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Trirhabda geminata (Coleoptera: Chrysomelidae) RESISTANCE TO THE DIRECT IMPACT OF SIMULATED ACIDIC FOG ON LARVAL GROWTH AND MORTALITY

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Abstract

The direct effects of acidic fog (pH 2·75) upon the mortality and growth of Trirhabda geminata *Horn (Coleoptera: Chrysomelidae), the dominant herbivore of the California coastal sage scrub,* Encelia farinosa *(Compositae: Asteraceae), were evaluated. Although there was a consistent pattern among and between experiments, suggesting that acidic fogs could reduce insect growth and survivorship within the first few days following application of treatments, an exposure to three consecutive, 3-h fogs over a five day period did not significantly affect mortality, biomass gain, or larval growth rate. There are two important implications from this study. First, even the highly acidic fogs found in southern California will have minimal direct effects on* T. geminata *performance. Second, the impacts on* T. geminata *biology observed in previous studies were likely mediated by host-plant responses to acidic-fog episodes.*

Keywords: Acidic fog, coastal sage scrub, Insecta, *Trirhabda geminata, Encelia farinosa.*

INTRODUCTION

The impact of acid deposition on vegetation has been extensively reviewed (Cowling, 1982; Lee, 1982; Linthurst *et al.*, 1982; Treshow, 1984; Shriner, 1986; Treshow & Anderson, 1989). Typical responses of plants to acidic deposition include lesion development, weathering of cuticular wax, foliar leaching, premature abscission and abnormal growth or development and ultimately death of the plant. The majority of studies determining the effects of acidic deposition on biotic systems have investigated the influence of acidic rain. The physiological effects of acidic fog, however, are generally less well known. Acidic fogs typically exhibit a much lower pH (a pH of 2·0–2·5 is not uncommon) than other forms of acidic precipitation, and in southern California, acidic fogs contain considerably more nitric acid than the acidic rains of eastern North America (Waldman *et al.*, 1982; Hoffman, 1984; Hoffman *et al.*, 1985). The chemical composition of coastal California acidic fogs, and its relation to photochemical pollutants, have been documented in detail by Waldman *et al.* (1982).

Initial studies documenting the effects of acidic fog on plants describe a sequence of cellular collapse progressing from the upper to lower epidermis in affected vegetation (Middleton *et al.*, 1950; Thomas *et al.*, 1952). Under both laboratory and field conditions, long-term exposure to fogs generates necrotic lesions, alters the physical characteristics of the leaf surface, increases foliar cation and carbohydrate leaching, decreases net photosynthesis, reduces plant growth and crop yield, and may even cause plant death (Granett & Taylor, 1981; Granett & Musselman, 1984; Musselman & Sterrett, 1988; Musselman & McCool, 1989; Paoletti *et al.*, 1989*a,b*; Takemoto *et al.*, 1989; McCool *et al.*, 1990; Mengel *et al.*, 1990; Trumble & Walker, 1991).

Acidic fogs also are capable of influencing host-plant susceptibility and suitability to insect herbivores (for reviews see: Bedford, 1986; Riemer & Whittaker, 1989; Heliövaara & Väisänen, 1993). Plant tissue concentrations of water, nitrogen, soluble proteins, amino acids and defensive compounds have all been shown to be affected by acidic fog deposition (Trumble & Hare, 1989; Dercks *et al.*, 1990; Paine *et al.*, 1993, 1994; Redak *et al.*, unpublished data). Our previous work has focused upon determining the effects of acidic fog on the *Encelia farinosa* Gray (Asteraceae) – *Trirhabda geminata* Horn (Coleoptera: Chyrsomelidae) system. *Encelia farinosa* is a dominant shrub plant in the coastal and interior sage scrub communities surrounding the large urban areas of southern California. Its major insect herbivore is the beetle *T. geminata*, an *Encelia* specialist that feeds on plant foliage both as a larvae and an adult. The insect is active during the rainy season with larvae emerging to feed on young plant tissues in early winter. Larvae pass through three stadia and pupate in the soil. Adults are active in late winter to early spring and oviposit at this time. Summer aestivation occurs in the egg stage. The reader is referred to Redak *et al.* (in press) for a more thorough review of this insect's biology. Our earlier research investigating the impact of acidic fog in this system demonstrated that acidic fogging results in increased foliar concentrations of soluble proteins and water. These foliage quality changes resulted in increased insect larval growth and adult and larval consumption rates (Paine *et al.*, 1993, 1994; Redak *et al.*, unpublished data).

