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Source: *Journal of Applied Ecology*, Vol. 24, No. 3 (Dec., 1987), pp. 935-944

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2403990>

Accessed: 29/09/2014 15:02

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EFFECTS OF ADULT AND LARVAL *CYRTOBAGOUS SALVINIAE* ON THE FLOATING WEED *SALVINIA MOLESTA*

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SUMMARY

(1) Experiments were conducted in field cages to assess the effects of adult and larval *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae) on *Salvinia molesta* D.S. Mitchell (Salviniaceae) growing under different conditions of temperature and availability of nitrogen.

(2) Adult *C. salviniae* fed on meristematic tissues in buds and on young leaves and roots (probably meristematic tissue) of *S. molesta*. Larvae tunneled through buds, rhizomes and roots.

(3) Destruction of meristematic tissues was compensated for by increased development of buds, but compensation was complete only at high levels of nitrogen availability.

(4) Adult feeding for 14 days did not reduce relative growth rate (RGR) of ramets or of whole plant weight. Though roots were destroyed by adults, compensatory growth maintained the RGR of root weight.

(5) The plant was not able to compensate for ramets killed through larvae destroying vascular tissues. RGRs were reduced by 0.0018 ramets per ramet per day and 0.0014 g per g per day by each larvae present during the period from hatching to pupation, on plants initially containing seven ramets and four buds.

INTRODUCTION

Salvinia molesta D. S. Mitchell (Salviniaceae) is a sterile floating fern which has become an important pest of tropical and southern-hemisphere temperate freshwaters (Holm *et al.* 1977). Biological control of the weed has been achieved in tropical areas of Australia (Room *et al.* 1981; Forno 1985, 1987), India (Joy *et al.* 1986), Namibia (Giliomee 1986), Botswana (I. W. Forno, personal communication) and in Papua New Guinea (Thomas & Room 1986) with the weevil *Cyrtobagous salviniae* Calder & Sands (Coleoptera: Curculionidae).

S. molesta consists of ramets connected by rhizomes to form two-dimensional colonies (Room 1983). Each ramet has a node, three leaves, one of which is modified to act as a root (Croxdale 1981), an apical bud and lateral buds. The apical bud grows to form a new ramet extending the branch and colony by iteration and new plants are formed by fragmentation. Usually only one lateral bud develops on a ramet to form a side branch but others (secondary buds) may develop, forming secondary growth in nutrient-rich waters and as compensatory growth in response to manual removal of buds (Julien & Bourne 1986).

Damage to *S. molesta* is caused by both larvae and adult weevils; larvae feed mainly inside rhizomes and adults feed on buds (Forno, Sands & Sexton 1983; Forno & Bourne

TABLE 1. Experiments with *Cyrtobagous salviniae* arranged in increasing order of RGR

(a) Adults					
Experiment	1	2	5	4	3
Starting date	19 April 1983	13 Sept. 1983	7 Feb. 1984	10 Jan. 1984	28 Nov. 1983
Duration (days)	14	14	14	14	14
RGR number of ramets					
No urea	0.021	0.023	0.034	0.037	0.107
Urea†	0.021	0.023	0.039	0.046	0.115
Mean leaf temperature (°C)	22	23	29	28	25
Mean water temperature (°C)*	23	18	28	28	25
Nitrogen content (% dry weight)					
Initial	0.92	1.12	1.18	1.22	1.78
Final: no urea	**	1.27	1.26	1.40	1.92
urea†	**	1.30	1.45	1.60	2.18
Potassium content (% dry weight)					
Initial	2.42	3.02	4.23	4.03	3.50
Final: no urea	**	1.88	2.65	2.50	2.45
urea†	**	1.76	2.44	2.32	2.29
(b) Larvae					
Experiment	3	2	1		
Starting date	8 April 1984	28 Feb. 1984	27 Oct. 1983		
Duration (days)	29	16	20		
Mean leaf temperature (°C)	24	29	28		
Mean water temperature (°C)*	24	28	23		
Nitrogen content (% dry weight)					
Initial	1.47	1.35	1.13		
Final	1.54	1.07	1.27		
Potassium content (% dry weight)					
Initial	3.36	3.91	2.80		
Final	2.16	2.63	2.00		

* Mean water temperatures predicted from maximum air temperatures using the equation of Room & Kerr (1983).

