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Plant-mediated effects of soil salinity on a gall-inducing caterpillar *Epiblema scudderiana* (Lepidoptera: Tortricidae) and the influence of feeding guild

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Abstract. A greenhouse experiment was conducted to study the indirect effects of soil salinity on a caterpillar that induces gall formation on a non-halophilic plant. Larvae of *Epiblema scudderiana* (Clemens) were allowed to feed on potted goldenrods (*Solidago altissima* L.) treated with 3 concentrations of NaCl (0, 8,000, 16,000 PPM). Experiments were also carried out with the larvae of two species of leaf beetles, *Trirhabda borealis* Blake, a leaf-chewer, and *Microrhopala vittata* F., a leaf-miner, to determine the influence of feeding guild. Adding salt to the soil affected both the plant and insect herbivores. The biomass of roots and shoots as well as root/shoot ratios of salt-stressed plants were lower, relative to controls. The biomass of the fully grown larvae and galls were decreased for the plants treated with the highest salt concentration. The percentage of biomass allocated to the gall was increased by soil salinity. All gall-inducing larvae completed their development (from second to final instar) even though their biomass was significantly reduced in the 16,000 PPM treatment. Soil salinity increased nitrogen concentrations in both gall and stem (normal) tissues but the levels were always higher in the gall. The salt treatments also increased sodium and potassium concentrations in galls and stems. Interestingly, sodium concentrations as well as the ratio of sodium ions to potassium ions increased more rapidly in the stem compared with the gall. Responses of folivorous insects to salt-stressed plants varied. Leaf-chewing larvae ate smaller amounts of plant tissue with high salt content compared with control, which also resulted in shorter feeding periods. The performance of the leaf-mining insect was not affected. However, it was able to complete its larval development within a smaller portion of the leaves. This study showed that soil salinity has a strong negative effect on *S. altissima*, especially on root development. Conversely, salt stress effects seemed to be progressively decreasing from the stem to the gall to the gall-inducer, which suggests that the gall tissue might act as a buffer against drastic changes in the mineral balance of the host plant. Nevertheless, it seems that unless the host plant dies, larvae of *E. scudderiana* can always produce a gall in which they can complete their development. On the other hand, leaf-chewing insects appeared to be sensitive to salt-rich tissues since they were deterred by them. Leaf-miners could complete their development with fewer food without any effect on their growth, suggesting that the peculiar tissues on which they feed within leaves became more abundant or nutritious in salt-treated plants.

INTRODUCTION

Plant concentrations of most mineral elements may vary considerably. Mineral deficiencies or surpluses can affect the suitability of host plants for herbivores (Dale, 1988). The sodium content of non-halophilic plants is generally low and only trace amounts of sodium are required by insect herbivores (Allen, 1989; Dadd, 1977). Insects feeding on plants have indeed much more potassium than sodium ions in their body fluid (Boné, 1946, 1947;

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Tobias, 1948). Any dramatic increase of sodium concentrations in the host plant could therefore make it more difficult for insect herbivores to get an optimal balance of mineral elements. Such effects have been found by Clancy & King (1993) who showed that responses of *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) to phosphorus depended on magnesium concentrations in the diet, and vice versa. It follows that insect performance might be impaired by salted plants as well, especially for species adapted to non-halophilic hosts.

Elevated sodium concentrations in the tissues of non-halophilic plants can be artificially generated by the intense use of de-icing salt in roadside environments (Liem et al., 1985), where several studies on the effects of salt on plant-aphid interactions have been done. Braun & Fluckiger (1984) reported that the population densities of *Aphis pomi* DeGeer (Hemiptera: Aphididae) were higher on salt-sprayed hawthorns, which had higher amino acid and sugar concentrations in their phloem, relative to control plants. High concentrations of organic solutes may represent a protection against osmotic imbalances for non-halophytes growing under saline conditions (Greenway & Munns, 1980). In another study, however, the effect of salted roadside plants on aphids was not significant (Spencer & Port, 1988). Furthermore, Araya et al. (1991) have experimentally increased the salt content of cereals and an artificial diet and found negative effects on the performance of *Schizaphis graminum* Rondani (Hemiptera: Aphididae). Thus, there seems to be no consistent response of phloem-feeding insects to increased salinity conditions.

