Hym. Mymaridae), an egg parasitoid, has been highly successful in many areas (Tooke, 1955; Kidd and Jervis, 1997).

G. scutellatus was first found in 1991 in NW Spain (Mansilla, 1992). It is now widespread and causing severe defoliation to eucalypt stands. In South Africa, susceptible varieties of *E. viminalis* Labill. begin to be attacked when the tree is about 2 years old and at 60 months of age the average height of these varieties is only 3.4 m, when the resistant varieties have reached 7.12 m (Richardson and Meakins, 1986). This is a clear example of the considerable losses that the attack of *G. scutellatus* can cause in susceptible species.

G. scutellatus is a generalist herbivore of *Eucalyptus* spp. In Australia its favorite food plant is *E. viminalis* (Tooke, 1955). In spite of this specialization, it has been recorded feeding on apple in New Zealand and Australia (Moutia and Vinson, 1945; Frappa, 1950; Tooke, 1955). Where the biological control of *G. scutellatus* is unsuccessful, the alternative is to use resistant host plant species. Nevertheless, there are no studies on the effects of different species of *Eucalyptus* on success of this herbivore. The first aim of this study was to measure the amount of biomass consumption and the effect of three species of *Eucalyptus* on growth and fecundity of *G. scutellatus*. Specific tests were carried out to find if a varied diet could improve female fecundity. If that were the case, a mixture of different species in the same plot should be avoided. Tests were also done to assess if this species of beetle can use apple leaves as food. Finally, the degree of attack by *G. scutellatus* was measured on 20 species of *Eucalyptus*, to obtain information on the resistant species that might be used in highly attacked areas.

Methods

Feeding experiments

Three species of *Eucalyptus* were used in the experiments: *E. globulus*, *E. obliqua* L'Herit. and *E. cinerea* F. Muell. ex Benth., respectively a frequently attacked species (and dominant in Galician plantations), one rarely attacked and one not attacked in South Africa (Tooke, 1935). To determine if *G. scutellatus* can feed on apple, apple leaves were provided to a group of 50 newly hatched larvae. All experiments were carried out in a climatic room at 21°C during 14 hours of light and 19°C during 10 hours of darkness. The humidity was 80 per cent. The first experiment was carried out to evaluate the biomass consumed during larval development. Three groups of 16 newly hatched larvae each were raised on leaves of the three eucalypt species. Offered leaves were weighed to the nearest 0.1 mg, by means of an electrobalance (Denver XE Series Model 50). During the first week of life, larvae were maintained in pairs, in Petri dishes 5 cm in diameter. The consumption obtained in this way was divided by two to estimate the consumption per larva. When larvae reached the second instar, they were isolated in Petri dishes (9 cm diameter), to evaluate individual larval consumption. Leaves were carefully selected, to obtain two groups with similar weight and surface area. Of these groups, one leaf was offered as food to the larvae and the other was used as a control to estimate the loss of weight of the leaves. Fresh biomass consumption was estimated by calculating the difference between the initial weight and the final weight of the leaf after 24 hours. This weight was corrected by multiplying this value by the ratio between the final and initial weights of control leaves.

The second experiment was carried out to evaluate the effect of eucalypt species on larval development and survival and adult weight. It was carried out with 300 newly hatched larvae. All the larvae emerged on the same day and were randomly assigned to three treatments with two replicates. Each group (50 larvae) received fresh leaves of *E. globulus*, *E. cinerea* or *E. obliqua* every 2 days. Larvae were maintained in 1-litre plastic boxes until pupation. They were weighed individually every 4 days. For pupation, larvae were transferred to similar containers with 5 cm of soil. Adults were weighed and sexed on the day of their emergence (about 1 month later).

The third experiment was carried out to evaluate the effect of eucalypt species on fecundity and fertility of the female beetles. Adult *G. scutellatus* were collected on 22 February 1997 near Pontevedra (42°27′N 8°36′W) when they were starting their reproductive activity. Adults were maintained together and the spontaneously formed pairs were randomly assigned to four treatments (10 pairs per treatment). Three treatments received fresh leaves of *E. globulus*, *E. obliqua* or *E. cinerea* every 2 days. The fourth treatment received one of the previous species every other day, in an alternate way. Each pair was kept in isolation in a tube 6 cm high by 3.5 cm diameter. Females were maintained with the male that they spontaneously accepted, since there is experimental evidence that females of some species can lay more or fewer eggs depending on the characteristics of their mate (Eberhard, 1996). Counts were made of the number of egg masses laid each day and the number of emerged larvae for 1 month (or until the death of the female).