** Results unreliable because of delay in drying plants.

† Two concentrations of urea combined (15 or 30 g per cage).

1986). Sands, Schotz & Bourne (1983) suggested that the most destructive feeding was by larvae. The aim of this study was to measure and compare the response of *S. molesta* to damage by adults and larvae at densities that occur in the field in Australia. In experiments in Brazil, reductions in biomass of *S. molesta* were recorded following damage by adults and their larval progeny (Forno & Bourne 1986). In laboratory studies with very high densities of adults, biomass was reduced (Forno & Bourne 1985). *S. molesta* compensated for loss of reproductive potential but not for biomass following manual removal of buds (Julien & Bourne 1986) but no information was available on the response of the weed to damage by insect feeding under field conditions.

We report the results of five experiments on the interaction of *S. molesta* with adults of *C. salviniae* and three experiments on the interaction with larvae, on Wappa Dam, Queensland (26° 35'S). As temperature and N affect the growth rate of the plant (Room 1986a) and the rate of development of larvae (Sands, Schotz & Bourne 1983), experiments were conducted over a year to obtain different combinations of temperature and concentration of N in the plant. Results of these and other experiments are being used to

TABLE 2. Growth of *Salvinia molesta* and mean damage per plant resulting from one adult of *Cyrtobagous salviniae* feeding for 14 days. Means for plants with and without adults are shown, except when not significantly different, for all experiments. The estimates are means of three urea treatments

Experiment	1	2	5	4	3
RGR number of buds					
No adults	0.028	0.028	0.039	0.053	0.130
Adults	-0.026	0.003	0.022	0.012	0.137
Net number of buds					
No adults	3.9	4.0	6.9	8.5	25.2
Adults	2.0	3.1	5.8	5.7	27.7
Buds destroyed by adults	3.0	2.9	3.1	3.6	2.5
Total buds with adults	5.0	6.0	8.9	9.3	30.2
Buds damaged by adults	0.7	0.9	1.7	2.2	1.7
% net buds damaged	35	29	29	38	6
RGR number of leaves	0.021	0.023	0.037	0.043	0.113
Total leaves	16.1	16.6	23.7	25.8	68.1
New leaves	4.1	4.6	9.7	11.8	54.1
Damaged leaves	4.1	5.5	9.9	12.9	24.2
Damaged leaves (% of total)	25	33	42	50	36
Percentage of leaf damaged	13	25	20	24	22
Roots destroyed by adults			1.4	2.5	0.8
Secondary growth per plant					
No adults	0	0	0	0.1	1.2
Adults	0	1.6	1.9	2.4	8.0
Scored new growth					
Net new growth					
No adults	2.7	2.8	6.2	7.5	35.9
Adults	1.7	2.4	5.7	6.5	37.4
New growth destroyed	0.8	1.0	0.8	0.9	0.6
Total new growth with adults	2.5	3.4	6.5	7.4	38.0
RGR weight					
Whole plant	0.021	0.050	0.062	0.078	0.112
Roots	0.057	0.080	0.130	0.133	0.162
Tops: no adults	0.009	0.028	0.038	0.045	0.081
adults	0.009	0.030	0.040	0.052	0.086
Buds: no adults	-0.032	0.037	0.027	0.032	0.117
adults	-0.136	-0.043	0.021	-0.042	0.119

develop a simulation model of interactions between the weed, biological control agents and the environment (Room *et al.* 1985), to help with control strategies for the weed.

MATERIALS AND METHODS

In the five adult experiments and three larval experiments, thirty-six and sixteen floating cages, respectively, were held 1 m apart and 15 m from and parallel to the bank of Wappa Dam. The cages were 500 mm × 500 mm × 500 mm with sides of plywood, a top of fine nylon mesh and an open base. Each cage contained a floating sheet of styrofoam with a 200 mm diameter hole cut in it. *S. molesta* plants consisting of four terminal main branch ramets with side branches (usually comprising seven ramets and four buds) were trimmed from colonies growing in the mat on the dam and placed, five per cage, in loose contact with each other in the hole in the foam.