Previous studies concerning the impact of acidic fogs upon plant–insect interactions investigated the indirect, or plant-mediated, effects of such fogs upon insect herbivores. They all involved treating host plants with an acidic fog and subsequently using insects as bioassay organisms to detect changes in host-plant quality that may have occurred with acidic deposition. Our objective here was to determine the direct effects of acidic fog on *T. geminata* biology by exposing the insect directly to acidic-fog episodes. Specifically, we wished to determine the direct effect of acidic fog upon the mortality, biomass gain, and growth of *T. geminata* larvae.

MATERIALS AND METHODS

Experiment A: Direct effect of acidic fog upon *T. geminata* mortality

Trirhabda geminata larvae (second instar) were collected from areas of interior coastal sage-scrub habitat on the Box Springs Mountains located adjacent to and southeast of the University of California, Riverside, California. Larvae were brought into the laboratory greenhouse and maintained on *E. farinosa* cuttings taken from the sampling areas. Cuttings were kept alive for *ca* 1 week in plastic vials (50 ml) containing water and were replaced as needed.

Acidic (pH 2·75) or control (pH 5·60) treatment fogs were applied to groups of approximately 100 replicate second instar *T. geminata*. During fog application, insects were held in 1 mm screened plastic cages (15 cm high by 20 cm diameter). Fogs readily moved through the screening and into the interior of the cages. The experiment was replicated four times (four paired groups of acidic and control fogged insects consisting each of approximately 100 insects).

Acidic fogs were prepared by adjusting distilled water to pH 2·75 with reagent grade nitric and sulfuric acid mixed at a 2·5 : 1 (v : v) ratio. This acid ratio is typical of fogs in southern California (Waldman *et al.*, 1982). Control fogs consisted of distilled water adjusted to a pH of 5·60. The additional heavy-metal ionic components known to occur in southern California fogs were added to both control and acidic fog solutions (Munger *et al.*, 1983). Fogs were created within 1 m^3 chambers using a fogging apparatus designed by Musselman *et al.* (1985) and operated at 7·03 kg cm^{-2}. Within the greenhouse, temperatures during fogging ranged from 22 to 26°C. A shade cloth cover over the fogging chamber was used to prevent light intensities from exceeding 300 $\mu E\ s^{-1}\ m^{-2}$, thus more closely simulating actual conditions during an acidic fog episode. As not all treatment groups were placed in a single chamber for a particular fogging episode, four chambers were utilized, and chambers for control and acidic fogs were alternated between fogging episodes to eliminate potential chamber effects.

Acidic or control fogs were applied to each group of insects for a 3-h period every other day for a total of three applications over 5 days. Following fog applications, insects were held in paper cups and fed fresh field-collected *E. farinosa* foliage *ad libitium*. For each replicate experiment, mortality was determined 24 h after the second and third fogging episodes (Days 4 and 6 of the experiment, respectively). To determine the direct effect of acidic fog on beetle mortality, the number of insects surviving and dying due to treatment applications was compared between treatment groups using the Fisher exact test (Zar, 1984). All data analyses were conducted using SAS 6.03 (SAS, 1988).

Experiment B: Direct effects of acidic fog upon *T. geminata* growth

Eight second-instar larvae (collected as above, starved for 24 h and weighed using an analytical balance to the nearest 0·01 mg) were placed on each of 60 1-year old *E. farinosa* plants. Plants were germinated from wild seed by a commercial nursery (Tree of Life Nursery, San Juan Capistrano, CA). All plants were potted in 4-litre pots with UC mix No. 3 soil (Matkin & Chandler, 1957) and were watered and fertilized (Osmocote™, N : P : K = 14 : 14 : 14 at 2·5 g pot^{-1}, Sierra Chemical Co., Milpitas, CA) as necessary. To prevent larvae from moving from their assigned host-plant, insects were held on experimental plants using plastic acetate confinement cones coated with teflan. Each plant supporting eight larvae was randomly assigned to either an acidic fog (pH = 2·75) or control fog (pH = 5·60) treatment (30 replicate plants supporting eight larvae per treatment).