The effects of roadside conditions, including soil salinity, on gall-inducing insects and their host plant, have also been investigated (Martel, 1995a, b). Natural populations of *Epiblema scudderiana* (Clemens) (Lepidoptera: Tortricidae) and *Eurosta solidaginis* (Fitch) (Diptera: Tephritidae) were not affected by road-stressed plants (Martel, 1995a). A field experiment designed to separate temporally air pollutants and de-icing salts showed that the apparent positive effects of pollutants on the larval biomass of *E. solidaginis* could be tempered by negative effects of salts (Martel, 1995b). These results suggest that salt-stressed plants could affect gall-inducing insects but the effects are difficult to isolate. Nevertheless, the effects of fluctuating mineral concentrations in plants on gall-forming insects are poorly known. The gall may operate as an intercepting or a redirecting tissue for various nutrients, including minerals (Abrahamson & Weis, 1987; McCrea et al., 1985). It follows that changes in the mineral composition of normal tissues will not be automatically echoed in galls. For instance, a few studies have demonstrated that soil fertilisation unequally affects the growth and nutrient content of gall and normal tissues (Abrahamson & McCrea, 1986; Fay et al., 1996a; Hartley & Lawton, 1992). Mature gall tissue can be richer or poorer in P, K, Ca, Mg, Mn, Fe, B, Zn, Cu, Mo and Al, compared with its matching normal tissue (Abrahamson & McCrea, 1986; Andersen & Mizell, 1987; Bagatto et al., 1991; Brewer et al., 1987; Harris & Shorthouse, 1996; Jankiewicz et al., 1970; Paquette et al., 1993; Skuhravý et al., 1980). For sodium, the picture is similar, i.e. comparisons between gall and normal tissues ended with mixed results (Andersen & Mizell, 1987; Brewer et al., 1987; Skuhravý et al., 1980).

More consistent effects of high salt concentrations in plant tissues on insect herbivores have been reported for chewing species. Leuck et al. (1974) have found feeding deterrence by grass sprayed with sodium chloride in *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae). Negative effects of salted plants on a stem-boring beetle, *Agapanthia* *villosoviridescens* (DeGeer) (Coleoptera: Cerambycidae), and a generalist leaf-chewing beetle, *Popillia japonica* (Newman) (Coleoptera: Scarabaeidae), have also been documented (Hemminga & van Soelen, 1988; Stamp & Harmon, 1991). Conversely, the development of a leaf-mining caterpillar, *Bucculatrix maritima* (Stainton) (Lepidoptera: Bucculatricidae), feeding on a halophilic plant was not affected by the salinity conditions in an estuary, although high salinity might have had detrimental effects on larval growth in one location (Hemminga & van Soelen, 1992). In spite of this, most studies suggest that insects chewing leaves or stems are more sensitive to salt in their food, relative to gall-inducers.

Whereas plant-mediated effects of abiotic stress on insect herbivores have been extensively studied, we have a relatively poor knowledge of the impact of plant mineral content on the performance of insect herbivores (Mattson & Scriber 1987). Moreover, we know little on plant-mediated effects of soil salinity on insects (Dale, 1988). The main purpose of this study was to investigate the impact of high soil salinity on the growth, biomass allocation and nutritional status of a non-halophilic plant, and its consequences for a gall-inducing caterpillar. It was hypothesised that salt effects should be proportionally the same on the gall tissue and its connected normal tissue, assuming that they both have similar growth requirements. A second objective of this study was to examine the influence of feeding guild. Experiments were carried out to measure the impact of high salt content of plant tissues on a leaf-chewer and a leaf-miner. It was hypothesised that leaf-feeding insects are more directly exposed to salt-stress-induced changes in their food than insects living in their own food-providing gall. Leaf-feeding insects were thus expected to be more adversely affected by salinity conditions than gall-inducers. Direct comparisons of responses to stress-induced changes in plants for different insect guilds have rarely been done before (e.g. Larsson & Bjorkman, 1993).

MATERIAL AND METHODS

Study species

The experimental host plant was the tall goldenrod, *Solidago altissima* L. (Asteraceae). It is a non-halophilic, clonal, and perennial herb that has a broad tolerance to diverse environmental conditions and commonly invades and dominates patches of disturbed habitats, such as road edges, in eastern North America (Abrahamson et al., 1983; Melville & Morton, 1982; Werner et al., 1980).