In the experiments with adults, some plants were supplied with additional N in the form of urea, to increase the range of plant N experienced by adults. There were three replicates of a factorial design of four insect and three urea treatments. Adult *C. salviniae*, selected

TABLE 3. Growth of *Salvinia molesta* and damage per plant by larvae of *Cyrtobagous salviniae*. Estimates are means for larval density of three per plant

Experiment	3	2	1
RGR number of ramets*			
No larvae	0.028	0.031	0.034
Larvae	0.025	0.024	0.025
Net nodes*			
No larvae	15.8	11.5	13.8
Larvae	15.2	10.3	11.6
Nodes destroyed	0.6	1.2	2.2
Total nodes with larvae	15.8	11.6	13.8
RGR number of buds			
No larvae	0.029	0.030	0.035
Larvae	0.025	0.008	0.015
Net buds			
No larvae	9.2	6.5	8.1
Larvae	8.2	4.6	5.6
Buds destroyed	3.6	3.3	3.3
Total buds with larvae	11.8	7.9	8.9
Roots destroyed with larvae	2.2	1.9	1.4
RGR weight whole plant			
No larvae	0.038	0.052	0.041
Larvae	0.037	0.048	0.036
RGR weight of roots			
No larvae	0.078	0.122	0.062
Larvae	0.080	0.103	0.053
RGR weight of tops	0.016	0.033	0.026
RGR weight of buds	0.023	0.010	0.003

* Number of ramets is equivalent to number of nodes (see Results).

randomly from laboratory cultures, were placed in the cages at densities of 0, 0.6, 1 and 1.4 adults per plant. Urea (46%N) was applied at the rate of 0, 15 and 30 g per cage as granules in dialysis tubes suspended among the *S. molesta* roots and replaced every third day. The five experiments were conducted between April 1983 and January 1984 and each was limited to 14 days so that any larvae developing from eggs laid by adults would have little time to influence plant growth.

In the larval experiments, there were four replicates of four larval densities, 0, 2, 4 and 8 larvae per plant for experiment 1, and 0, 1, 2 and 4 larvae for experiments 2 and 3. Larvae from laboratory cultures were placed separately in buds, except with eight larvae per plant when two were placed in each of the four buds on the plants. The larval experiments ran for 16–29 days, between October 1983 and April 1984, depending on the mean development time for larvae, predicted from temperature and concentration of N in the plant for each experiment (Sands, Schotz & Bourne 1983).

At the beginning and end of the experiments, the rhizome of each plant was mapped. Each bud, node and root was assessed as undamaged, damaged or destroyed (absent or rotting) and damage to each leaf was rated either, 0, <25%, <50%, <75%, <95% or 100%. New growth was scored as 1 for a new ramet and 0.25, 0.5 or 0.75 for buds, depending on the stage of development. Thirty plants at the beginning, and all plants at the end of each experiment, were washed in deionized water, dissected into buds, tops and roots, and each portion was dried to constant weight at 70°C. Prior to the dissection of plants, adults and pupae were removed. Some insects were not recovered and a few larvae

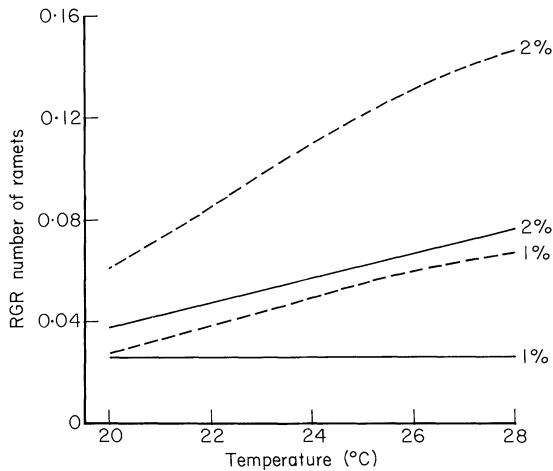


FIG. 1. The relationship of RGR ramets to water temperature for observed trimmed (—) and for predicted (Room 1986a) untrimmed (---) plants of *Savina molesta* containing N at 1% and 2% dry weight.