Acidic or control fogs were applied to each replicate plant and associated larvae for a 3-h period every other day for a total of three applications over 5 days. As not all plants within a treatment were placed in a single chamber for a particular fogging episode, six chambers were utilized, and chambers for control and treatment fogs were alternated between fogging episodes to eliminate potential chamber effects. Insects were allowed to feed and grow throughout this period and for an additional 5 days following the final fog application. On Day 10, larval mortality for each replicate plant was determined. Larvae were then removed from their host plants, starved for 24 h, and their biomasses determined. At the time of removal, larvae were in the third instar. Using the average initial (n = 8 insects $plant^{-1}$) and final (n = 0–8 insects $plant^{-1}$, depending on mortality) insect biomass estimates, the average larval biomass gain and larval growth rate were calculated for each experimental replicate (Waldbauer, 1968; Kogan & Parra, 1981). To determine the direct effect of acidic fog on larval growth, a two sample t-test was used to compare the mean values of average biomass gain between treatments. As the mortality and growth data were non-normal with unequal variances, the Wilcoxon–Mann–Whitney test was used to compare average growth rates and per cent mortality between treatments (Zar, 1984).

Experiment C: Direct and plant-mediated effect of acidic fog upon *T. geminata* growth

Using the above methodology (see Experiment B

above), 160 1-year-old *E. farinosa* plants growing in 4-litre pots were randomly assigned to either an acidic (pH = 2·75) or control fog (pH = 5·60) treatment. Each treatment was replicated 80 times (80 plants per treatment) and fogs were applied to each replicate plant for a 3-h period every other day for a total of three applications over 5 days.

Simultaneous to the production of experimental plants, acidic (pH 2·75) or control (pH 5·60) treatment fogs were applied to groups of approximately 400 field-collected third instar *T. geminata* as in Experiment A above. Again, acidic or control fogs were applied to each group of insects for a 3-h period every other day for a total of three applications over 5 days. Between fog applications, insects were held in paper cups and fed fresh field collected *E. farinosa* foliage *ad libitium*.

Following insect and plant treatment applications, four acidic-fogged or four control-fogged larvae (starved for 24 h and weighed to the nearest 0.01 mg) were randomly assigned and placed on each of the control or acidic fogged experimental plants. This approach yielded a two-factor experimental design with fog treatment of plant and fog treatment of insects as main effect factors, each at two levels (control and acidic). Each of the four treatment combinations (control fogged plants–control fogged insects, control fogged plants–acidic fogged insects, acidic fogged plants–control fogged insects, and acidic fogged plants–acidic fogged insects) was replicated 40 times. Larvae were held on experimental plants using confinement cones as described above. Insects were allowed to feed and grow for 7 days at which time larvae were removed from their host plants, starved for 24 h, and their biomasses determined. Average larval biomass gain and average larval growth rate was calculated for each experimental replicate. The relative importance of direct and plant-mediated effects on beetle growth was assessed using two-way analysis of variance with plant fog and insect fog as main effect treatments, each at two levels (control and acidic) with average larval biomass gain and average larval growth rate as dependent variables (Zar, 1984).

RESULTS

Experiment A: Direct effect of acidic fog upon *T. geminata* mortality

Neither two or three 3-h exposures of acidic fogs to second instar *T. germinata* had detectable impact on beetle mortality (Table 1). When mortality was assessed 24 h after the second or third of three fogging episodes, larval mortality was low in both control-fogged and acidic-fogged groups. Regardless of treatment application or experimental replicate, larval survivorship ranged from approximately 95 to 100%.

