Retrospective host testing of *Aconophora compressa*; reproduction and survival on the target weed, *Lantana camara*, and non-target species

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Summary *Aconophora compressa* Walker (Hemiptera: Membracidae) has been released as a biological control agent against *Lantana camara* L. (lantana) (Verbenaceae), a noxious pastoral and environmental weed. In no-choice tests conducted post-release, adult survival was statistically equivalent across the four verbenaceous plant taxa tested, *Citharexylem spinosum* L. (fiddlewood), lantana and *Duranta erecta* L. (var. geisha girl and var. Sheena's gold), but much lower on the two non-verbenaceous host plants, *Jacaranda mimosifolia* D.Don (jacaranda) (Bignoniaceae) and *Myoporum acuminatum* R.Br. (Myoporaceae). Significantly more eggs were deposited on fiddlewood than on lantana, geisha girl and Sheena's gold; oviposition was not observed on jacaranda or *M. acuminatum*. Nymphal development was fastest on fiddlewood followed by lantana, geisha girl, and Sheena's gold. Nymphal survival across verbenaceous host plants ranged from 42 to 65%, but differences were not significant. *A. compressa* can survive and reproduce on lantana and build up to high numbers in laboratory settings but this is rarely observed in the field. This disparity between laboratory and field results warrants further investigation.

Keywords *Aconophora compressa*, sap-sucking bug, host testing, lantana, biological control.

INTRODUCTION

Aconophora compressa was released in Australia from Mexico for biological control against lantana in 1995 (Palmer *et al.* 1996). Host-specificity testing prior to its release implied a narrow host range (Palmer *et al.* 1996). Since its release, however, *A. compressa* has been found on several plant species in the field, but is mostly associated with fiddlewood, an exotic ornamental tree (Palmer *et al.* 2004, Dhileepan *et al.* in press). Outbreaks of *A. compressa* on urban fiddlewood have caused complete defoliation of the trees, and honeydew from the insects allows black sooty mould to grow on anything beneath the trees, resulting in numerous complaints from the public (Maher *et al.* 2004).

Initial field surveys across several host species showed that fiddlewood was the most heavily used host by *A. compressa* in terms of percentage of infested plants, percentage of infested branches, and numbers of individuals per plant; lantana was second with much lower use (Dhileepan *et al.* in press). These two hosts were the only ones upon which *A. compressa* development occurred throughout the year All other hosts sampled (geisha girl, Sheena's gold, jacaranda and *Aviciennia marina* (Forssk.)) were located nearby fiddlewood trees on which *A. compressa* was abundant (Dhileepan *et al*. in press).

In the study presented here, we quantified *A. compressa* development time, survival (adults and nymphs) and reproduction on six host plant species under laboratory conditions. This work was undertaken to investigate the disparity between post-release field observations and pre-release laboratory derived expectations.

MATERIALS AND METHODS

Plants Six plant taxa were included in no-choice tests: fiddlewood, lantana, geisha girl, Sheena's gold, jacaranda, and *M. acuminatum*. Plants that became heavily infested with mites or aphids during tests were excluded from analysis because *A. compressa* mortality increased substantially on infested plants.

Adult survival and reproduction Ten males and ten female newly emerged adults were placed in cages with a single plant of one of the test species. Additional plants were required for cages with fiddlewood, and occasionally lantana, required additional plants to sustain nymphs and adults. Individuals readily moved between plants as long as branches were touching. Two trials of five replicates each were conducted in a randomised complete block design, commencing on April 4, 2005 and July 2, 2005. The numbers of live adults and egg batches deposited were recorded every other day for 70 days.

The effect of host species on adult survival was analysed using parametric survival methods (Tableman and Kim 2004). All slope estimates were made with respect to fiddlewood, i.e. slope estimates of other treatments, plus standard errors, that included zero were not significantly different from fiddlewood. Weibull and log-logistic distributions were fitted to trials one and two respectively, therefore slope estimates for trials one and two were not directly comparable.