TABLE 4. Estimated regression coefficient (b) for density of adults and larvae on plant growth with standard error (S.E.) and the mean value for one insect

	b	S.E.	Mean
Adults			
Number of buds destroyed	1.16	0.36	3.0
Number of roots destroyed	0.59	0.026	1.6
Number of new growths destroyed	0.30	0.111	0.8
Proportion of leaves damaged	0.12	0.019	0.37
RGR number of buds	-0.032	0.003	0.003
RGR weight of buds	-0.058	0.011	-0.055
Larvae			
Number of nodes destroyed			
Experiment 1	0.66	0.060	0.77
2	0.35	0.067	0.51
3	0.19	0.067	0.20
Total buds produced			
Experiment 1	0.51	0.093	8.3
2	0.37	0.104	7.2
3	0.97	0.104	9.9

may have remained in the tissues. The percentage dry weight of N, P and K in the combined material from each cage was determined after grinding (Johnson *et al.* 1985). Leaf temperatures were measured using a Grant recorder and air temperatures were recorded in a Stevenson screen using a thermograph.

Data analysis

Analysis of variance was carried out on the combined data from the adult experiments to assess differences between experiments, adult numbers, applied urea and interactions.

Cage means of the plant parameters were used for the analysis, with transformation to make variance independent of the mean. Covariate analysis confirmed that addition of urea to a cage did not affect the growth of plants in adjacent cages. Results from the three larval experiments were also combined for analysis, allowing for the different numbers of larvae in the experiments. As four and eight larvae per plant gave the same results, suggesting that two larvae could not survive in one bud, both treatments were included in the analyses as four larvae per plant. For brevity and clarity, estimates have been presented for one adult and three larvae per plant in Tables 2 and 3, respectively, and density effects reported separately.

In a regression analysis relating RGR of trimmed plants to temperature and N, data from experiments by Room & Thomas (1986a), covering a range of plant N from 0.8% to 2.8% and temperatures from 18 to 28 °C, were included.

RESULTS

Growth of undamaged S. molesta

The relative growth rates (RGR) of ramets (r) of undamaged *S. molesta* for the two sets of experiments ranged from 0.021 to 0.115 $r\ r^{-1}\ \text{day}^{-1}$ (S.E. 0.002) at mean leaf temperatures of 22–29 °C and final plant N of 1.1–2.2% (S.E. 0.02) (Tables 1, 2 and 3). These measured growth rates of plants trimmed from colonies were lower than those predicted for uncrowded intact plants (Room 1986a). Figure 1 shows the relationship of RGR ramets of trimmed plants to water temperature and plant N together with that for untrimmed plants. Temperature had much less effect on the growth rate when plants were trimmed.

Experiments with adults of C. salviniae

Damage by adults

Adults destroyed or damaged buds, roots and the youngest leaves of *S. molesta* (Table 2). Young buds were killed by adults feeding on them. Feeding on older buds damaged leaflets but not the meristematic tissue and ramets developed having damaged leaves. Both damage and destruction increased with increasing insect density over the range 0.6–1.4 adults per plant (Table 4) but the fitted lines did not extrapolate to zero damage without insects, indicating some competition between adults.

The number of buds destroyed (3.0 per plant) and the score for new growth destroyed (0.8 per plant) by one adult were substantially the same for all experiments (Table 2) but the percentage of buds damaged was much less (6%) when the RGR was high in Experiment 3 than in the other experiments (29–38%) (Table 2).

Most new leaves were damaged by adults but the average damage to each leaf was slight (<26%). The percentage of total leaves damaged ranged from 25% to 50% (S.E. 1.4). The number of roots destroyed differed between the three experiments for which data were collected (S.E. 0.17 in Table 2), fewer being destroyed in treatments with urea. This was the only effect of added urea on damage by adults, hence results presented in Table 2 are means of all urea treatments.