Feeding preferences in the field

Feeding preferences were estimated in the eucalypt plots (established in 1955) at the Center of Forest Research of Lourizán (Pontevedra), at the end of the period of reproduction of *G. scutellatus* in the spring of 1996. To evaluate the preferences of *G. scutellatus* for different species of eucalypts, at least three trees per species were examined using binoculars. Damage by *G. scutellatus* is very characteristic and is concentrated on the terminal buds. An arbitrary scale was used, varying from 0 (absence of damage) to 5 (all the terminal branches severely attacked). If *G. scutellatus* has any preference for certain species it has the opportunity to choose among them in the same locality.

Results

Experiment 1. Leaf consumption in three species of Eucalyptus

Figure 1 shows the daily biomass consumed by the larvae. Results are similar for *E. globulus* and

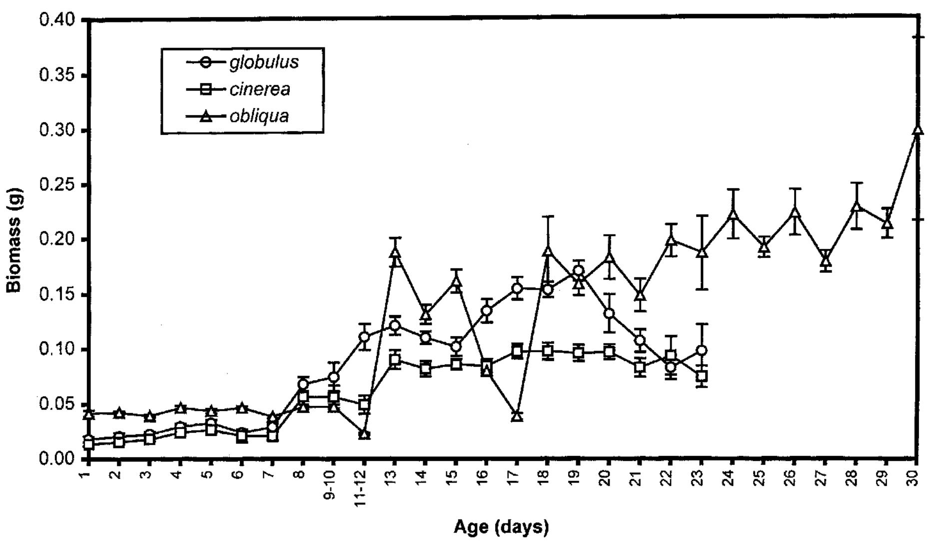

Figure 1. Daily biomass consumption by *Gonipterus scutellatus* larvae on three *Eucalyptus* species. The minumum on days 16 and 17 for *E. obliqua* was due to a temporary unavailability of fresh leaves. Mean ± s.e.

E. cinerea, with a daily consumption around 0.10–0.15 g for mature larvae. Consumption was lower towards the end of the feeding period for *E. globulus* because some larvae reached the prepupa and ceased feeding. By contrast, for *E. obliqua*, leaf consumption in the first instar larvae was very low and increased when the surviving larvae reached the second instar. Daily consumption remained around 0.2 g, with the exception of days 15 and 16, due to the unavailability of fresh leaves.

Throughout their development, larvae of *G. scutellatus* consumed a quantity of biomass that varied between 1.0 and 4.6 g (Table 1). Consumption was significantly different between tree species (ANOVA, $F = 209.34$ d.f. = 2, $P < 0.001$), being specially high *E. obliqua* (test Scheffé, $P < 0.05$). This species had low palatability, so that it was impossible to rear the 16 larvae initially used for the experiment (see also below). No differences were detected in the consumption of leaves of *E. globulus* and *E. cinerea*.

Experiment 2. Effect of food on the development of G. scutellatus

Different feeding treatments had very significant effects on survival probability (Figure 2). Larvae fed with *E. obliqua* suffered a higher mortality throughout the duration of the experiment. The groups fed with *E. globulus* and *E. cinerea* followed a very similar pattern, with the exception of the emergence of the adults, where one of the groups fed with *E. globulus* suffered a very high mortality (whose cause was unknown) during the pupal phase.