Experiment B: Direct effects of acidic fog upon *T. geminata* growth

The biomass gained by second instars was not affected by the direct application of acidic fog to larvae feeding on *E. farinosa* ($t_{0\cdot05,\ 2\text{-tail}} = 0\cdot577$, df = 46, $P = 0\cdot567$; Fig. 1(A)). Acidic fog-treated larvae gained an average of 12·6 mg (±1·4 SEM) while control fog-treated larvae gained 13·8 mg (±1·4 SEM). Additionally, the average growth rate of these larvae was not affected by the acidity of treatment fog ($Z = 0\cdot640$, $P = 0\cdot522$; Fig. 1(B)). Acidic fog-treated larvae demonstrated an average growth rate of 0·114 mg mg^{-1} day^{-1} (±0·009 SEM) as compared to 0·124 mg mg^{-1} day^{-1} (±0·006 SEM) for control-treated larvae. As with Experiment A, the mortality of larvae treated with acidic fog was not significantly different than larvae treated with control fog ($Z = 0\cdot752$, $P = 0\cdot452$; Fig. 1(C)). Mortality for acidic fog-treated insects was 26·3% (±3·5 SEM); that for control fog-treated insects was 30·0% (±3·9 SEM).

Experiment C: Direct and plant-mediated effects of acidic fog upon *T. geminata* growth

Larvae reared on control fog-treated plants exhibited larger average biomass gains than larvae reared on acidic fog-treated plants (5·12 mg ± 0·78 SEM for controls vs 3·71 mg ± 0·78 SEM for acidic treated, Fig. 2(A)); however, this difference was not significant (Table 2). Similarly, larvae reared on control fog-treated plants demonstrated larger average growth rates than those reared on acidic fog-treated plants (0·0527 mg mg^{-1} day^{-1} ± 0·0079 SEM for controls vs

Table 1. Direct impact of acidic fog (pH 2·75) on *T. geminata* second instar mortality

Replicate experiment	Treatment fog	After two 3-h fogs		After three 3-h fogs	
		Survival (%)	Fisher Exact (*P*)	Survival (%)	Fisher Exact (*P*)
1	Control	96·7		100·0	
	Acidic	98·9	0·624	96·9	0·250
2	Control	98·1		96·8	
	Acidic	96·0	0·438	100·0	0·246
3	Control	99·1		99·0	
	Acidic	94·3	0·089	99·0	1·000
4	Control	96		100·0	
	Acidic	96·8	1·000	100·0	NC[a]
Pooled	Control	97·6		98·9	
	Acidic	96·5	0·393	99·4	0·686

[a]Both treatments exhibited no mortality; the statistic was not calculable.

0·0384 mg mg^{-1} day^{-1} ± 0·0079 SEM for acidic treated, Fig. 2(B)), yet this difference also was not significant (Table 2). Additionally, there was no significant interactions between treatments with regard to their impact on larval biomass gain or growth rate (Table 2, Fig. 2(A) and (B)).