Plant growth

Adult feeding stimulated the production of buds by 30.6% (S.E. 3.4) but there was a significant net loss ($P < 0.001$) of buds except in Experiment 3 (Table 2). The RGRs of

number and weight of buds decreased linearly as adult density increased from 0 to 1.6 per plant with the other four experiments (Table 4).

Some stimulation of growth occurred in the leaves and rhizomes as RGR top weight (excluding buds) increased slightly but significantly for all experiments (Table 2) up to one adult but the effect was reduced at the higher density. Mean RGRs top weight for 0, 0.6, 1 and 1.4 adults per plant were 0.040, 0.044, 0.044 and 0.042 g g⁻¹ day⁻¹ (S.E. 0.008), respectively. Similarly, feeding stimulated root growth as RGR root weight was maintained though some roots were destroyed. Secondary growth of lateral buds also increased with adult feeding (Table 2), averaging 1.95 (S.E. 0.40) buds per adult.

The score for undamaged new growth was the same for plants with or without adults in Experiment 3 but was reduced by 22% (S.E. 1.10) by adults in the other experiments (Table 2). However, RGR ramets and RGR whole plant weight were not reduced by adult feeding (Table 2).

Experiments with larvae of C. salviniae

Damage by larvae

Larvae damaged leaves and destroyed the buds on which they were placed, as well as nodes, other buds, sections of rhizome and roots (Table 3). The roots that were destroyed were not always on damaged ramets. Destruction of nodes increased with larval density (Table 4).

Only about 12% of leaves were damaged, ratings for damage being 29–44% per leaf. Numbers of damaged leaves increased with density of larvae but the damage per leaf did not. The same number of buds was destroyed in each experiment, 1.04 (S.E. 0.045) buds per plant per larva, though experiments ran for different times. Numbers of nodes and roots destroyed differed (Table 2) but the number of ramets with either or both the node and root destroyed was the same for the three experiments (the mean for three larvae was 2.5) and increased with density of larvae; 0.731 (S.E. 0.052) per larva.

Plant growth

Feeding by larvae also stimulated bud production, and destruction of buds resulted in a decrease in net RGR number of buds (Table 3). The total number of buds produced increased with numbers of larvae, the greatest effect occurring in the low-temperature experiment that ran for the longest time (Table 4). The stimulation of secondary lateral buds by larvae was minor, <0.2 per plant per larva.

Plants with and without larvae produced the same number of new ramets but destruction of nodes by larvae resulted in a significant reduction of RGR ramets; 0.0018 (S.E. 0.0004) per larva (Table 3). Destruction of a node prevented further buds developing from that ramet.

In each experiment, there was a consistent reduction in RGR whole plant weight of 0.0014 (S.E. 0.0004) per larva. Root weight rather than top weight was reduced by larval feeding (Table 3). However, larvae had no effect on RGR weight of roots in plants containing the most N, which were also the plants on which the most roots were destroyed.

Nitrogen and potassium in plant tissue

Feeding by adults or larvae did not significantly affect whole-plant N. Plant N increased during most experiments (Table 1). Adding urea (both levels) increased N by

0.21% dry weight (S.E. 0.03) only in the last three adult experiments giving an increase of 0.0076 (S.E. 0.0015) in RGR ramets but urea did not affect whole-plant weight.

Plant K decreased during the experiments, the greatest loss being from plants attacked by adults, 0.015% (S.E. 0.022) per adult, and by larvae, 0.04% (S.E. 0.01) per larva and in plants with applied urea, 0.15% (S.E. 0.03). There were no significant changes in P content.

Throughout these experiments, damage on plants without adults or larvae was negligible.

DISCUSSION

Stable mats of *S. molesta* in Australia have an average density of 601 plants m^{-2} (Julien & Forno, unpublished data) and control of the weed by *C. salviniae* occurs with populations of less than 500 adults m^{-2} (Forno 1987). This is close to the mean of one adult per plant used in our experiments. The theoretical stable age distributions of *C. salviniae* achieved with unrestricted population growth (Sands, Schotz & Bourne 1986) predict that three larvae will be associated with each adult. Therefore, the mean densities of 2.3 larvae and one adult used in these experiments are representative of weevil populations under control conditions.