Table 1: Leaf consumption estimates during larval development of *Gonipterus scutellatus* in three eucalypt species

Species	Leaf consumption (g)	Minimum	Maximum
globulus	1.73 ± 0.07 (16)	1.33	2.41
cinerea	1.24 ± 0.03 (16)	1.01	1.55
obliqua	3.49 ± 0.17 (11)	2.65	4.63

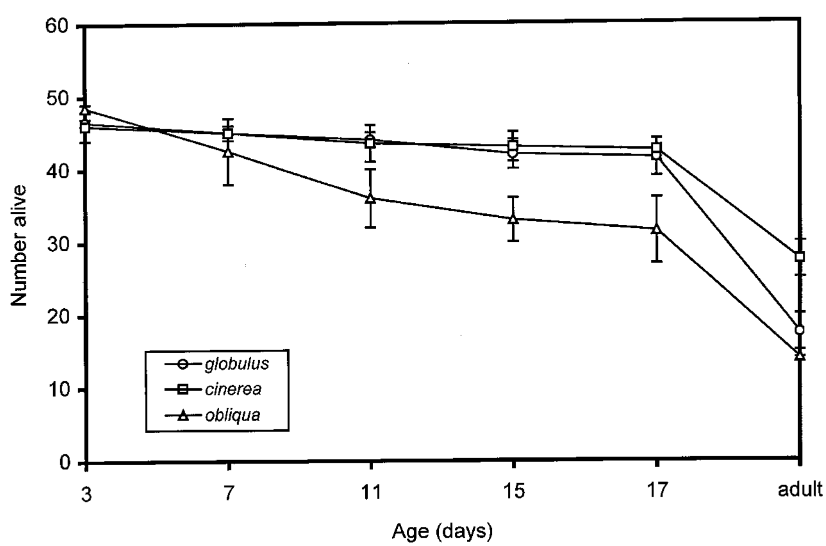

Figure 2. The effect of diet on the survival of *Gonipterus scutellatus* fed on three species of *Eucalyptus*. Mean ± s.e.

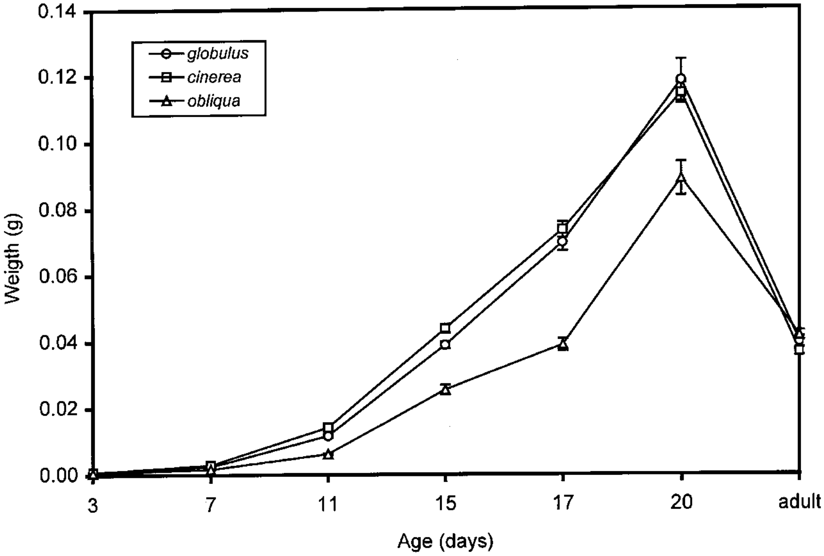

Figure 3. The effect of feeding on three species of *Eucalyptus* on the growth rate of *Gonipterus scutellatus*. Note that *E. obliqua* was clearly the worst diet. Mean ± s.e.

The growth curve is presented in Figure 3. It is clear that larvae fed with *E. obliqua* grew more slowly than those fed on the other two species. The effects of eucalypt species on the weight of larvae was significant from an early stage (3 days of age) and was manifested clearly in the mature larvae (ANOVA, $P < 0.05$ at all the ages). Significant differences between replicates were found in almost all the cases, and there was a food-replicate interaction in some ages of larvae.