Three species of insect herbivores that differed in their mode of feeding were used in this study. Larvae of *E. scudderiana* induce an elliptical gall on the stems of *Solidago* spp. (Meaden, 1956; Miller, 1976). Gall-formation is preceded by mining of the apical bud. After about a week, the larvae enter the stem 7.5–10 cm below the tip of the plant and just above the axil of a leaf (Meaden, 1956). Gall-inducing caterpillars feed on the vascular tissues and may severely affect the connections between the lower and upper parts of the stem and induce lateral branching (Blum, 1953). Debris and frass are evacuated through an opening in the gall that is kept closed with silk when not in use. The larvae of *Trirhabda borealis* Blake (Coleoptera: Chrysomelidae), one of the most abundant herbivores of *Solidago* spp. in North America, chew the young leaves of goldenrods and asters (Messina & Root, 1980). The gregarious larvae of *Microrhopala vittata* F. (Coleoptera: Chrysomelidae) bore into the leaves of *Solidago* spp. and form blotch-type mines (Messina & Root, 1980). The larvae may burrow mines in several leaves to complete their development but if they do so they rarely stay in groups (Damman, 1994). Pupation and adult emergence take place in the mine.

Experimental plants

Seedlings of *S. altissima* were grown from seeds collected in the Ottawa area. Road edges were avoided to prevent the use of plants that might be adapted to a saline environment (Pitelka & Kellogg, 1979). All plants were grown in the greenhouse facility (ELBA) at Carleton University where the environmental conditions (photoperiod, temperature, humidity) were not controlled and thus similar to natural conditions. Seedlings were grown individually (pot diameter = 12 cm) in a potting mix that contained equal amounts of top soil (sandy loam), peat moss, and perlite. A preliminary experiment showed that 16,000 PPM is the highest concentration of salt that most seedlings of *S. altissima* could tolerate. For the first week (mid-May), experimental plants (about one month old) were watered daily with 50 ml of 0, 8,000, or 16,000 PPM NaCl solutions. Then, the plants were watered every 3 weeks with 75 ml of the solutions described above. Similar volumes of a fertiliser (Plant-Prod 20-20-20 at 1% of the recommended concentration) were applied to each plant during non-treatment weeks. The low concentration of fertiliser was used to temper the difference between experimental and natural plants. Between salt treatments and fertilisation, plants received supplementary watering (75 ml each time to all plants) throughout the experiment when the soil mixture was drying. The volumes used for salt treatments, fertilisation and watering were found to humidify the soil mixture without any excessive loss from the pots in trials.

Gall-inducer experiment

Second-instar larvae of *E. scudderiana*, which have a total of 5 instars, were collected in the field (early July) from *S. altissima* stems prior to gall formation. The larvae were then transferred to the experimental plants. At the end of the experiment (late September), the galls were dissected and the above- and below-ground plant tissues were separated. All plant and animal tissues were oven-dried at 60°C and weighed.

Chemical analyses followed standard procedures. Stem and gall tissues were ground using a mill (mesh size = 0.4 mm) and then digested in concentrated sulphuric acid for the determination of nitrogen, potassium and sodium concentrations. Mercury was used as the catalyst and lithium sulphate salt was added to increase the boiling temperature. One half of the digested product was used for the semi-micro-Kjeldahl nitrogen analysis (McKenzie & Wallace, 1954). The other half was used for the determination of potassium and sodium concentrations with an atomic absorption spectrophotometer (Perkin-Elmer model 703). Atomic absorption K and Na standard solutions were used (Aldrich Chemical Co., Milwaukee, Wisconsin).

Leaf-chewer and leaf-miner experiments

To test the effect of feeding guild, two other experiments were conducted with a subsample of the plants used for the gall-inducing caterpillar. A no-choice test was performed with the leaf-chewing beetle larvae in mid-June. A longer experiment covering the whole development of these insects would not have been possible without a substantial loss of foliage or plants as well as a great overlapping period and interference with the gall-inducing caterpillar. Leaf sections sampled on the greenhouse plants were presented in petri dishes to starved (12 h) third-instar larvae of *T. borealis* for a period of 2.5 h. The leaf sections were inserted between two wet filter papers. The filter paper that was on top of the leaf was punched 3 times so that the larvae had only access to the equivalent of 3 leaf discs of equal size (diameter = 7 mm). The activity of the larvae (feeding, resting, moving) was noted every 15 min. The area chewed was then measured by tracing the leaf sections on paper and using the weight of the pieces of paper. Leaves were also oven-dried and analysed for total nitrogen, potassium and sodium (as above).