Damage by adults and larvae together have achieved biological control of *S. molesta* in numerous tropical countries where RGRs ramets have exceeded those recorded in our experiments (Room 1986b; Room & Thomas 1986a). Since the plant fully compensated for damage by adults when the RGR ramets was high and larvae had a greater effect than adults in reducing growth, it follows that the larval stage of *C. salviniae* was the most important in controlling the weed.

S. molesta compensated for insect damage by increasing total production of buds but this was insufficient to prevent net losses, except in the experiment with adults and high plant N. Compensation following destruction of meristematic tissues by adults, which maintained RGR ramets and increased secondary bud production, was similar to that observed in plants disbudded manually (Julien & Bourne 1986) except that there was no reduction in root weight. Destruction of roots—submerged leaves (Croxdale 1981)—by adults was observed for the first time during these experiments and probably resulted from feeding on root meristems. The plants compensated in the same way as in the tops, and root weight was maintained. It is likely that the small amount of damage to leaves had little effect on growth. Feeding by adults had the same effect on the habit of the plants as manual disbudding (Julien & Bourne 1986) but, since buds were continuously destroyed, traumatic reiteration was restricted.

Compensation by the plant for damage caused by larvae tunnelling in the rhizome was less successful. Feeding inside the rhizome destroyed vascular tissue, disrupting the mobilization of assimilates required for regrowth following damage (Jameson 1963; Davidson & Milthorpe 1966; Crawley 1983). There was little secondary lateral-bud stimulation by larvae compared with that by adults. The destruction of nodes prevented regrowth from those ramets, while destruction of rhizomes isolated one ramet from another. Consequently, little change occurred in the habit of the plant. The number of roots destroyed increased with plant N, but some may have been shed by the plant in response to damage (Sands, Schotz & Bourne 1983). Compensation for loss of roots by maintaining root weight occurred only in one experiment, when plant N was highest.

The fact that adults destroyed the same number of buds in each experiment suggests that damage to tops by adults may be independent of temperature and N. However, temperature and N affect adult fecundity, oviposition behaviour and longevity (Sands, Schotz & Bourne 1986) and, hence, the population dynamics of *C. salviniae*. Such changes in population dynamics affect insect-plant interactions and have been observed to alter rates of damage to *S. molesta* (Forno, Julien & Room, unpublished data).

Room & Thomas (1985) observed increases in concentrations of N in new growth by plants damaged by *C. salviniae*. In our experiments damage by larvae and adults had no effect on N in whole plants. Had discrete portions of plants been analysed, changes in concentration probably would have been detected. Manual disbudding of *S. molesta* stimulated increased N in new growth but the increase was not detectable in the whole plant analysis (Julien & Bourne 1986). The correlation between concentration of N in plants and production of secondary buds (Julien & Bourne 1986) was maintained when plants were damaged by adults (Tables 1 & 2).

Room & Thomas (1986b) found a negative correlation ($r = -0.67$, $P < 0.001$) between concentration of K and damage by *C. salviniae*. We found that the loss of K increased with increased densities of insects and that damage by larvae caused a greater loss than damage by adults. There was a consistent loss of K from all plants and this may have been due to the damage inflicted manually by trimming plants.

Trimming plants to a uniform size reduced relative growth rates and probably reduced the capacity of the plant for regrowth and compensation after damage. Fewer ramets per plant resulted in fewer resources from which assimilates could be drawn and fewer nodes with dormant buds for regrowth. Untrimmed plants may have no advantage, however, when vascular tissues are destroyed preventing movement of assimilates.

The most damaging herbivores are those that destroy the ability of a plant to maintain a regenerative link between shoot and root (Harper 1977). This appears to be the case when comparing the effects of different stages of the same species of herbivore. The internal damage to plant tissues caused by larvae was more debilitating to *S. molesta* and plants were less able to compensate for such damage than when only meristematic tissue was destroyed by adults.

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(Received 30 September 1986; revision received 9 March 1987)