Taking into account the effect of sex on adult weight (females are heavier than males), the weights of the adults were also affected by the food species (ANOVA, food, $F = 3.502$, d.f. = 2, $P = 0.034$; replicate, $F = 0.787$, d.f. = 1, $P = 0.377$; sex, $F = 34.477$, d.f. = 1, $P < 0.0001$; no interaction was significant). In this case the few adults reared on *E. obliqua* weighed more than the other treatments (Figure 3).

Experiment 3 Effect of food on fecundity and fertility of female beetles

Significant differences were detected among treatments in the number of egg masses laid ($F = 4.85$, d.f. = 3, $P = 0.006$). The average values (± s.e.) were 31.8 ± 1.8 egg masses (1.1 egg masses per day) for the females fed with *E. obliqua*, 18.8 ± 3.3 (0.7 per day) for *E. globulus*, 22.1 ± 2.2 (0.8 per day) for *E. cinerea* and 22.8 ± 2.6 (0.8 per day) for those that received the alternated food. Nevertheless, the numbers of larvae that hatched were not significantly different between treatments: 186.1 ± 25.9 for *E. obliqua*, 112.1 ± 25.6 for *E. globulus*, 123.9 ± 17.6 for *E. cinerea* and 122.2 ± 20.8 for alternated food ($F = 2.20$, $P = 0.105$).

The fertility of the females tended to diminish with increasing age (Figure 4; correlation between age and number of larvae produced: *E. globulus* Spearman $r = -0.31$, $P = 0.098$; *E. cinerea*, $r_s = -0.78$, $P < 0.001$; alternate, $r_s = -0.58$, $P = 0.001$), except for the group of females fed with *E. obliqua* that increased their fertility around 20 days of age ($r_s = 0.03$, $P = 0.896$).

Feeding preferences

The tests with young apple leaves indicated that *G. scutellatus* cannot feed on this species of tree: all the larvae died in 2–3 days, although they tasted the offered leaves. Table 2 presents the attack scores observed in different species of *Eucalyptus* in the plots at the Center of Forest Research of Lourizán (Pontevedra). The results indicate that besides *E. globulus*, *G. scutellatus*

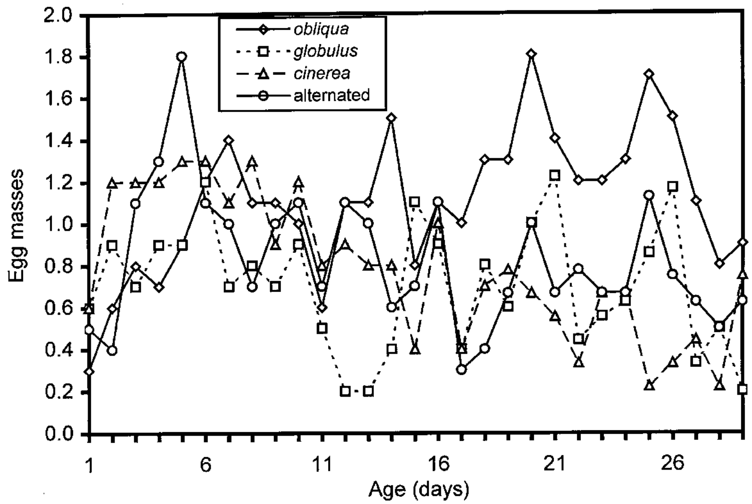

Figure 4. The effect of feeding on single *Eucalyptus* species or alternating species on fecundity of *Gonipterus scutellatus* females. Age refers to days since the start of the experiment.

Table 2: The attack degree by *Gonipterus scutellatus* on trees at the eucalypt plots of the Forest Research Center of Lourizán (NW Spain) in May 1997. The scale is arbitrary, from 5 (maximum attack) to 0 (no attack). Mean ± s.e. (*n*)