The total number of eggs laid and the mean number of eggs laid per egg batch (square root transformed) was assessed using linear mixed-effects ANOVA (Pinheiro and Bates 2000). The mean time taken for the first female to oviposit was calculated for each host plant.

Three replicates of Sheena's gold and one of geisha girl were excluded due to mite or aphid infestation.

Nymphal survival and development Between 50 and 75 newly emerged 1st instar nymphs were transferred to cages with a single plant of one of each test plant except *M. acuminatum*. Nymphs were then counted by instar three times per week until all had died or emerged as adults. Newly emerged adults were removed from the cage. Ten replicates (one plant per cage) were set up for each species, except Sheena's gold (four replicates) and *M. acuminatum* (not assessed in this trial).

The effect of host species on nymphal survival was assessed using a one way ANOVA. The effect of host plant on total nymphal development time was determined using a one way ANOVA; jacaranda was excluded from the analysis because nymphs completed development on only one replicate. Two replicates of fiddlewood and lantana and one replicate of geisha girl and Sheena's gold were excluded due to mite or aphid infestation.

RESULTS

Adult survival and reproduction Adult survival on fiddlewood, lantana, geisha girl, Sheena's gold, and jacaranda did not differ statistically (Table 1). However, the survival curve for jacaranda were similar to that for *M. acuminatum* (Figure 1), which was significantly lower than on any other host plant (Table 1, Figure 1).

The total numbers of eggs and egg batches laid were significantly influenced by host plant, with fiddlewood supporting most oviposition (Table 2). Lantana received approximately 60% of the number of eggs laid on fiddlewood and were distributed across a similar number of egg batches (Table 2). The number of eggs laid on geisha girl and Sheena's gold were statistically similar, with approximately 25% or less eggs laid and significantly fewer egg batches than on fiddlewood (Table 2). Oviposition was first recorded on fiddlewood, followed by lantana, geisha girl and Sheena's gold (Table 3). No oviposition was observed on jacaranda or *M. acuminatum*.

Nymphal survival and development Nymphal survival was not significantly different between host plants ($F = 1.7653$, $df = 3$, $P = 0.1795$), but ranged between 42 to 65% (Table 4). Nymphal development was completed on only one of ten plants (replicates) of jacaranda. Nymphal development time was, however, highly significantly different across host taxa ($F = 33.592$, $df = 3$, $P < 0.0001$) with development times on each host being significantly different from all others (Table 4).

Table 1. Slope estimates, by trial, of the effect of host plant species on adult survival of *A. compressa*. See methods for model details.

Source	Slope estimate	Standard error	Z	P
Trial 1				
Intercept	4.5862	0.3213	14.274	<0.0001
Geisha girl	0.3418	0.5323	0.642	0.521
Jacaranda	−0.4939	0.8125	−0.608	0.543
Lantana	0.0672	0.5325	0.126	0.900
M. acuminatum	−1.7044	0.3623	−4.705	<0.0001
Sheena's gold	0.2777	0.8333	0.333	0.739
Trial 2				
Intercept	4.220	0.4248	9.9346	<0.0001
Geisha girl	−0.102	0.5757	−0.1776	0.859
Jacaranda	−0.020	0.7459	−0.0268	0.979
Lantana	0.553	0.6310	0.8757	0.381
M. acuminatum	−0.968	0.7332	−1.3201	0.187
Sheena's gold	0.515	0.6351	0.8103	0.418

DISCUSSION

Although *A. compressa* was introduced as a lantana specialist, it performed significantly better on fiddlewood (Tables 2–4). In terms of the total number of eggs laid, the number of egg batches laid, the time taken to initiate oviposition, and nymphal development time, *A. compressa* performs best on fiddlewood, followed by lantana, geisha girl and Sheena's gold, respectively. Nevertheless, adult survival did not vary significantly across the verbenaceous hosts. Thus far, there is little basis to distinguish between jacaranda and *M. acuminatum*, the only two non-verbenaceous hosts. There was no oviposition on either host plant, and adult survival did not differ between them.