The larval development and adult biomass of the leaf-mining beetle larva were also studied. Second-instar larvae of *M. vittata* were collected in the field (mid-June) from *S. altissima* leaves and then transferred to a subsample of the plants used for the experiment with the gall-inducer. This experiment ended with the emergence of the adults one month later (mid-July) so that there was only a small overlap period (about one week) with the gall-inducing caterpillar. The beetles were oven-dried and weighed. The mined leaves were cut off the plants. The area mined was measured as described above.

Data analysis

The pots were considered the experimental units for this study. The experimental design was originally blocked but possibly because of plant mortality and the relatively small space used for the experiment compared to the size of the greenhouse (cf. in-house gradients), the blocking factor was not found significant and therefore dropped out from the analyses. Variations caused by salinity conditions and plant tissue when applicable were analysed by 1-way ANOVA and MANOVA. The difference between gall and stem

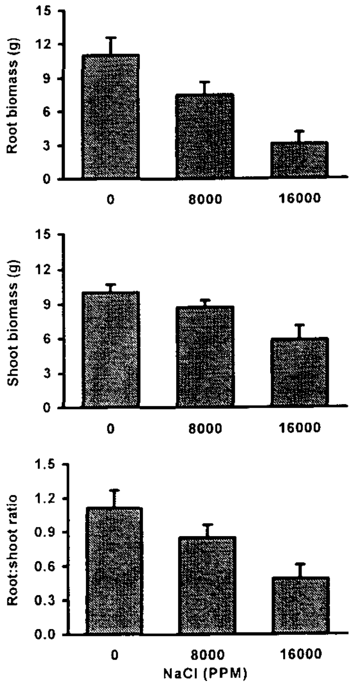

Fig. 1. Effect of soil salinity on the growth and biomass allocation of *S. altissima*. Means + 95% confidence limits.

contents was used to measure the interaction between treatment and plant tissue in the 1-way MANOVA. A non-parametric statistical analysis (Kruskal-Wallis test) was used for larval biomass of *E. scudderiana* because the assumptions for ANOVA were not met for that variable. Pillai's test statistics were used for MANOVA because it is less susceptible to violations of assumptions of parametric analysis (Scheiner, 1993). The angular (arcsine-square root) transformation was used prior to data analysis for percentages (Sokal & Rohlf, 1995). Unless otherwise stated, sample sizes for the 0, 8,000, and 16,000 PPM treatments were as follows: (1) Gall-inducer data: n = 20, 22, and 12; (2) Leaf-chewer data: n = 15, 14, and 10; (3) Leaf-miner data: n = 11, 5, and 5. Uneven sample sizes among treatments were generated by plant mortality caused by salinity or insects falling on the soil prior to gall or mine formation.

RESULTS

Increasing soil salinity had a highly significant impact on the growth of *S. altissima* (Table 1). The whole plant biomass allocation pattern was indeed altered by soil salinity. Root biomass was reduced by 32–72% whereas shoot biomass was reduced by 13–41% (Fig. 1). Root/shoot ratios confirm that the root system was more severely affected by salt than shoot; the values were abated by 23–56% (Fig. 1). Salt effects on growth and biomass allocation peaked at the highest concentration of NaCl applied to the plants.

TABLE 1. Results for the statistical analyses performed on the biomass variables considered for the experiment conducted with the gall-inducing caterpillar (*E. scudderiana*) and its host plant (*S. altissima*). 1-way ANOVA testing were used for all variables, except for larval biomass (Kruskal-Wallis test).

Variables	Salt treatment*
Host plant	
Root	$P < 0.001$ ($F_{2,51} = 31.73$)
Shoot	$P < 0.001$ ($F_{2,51} = 28.59$)
Root : shoot ratio	$P < 0.001$ ($F_{2,51} = 19.33$)
Gall-inducer/gall	
Larva	$P = 0.031$ ($\chi^2_{2,51} = 6.97$)
Gall	$P = 0.009$ ($F_{2,51} = 5.21$)
Allocation to gall	$P < 0.001$ ($F_{2,51} = 10.49$)

* NaCl (0, 8,000, 16,000 ppm).