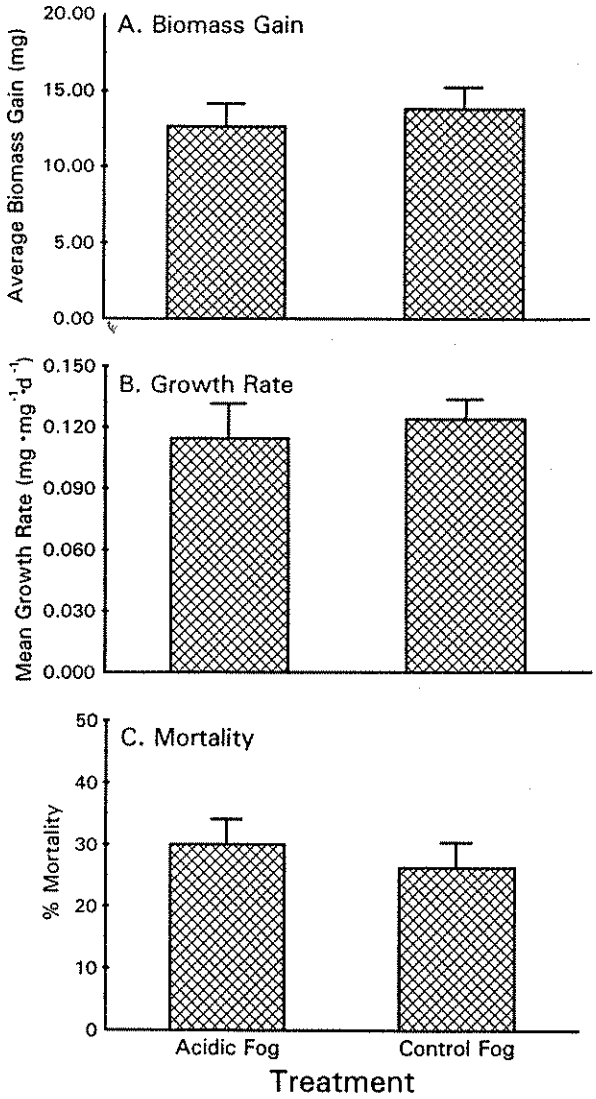

Fig. 1. The direct effect of acidic fog upon *T. geminata*. (A) Average biomass gain. (B) Average larval growth rate. Plotted values are means; vertical lines indicate 1 SEM.

Table 2. Analysis of variance for the direct and plant-mediated effects of acidic fog on insect biomass gain and growth

Source	df	Mean square	*F*	*P*
Dependent variable: Biomass gain				
pH of fog applied to plants	1	73·89	1·60	0·208
pH of fog applied to insects	1	39·01	0·85	0·359
Interaction	1	10·71	0·23	0·631
Error	146	46·13		
Dependent variable: Growth rate				
pH of fog applied to plant	1	0·0076586	1·61	0·206
pH of fog applied to insects	1	0·0008914	0·19	0·665
Interaction	1	0·0003559	0·08	0·785
Error	146	0·0047443		

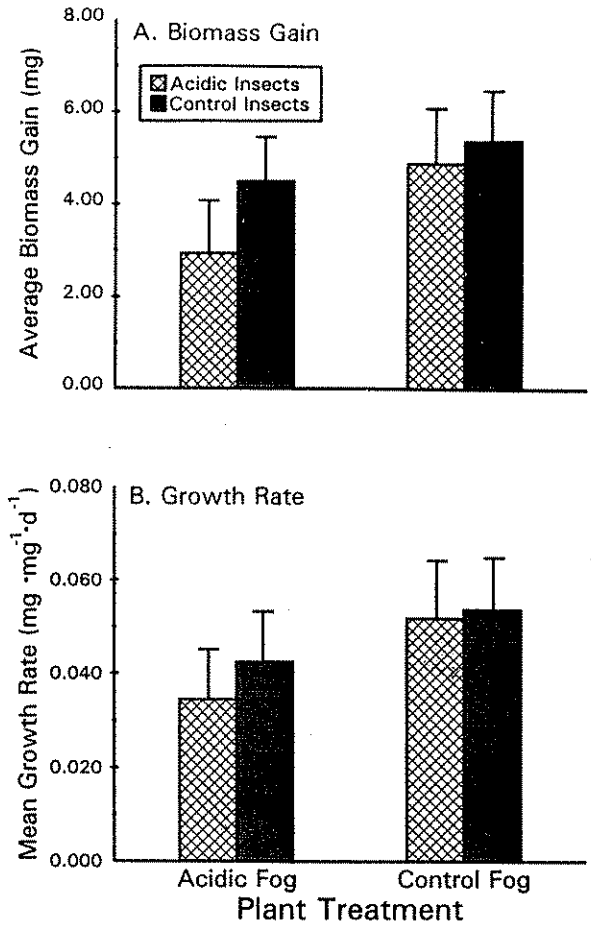

Fig. 2. The direct and plant-mediated effects of acidic fog upon *T. geminata*. (A) Average biomass gain. (B) Average larval growth rate. Plotted values are means; vertical lines indicate 1 SEM.