Species	Attack degree
globulus	5.0 ± 0.0 (3)
longifolia	5.0 ± 0.0 (3)
grandis	4.0 ± 0.0 (3)
propinqua	3.7 ± 0.3 (3)
ovata	2.7 ± 0.3 (3)
citriodora	2.5 ± 0.5 (2)
viminalis	2.0 ± 0.0 (3)
pauciflora	1.7 ± 0.7 (3)
microcorys	1.0 ± 0.8 (3)
rubida	0.8 ± 0.8 (4)
alpina	0.7 ± 0.7 (3)
dives	0.3 ± 0.3 (3)
pilularis	0.3 ± 0.3 (3)
saligna	0.3 ± 0.3 (3)
cornuta	0.0 ± 0.0 (3)
fastigata	0.0 ± 0.0 (3)
ficifolia	0.0 ± 0.0 (2)
niphoploia	0.0 ± 0.0 (3)
obliqua	0.0 ± 0.0 (2)
amygdalina	0.0 ± 0.0 (3)

attacks preferably *E. longifolia* Link and Otto, *E. grandis* Hill ex Maiden, *E. propinqua* Deane and Maiden, *E. ovata* Labill., *E. citriodora* Hook. *E. viminalis* and *E. pauciflora* Sieber ex Sprengel.

Samplings carried out in mixed plots agree with the data presented above. *G. scutellatus* clearly prefers to attack *E. globulus* rather than *E. obliqua* in plots located in Lourizán, where both species grow in mixture (Table 3). In Folgoso (Forcarei), *G. scutellatus* showed again a marked preference for *E. globulus* (Table 3). In this locality, the density of *G. scutellatus* in *E. globulus* reached a maximum of 78 egg masses and more than 600 larvae in a tree of about 4 m height, but only two attacked trees of *E. camaldulensis* were found among 50 examined. *E. camaldulensis* has low palatability for *G. scutellatus*, but surprisingly not for European insect fauna, since abundant geometrid larvae were found feeding on this species.

Discussion

In the different countries where it has spread, *G. scutellatus* has shown marked preferences for several species of eucalypt. Tooke (1935, 1955) presented a list of four groups of species in relation to the degree of attack observed in South Africa. On the island of Mauritius *E. robusta* Smith, *E. tereticornis* Smith and *E. kirtoniana* Maiden are cited as the most susceptible (Williams *et al.*, 1951). In Kenya, the attacked species were *E. globulus*, *E. maidenia* F. Muell., *E. robusta* and *E. smithii* R.T. Baker, while *E. saligna* Smith and

Table 3: The mean number of adults, egg masses and larvae of *Gonipterus scutellatus*, on different eucalypt species. Trees were 1–4 m high

Species and locality	Adults	Egg masses	Larvae
Lourizán, April 1996			
globulus (*n* = 60)	0.4 ± 0.11	22.0 ± 2.83	1.7 ± 0.31
obliqua (*n* = 60)	0.05 ± 0.03	8.2 ± 1.76	0.2 ± 0.09
Forcarei, April 1997			
globulus (*n* = 50)	0.4 ± 0.05	22.0 ± 3.11	147.2 ± 20.82
camaldulensis (*n* = 50)	0.0 ± 0.00	0.6 ± 0.09	2.7 ± 0.38
viminalis (*n* = 25)	0.1 ± 0.06	4.7 ± 2.96	5.8 ± 3.18

E. citriodora were cited as practically immune (Kevan, 1946). In Madagascar the most susceptible were *E. cornuta*, *E. viminalis*, *E. punctata*, *E. globulus*, *E. urnigera* and *E. rostrata* (= *E. camaldulensis*) (Frappa, 1950). In Italy *G. scutellatus* showed a clear preference for the leaves of *E. globulus*, not attacking the plants of *E. cinerea*, *E. gunnii* Hook. f., *E. polyanthemos* Schauer, *E. stuartiana* and *E. rostrata* (Arzone and Meotto, 1978). Finally in Galicia only damages to *E. globulus* and *E. obliqua* have been reported (Mansilla and Pérez Otero, 1996). Comparing the present results with the literature it clearly emerges that the species most cultivated in Galicia, *E. globulus*, is one of the favorite species of *G. scutellatus*. Nevertheless, the choice of eucalypt species by *G. scutellatus* clearly depends on availability, as the results of Clarke *et al.* (1998) indicate. They found that in Tasmania, *G. scutellatus* avoids *E. globulus* and *E. viminalis*, laying most eggs in *E. pulchella* Desf.