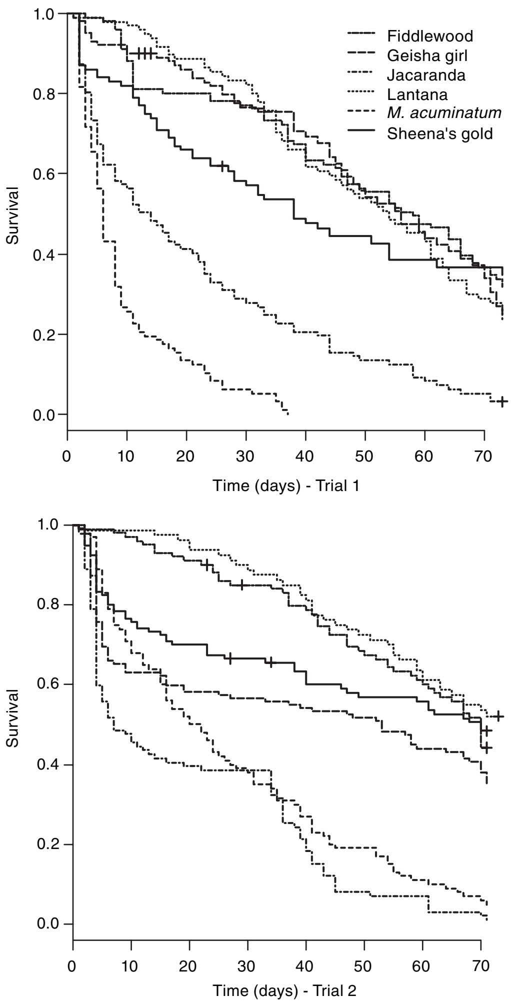

Figure 1. Survival of adult *A. compressa* over 70 days on six plant species for trials one (above) and two (below).

Recent host testing of *A. compressa* conducted in South Africa provides comparable results to that found in this study for lantana; adult survival was high and an average of 51.7 ± 3.6 eggs were laid per egg batch (Heystek and Baars 2005) (Table 2). However, Heystek and Baars (2005) found no adult survival on jacaranda after three weeks, and less then 30% survival on *D. erecta* (variety not specified) with no egg batches laid. Survival in our study was much higher for both jacaranda and *D. erecta* (geisha girl and Sheena's gold) (Figure 1). In addition, oviposition began on both geisha girl and Sheena's gold within three weeks in trial 1 but not trial 2 (Table 3). Differences in host plant variety and physiological condition, perhaps modified by abiotic conditions, could account for the differential survival recorded across the studies. If Heystek and Baars (2005) had tested survival for more than three weeks, it is possible that oviposition would have been initiated on *D. erecta*.

Table 2. Mean total number of eggs and mean number of egg batches laid on verbenaceous host plants ± standard errors. Different letters in each column indicate significant differences between treatments.

Treatment (n)	Total eggs	Egg batches
Fiddlewood (10)	1298 ± 84 a	13.3 ± 1.1 a
Lantana (10)	740 ± 140 b	10.6 ± 0.6 a
Geisha girl (9)	334 ± 54 c	6.4 ± 0.9 b
Sheena's gold (7)	174 ± 34 c	5.4 ± 1.4 b

Table 3. Preoviposition period (days) for *A. compressa* across host types ± standard errors (n).

Treatment	Trial 1	Trial 2
Fiddlewood	11.0 ± 0.6 (5)	14.4 ± 0.5 (5)
Lantana	15.6 ± 0.8 (5)	15.6 ± 0.5 (5)
Geisha girl	19.0 ± 1.6 (4)	32.4 ± 3.6 (5)
Sheena's gold	31.0 ± 9.7 (3)	41.5 ± 4.6 (5)

Table 4. Mean nymphal survival (1st instar to adult) of *A. compressa* and nymphal development time ± standard errors. Different letters in each column indicate significant differences between treatments.