DISCUSSION

Our results indicate that direct deposition of acidic fog upon *T. geminata* larvae does not significantly affect their mortality or growth. While few studies have investigated the direct impact of acidic deposition upon insect herbivores (Heliövaara & Väisänen, 1993), the lack of impact we document here coincides with the general pattern exhibited in other terrestrial systems (Gunnarsson & Johnsson, 1989; Heliövaara *et al.*, 1992; Heliövaara & Väisänen, 1993). Indeed, with the exception of direct toxicity in aquatic systems, the impact of acidic pollution on herbivorous insects appears to be entirely plant-mediated (Heliövaara & Vaisanen, 1993). Our own research investigating the impact of acidic fog in several systems supports this view (Trumble & Hare, 1989; Paine *et al.*, 1993; Redak *et al.*, unpublished data). Nonetheless, given the pH of the acidic treatments (pH = 2·75) used in this study, we feel these results demonstrate a powerful ability of *T. geminata* larvae to withstand the physiological stresses imposed by direct contact with solutions of this acidity.

The plant-mediated effects of acidic fog upon *T. geminata* larval growth presented here are somewhat in

contrast to findings from our earlier research in this system. While the study presented here demonstrates no significant direct or plant-mediated effects on insect biomass gain or growth due to acidic fogging, there does appear to be a consistent trend to suggest that acidic fogging may negatively influence *T. geminata* performance. Although not statistically significant, control values for biomass gain, larval growth, and survivorship are consistently higher than acidic treatments. Investigating the same plant–insect association, Paine *et al.* (1993, 1994) found that applications of acidic fog alter *E. farinosa* foliage quality (increased concentrations of nitrogen and soluble protein) such that *T. geminata* larval and adult consumption are increased. Similarly, in the lima bean (*Phaseolus lunatus* L.) — *Trichoplusia ni* Hübner (Lepidoptera: Noctuidae) system, Trumble and Hare (1989) showed that when plants were treated with acidic fogs (pH = 3·0), the foliar concentration of total nitrogen increased to a level that presumably resulted in enhanced insect growth and consumption rates. Treatment applications of fogs with lower pH values (2·5 and 2·0), while altering bean foliage quality (increased concentrations of total nitrogen, soluble protein, and various amino acids) did not significantly alter insect growth or consumption (Trumble & Hare, 1989).

The differences between our earlier studies and the results presented here may be due, in part, to methodological differences. Paine *et al.* (1993) did not initiate insect bioassays of fog-treated host plants until 7 days after the final fog applications (thus allowing 12 days for the treatments to affect host plant quality). In this study, experimental design constraints required feeding trials to be initiated and completed prior to Day 12 and in the case of Experiment B by Day 10. Theoretically, the strong positive influence of acidic fog on insect growth, demonstrated in our earlier study, may require at least 12 days to influence *E. farinosa* host-plant quality such that insect growth and consumption are affected. The consistent pattern of reduced growth with acidic fog treatment (either direct or plant-mediated) shown here, although not statistically significant, may be indicative of a direct, yet small, negative impact upon insect growth and/or a short-term (less than 12 days), negative plant-mediated impact upon insect growth. Differences between the study presented here and that of Trumble and Hare (1989) may be due to different experimental systems employed (*T. ni–P. vulgaris* vs *T. geminata–E. farinosa*) as well as different treatment methodology (different pH of fogs used, different treatment exposure times). It is interesting to note that where Trumble and Hare used similar pH values for treatment fogs as those used here, they failed to demonstrate a significant impact on *T. ni* biology (Trumble & Hare, 1989).

In conclusion, our results demonstrate that the direct impact of acidic fogs on *T. geminata* mortality, biomass gain, and growth is minimal. There is an indication (although non-significant) that over the short-term (less than 12 days) direct acidic fogging may be detrimental to insect growth and survivorship. It should be noted that direct long-term impacts of acidic fog on herbivorous insects populations (i.e. impact on insect fitness over several generations) was not tested and is not known. Furthermore, the impact of acidic fog, either direct or plant-mediated, on such parameters as adult host-plant choice, oviposition, mating, and reproduction are unknown as well. As acidic-fogs affect significant areas of coastal North America and Europe, including areas of agricultural and natural biotic importance, further studies investigating both the direct and plant-mediated impact of acidic-fog upon plant–insect interactions are warranted.

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