Among the species with the highest attacks in Lourizán, all except *E. grandis* and *E. citriodora* are mentioned by Tooke (1935) as highly susceptible. *E. grandis* does not appear in Tooke's list. The difference in the susceptibility of *E. citriodora* may be due to varietal differences, as was found for *E. viminalis* (Richardson and Meakins, 1986). On the other hand, the species least attacked in Lourizán are also those mentioned by Tooke (1935) as not very susceptible. The present evaluation of the damage by *G. scutellatus* was made without knowledge of Tooke's list, and therefore the results are independent. Clearly the most susceptible species in South Africa and other countries are the most susceptible in NW Spain. Results of this study might therefore be used as a guide to resistance in other countries.

It seems that *G. scutellatus* cannot survive on apple leaves. The literature citations of this species feeding on apples are probably due to adults that may be found resting on different species of plants, but they would not serve as a substitute food.

Significant differences in the leaf consumption by *G. scutellatus* were detected on the three studied tree species. However, the method used to estimate consumption is intrinsically subject to high errors, due to the different morphologies and densities of the leaves of the different species (Waller and Jones, 1989). Results indicate that the larvae of *G. scutellatus* consume approximately 11–15 times their final weight during their development, when they are fed respectively with *E. cinerea* or *E. globulus*, but the value rises to 27 times when the food is *E. obliqua* (the final weight of the larvae fed with this species was significantly smaller). Freitas (1991) fed the larvae of *Gonipterus gibberus* with leaves of *E. saligna*, a species lightly attacked according to Tooke (1935). It was estimated that *G. gibberus* consumed a total of about 12 times their weight, using the method of Waldbauer (1962), that accurately corrects for differences between the weight of experimental and control leaves. The value found in the present experiments with *G. scutellatus* fed with *E. globulus* and *E. cinerea* is therefore very similar, which suggests that the method was acceptable. When the density of *G. scutellatus* larvae is very high, they can produce almost complete defoliation of trees (one tree with 300 larvae can lose more than 500 g of fresh leaves). *Eucalyptus globulus* is nevertheless highly resistant to insect damage, because 50 per cent defoliation in spring or summer, but not in autumn, does not significantly reduce initial height growth

(Abbott and Wills, 1996). There are no estimates of productivity losses due to *G. scutellatus* on *E. globulus*, but if it behaves similarly to *E. marginata*, more frequent low intensity defoliations will reduce growth more than less frequent higher intensity defoliations (Abbott *et al.*, 1993).

The results of experiment 2 indicate that not all tree species are suitable. *E. cinerea* that supposedly was a non-attacked species (Tooke, 1935; Arzone and Meotto, 1978) was similar to *E. globulus* in its palatability. *E. obliqua*, a species that is used rarely in the field (Table 3), is not appropriate for larval development of *G. scutellatus*. Surprisingly, the few adults that emerged from larvae fed with this species were heavier than individuals fed with *E. globulus* or *E. cinerea*. This suggests that even less palatable species might be used by the insect if the preferred species are absent.

It is possible that if *G. scutellatus* has several eucalypt species in the same plot the fecundity of the females increases due to a richer diet. The results of this study suggest that the planting of several species with different palatabilities does not increase the fertility of *G. scutellatus*. Nevertheless, only three species were tested, and it is still possible that some combinations of species could produce the mentioned effect.

The surprising result obtained with *E. obliqua* and adult fecundity contrasts with the results mentioned for larval feeding. This might be due to females fed with *E. obliqua* being younger, because they did not reduce their fertility with age (Figure 4). The low fecundity of females fed with *E. globulus* could be due to the fact that they were fed from buds collected from trees showing little attack, and for that reason the least palatable trees of this species could have been selected unconsciously. This suggests that there is variability to the attack by *G. scutellatus* within *E. globulus* stands.

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References

Anonymous, 1997 *State of the World's Forests*. FAO, Rome, 200pp.

Abbott, I., van Heurck, P. and Burbridge, T. 1993 Impact of frequency and intensity of defoliation on growth of Jarrah (*Eucalyptus marginata*): an experimental study with saplings. *For. Ecol. Manage.* **56**, 175–183.

Abbott, I. and Wills, A. 1996 Growth of young *Eucalyptus globulus* in plantations after manual defoliation simulating insect herbivory. *CALMScience* **2**, 129–132.

Arzone, A. and Meotto, F. 1978 Reperti biologici su *Gonipterus scutellatus* Gyll. (Col. Curculionidae) infestante gli eucalipti della Riviera Ligure. *Redia* **61**, 205–222.