Treatment (n)	Survival (%)	Development time
Fiddlewood (8)	65.4 ± 7.4 a	40.6 ± 1.3 a
Lantana (8)	50.8 ± 8.7 a	48.8 ± 2.5 b
Geisha girl (9)	47.2 ± 8.1 a	59. 0 ± 2.7 c
Sheena's gold (3)	41.9 ± 7.4 a	75.4 ± 8.8 d
Jacaranda (1)	36.2	66.0

Further experiments will be completed to assess nymphal survival and development on *M. acuminatum*, Sheena's gold and jacaranda. However, given that nymphal development was completed on only one replicate of jacaranda, considerable attention should be given to ensure that host plants are as acceptable as possible to the insect. Of course, this proves difficult when dealing with the biology of an insect that is largely unknown. Increasing replication in tests, as well as including plants of different sizes or condition, is a strategy that should have been followed in pre-release tests to increase chances of detecting non-target species that can be utilised by the insect.

Whereas fiddlewood was clearly the most appropriate host for *A. compressa* in laboratory trials, lantana still attracted considerable oviposition (approximately 60% of that on fiddlewood) and high adult and nymphal survival (Figure 1, Table 1 and Table 2). Clearly, the low abundance of adults, nymphs and egg batches on lantana in the field (Dhileepan *et al.* in press), relative to densities on fiddlewood, cannot be explained by survival and reproduction parameters of the insect on lantana, relative to fiddlewood, under laboratory conditions. Given that lantana and fiddlewood often exist in close proximity in the field, it is unlikely that spatial considerations cause the disparity between field and glasshouse results. The lower use of lantana by *A. compressa* in the field compared to fiddlewood must thus have an alternative explanation. Two possible explanations exist: 1) *A. compressa* does not locate lantana effectively, i.e. the insects are not attracted to the plant, or 2) *A. compressa* locates lantana but, once on the plant, rejects it for some reason.

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REFERENCES

Dhileepan, K., Trevino, M. and Raghu, S. (in press). Temporal patterns in incidence and abundance of *Aconophora compressa* (Hemiptera: Membracidae), a biological control agent for *Lantana camara*, on target and non-target plants. *Environmental Entomology*.

Heystek, F. and Baars, J.R. (2005). Biology and host range of *Aconophora compressa*, a candidate considered as a biocontrol agent of *Lantana camara* in Africa. *Biocontrol* 50, 359-73.

Maher, P.E., Davis, B.J., Day, M.D., Mackey, A.P., Palmer, W.A. and Snow, E.L. (2004). What happens when a biocontrol agent attacks exotic but desired ornamentals? Proceedings of the 14th Australian Weeds Conference, eds B.M. Sindel and S.B. Johnson, pp. 187-9. (Weeds Society of New South Wales, Sydney).

Palmer, W.A., Day, M.D., Dhileepan, K., Snow, E.L. and Mackey, A.P. (2004). Analysis of the non-target attack by the lantana sap-sucking bug, *Aconophora compressa*, and its implications for biological control in Australia. Proceedings of the 14th Australian Weeds Conference, eds B.M. Sindel and S.B. Johnson, pp. 341-4. (Weeds Society of New South Wales, Sydney).

Palmer, W.A., Willson, B.W. and Pullen, K.R. (1996). The host range of *Aconophora compressa* Walker (Homoptera: Membracidae): a potential biological control agent for *Lantana camara* L. (Verbenaceae). *Proceedings of the Entomological Society of Washington* 98, 617-24.

Papaj, D.R. and Rausher, M.D. (1983). Individual variation in host location by phytophagous insects. *In* 'Herbivorous insects: host-seeking behaviour and mechanisms', ed. S. Ahmad, pp. 77-124. (Academic Press, New York, USA).

Pinheiro, J.C. and Bates, D.M. (2000). 'Mixed-effects models in S and S-PLUS'. (Springer-Verlag, New York).

Tableman, M. and Kim, J.S. (2004). 'Survival analysis using S: analysis of time-to-event data'. (Chapman & Hall/CRC, Boca Raton).