Calvo de Anta, R. 1992 *El Eucalipto en Galicia. Sus relaciones con el medio natural*. Univerisidade de Santiago de Compostela, Santiago de Compostela, 211pp.

Clarke, A.R., Paterson, S. and Pennington, P. 1998 *Gonipterus scutellatus* oviposition on seven naturally co-occurring *Eucalyptus* species. *For. Ecol. Manage.* **110**, 89–99.

Eberhard, W.G. 1996 *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton University Press, Princeton, N.J., 501pp.

Fox, L.R. and Morrow, P.A. 1983 Estimates of damage by herbivorous insects on *Eucalyptus* trees. *Aust. J. Ecol.* **8**, 139–147.

Frappa, C. 1950 Sur la présence de *Gonipterus scutellatus* Gyll. dans les peuplements d'*Eucalyptus* de Madagascar et l'acclimatement d'*Anaphoidea nitens* Gir., insecte auxiliaire parasite. *Rev. Pathol. Veg. Entolom. Agric. Fr.* **29**, 183–189.

Freitas, S. 1991 Observaçoes sobre a alimentaçao de *Gonipterus gibberus* (Boisduval, 1835) (Coleoptera, Curculionidae) em eucaliptos. *An. Soc. Entomol. Bras.* **20**, 333–338.

Kevan, D.K.M. 1946 The *Eucalyptus* weevil in East Africa. *East Afr. Agric. J.* **12**, 40–44.

Kidd, N.A.C. and Jervis, M.A. 1997 The impact of parasitoids and predators on forest insect populations. In *Forests and Insects*. A.D. Watt, N.E. Stork and M.D. Hunter (eds). Chapman and Hall, London, 49–68.

Lowman, M.D. and Heatwole, H. 1992 Spatial and temporal variability in defoliation of Australian eucalypts. *Ecology* **73**, 129–142.

Mansilla, J.P. 1992 Presencia sobre *Eucalyptus globulus* Labill de *Gonipterus scutellatus* Gyll. (Col. Curculionidae) en Galicia. *Bol. San. Veg. Plagas*, **18**, 547–554.

Mansilla, J.P. and Pérez Otero, R. 1996 El defoliador del eucalipto *Gonipterus scutellatus*. *Phytoma (España)* **81**, 36–42.

Montoya, J.M. 1995 *El eucalipto*. Mundi-Prensa, Madrid, 125pp.

Morrow, P.A. 1977 The significance of phytophagous insects in the *Eucalyptus* forests of Australia. In *The Role of Arthropods in Forest Ecosystems*. W.J. Mattson (ed.). Springer-Verlag, New York, 19–29.

Moutia, L.A. and Vinson, J. 1945 Le charançon de l'*Eucalyptus*, *Gonipterus scutellatus* Gyll. *Rev. Agricole et Sucriere de l'Ile Maurice* **24**, 25–30.

Paiva, J. 1992 As plantaciόns de eucaliptos e a flora e fauna portugesa. *Cadernos da Área de Ciencias Biolóxicas. Seminario de Estudos Galegos* **4**, 71–84.

Richardson, K.F. and Meakins, R.H. 1986 Inter- and intra-specific variation in the susceptibility of eucalypts to the snout beetle *Gonipterus scutellatus* Gyll. (Coleoptera: Curculionidae). *S. Afr. For. J.* **139**, 21–31.

Tooke, F.G.C. 1935 The eucalyptus snout beetle. Extent to which different kinds of *Eucalyptus* are attacked. *Fmg S. Afr.* **10**, 174.

Tooke, F.G.C. 1955 The *Eucalyptus* snout-beetle, *Gonipterus scutellatus* Gyll. A study of its ecology and control by biological means. *Ent. Mem. Dept. Agric. U. S. Afr.* **3**, 1–282.

Waldbauer, G.P. 1962 The growth and reproduction of maxillectomized tobacco hornworms feeding on normally rejected non-solanaceous plants. *Entomol. Exp. Appl.* **5**, 147–158.

Waller, D.A. and Jones, C.G. 1989 Measuring herbivory. *Ecol. Entomol.* **14**, 479–481.

Williams, J.R., Moutia, L.A. and Hermelin, P.R. 1951 The biological control of *Gonipterus scutellatus* Gyll. (Col. Curculionidae) in Mauritius. *Bull. Entomol. Res.* **42**, 23–28.

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