Growing goldenrods at high salinity conditions affected the biomass of *E. scudderiana* larvae significantly (Table 1) but did not cause mortality. Also, all larvae completed their

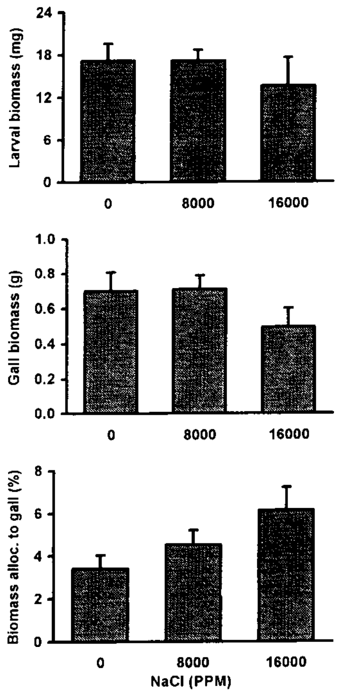

Fig. 2. Effect of salinity conditions on the biomass of fifth instar *E. scudderiana* larvae and the gall tissue formed on *S. altissima*. Means + 95% confidence limits.

development, i.e. second to fifth (final) instar, in spite of the treatments. The gall-inducing caterpillars attained a lower biomass (20% lower than control) when fed on goldenrods treated with the highest salt concentration whereas the intermediate treatment did not generate any changes in larval biomass relative to controls (Fig. 2). The effect of soil salinity on the growth of gall tissue was highly significant (Table 1). The biomass of galls induced on *S. altissima* treated with the 16,000 PPM NaCl solution was 30% lower than those on control plants but again, the 8,000 PPM treatment did not affect gall tissue (Fig. 2). Meanwhile, the percentage of the total biomass of the host plant represented by the gall increased significantly with the amount of salt added to the soil (Table 1), meaning that on high-salt plants gall and other tissues were not equally affected. The gall tissue represented a 32% and 79% higher proportion of the whole plant biomass for the 8,000 and 16,000 PPM treatments vs. control, respectively (Fig. 2).

The chemical composition of plant tissues was altered by the application of salt to goldenrods. Soil salinity affected nitrogen concentrations in both gall and stem (normal) tissues significantly (Table 2). The effect of the treatments on nitrogen was the same for both plant tissues, as shown by the nonsignificant gall-stem response variable. Applying a salt solution to the soil resulted in an increase of total nitrogen concentrations (12–67% for the gall and 28–108% for the stem; Fig. 3). Nitrogen concentrations found in the gall tissue were at least two times higher than the concentrations in the stem tissue for all treatments (Table 2 and Fig. 3). Soil salinity had a significant impact on mineral concentrations of gall and stem tissues (Table 2). There was an interaction between treatments and plant tissue for sodium but not for potassium, meaning that gall and stem tissues were equally affected only for the latter. Na concentrations were much higher for the 8,000 PPM treatment (more than twice) and reached 15–30 times higher values for the 16,000 PPM treatment, relative to controls (Fig. 3). Gall and stem tissues of control plants had the same very small amounts of sodium. On the other hand, K concentrations were always higher (42–76%) in gall than stem tissue (Fig. 3). Salt treatments resulted in increased levels of potassium (8,000 PPM: 17–32%; 16,000 PPM: 23–52%). Most important, sodium/potassium ions ratio in both gall and stem tissues increased significantly with the amount of salt added (Table 1), with sodium ion concentrations attaining levels almost equal to those of potassium in the stem tissue in the 16,000 PPM NaCl treatment (Fig. 3). The mean ratio of sodium to potassium in the stem of goldenrods watered with the 16,000 PPM NaCl solution was almost three times higher than the same mean ratio measured in the gall. The ions ratio increased more rapidly in the stem than the gall tissue and the interaction between treatment and plant tissue was significant (Table 2).

TABLE 2. Results for the statistical analyses performed on the chemistry variables considered for the experiment conducted with the gall-inducing caterpillar (*E. scudderiana*) and its host plant (*S. altissima*). 1-way MANOVA and ANOVA testing for salt treatment[a] effect were used for all variables. The difference between gall and stem contents was used to measure the interaction between treatment and plant tissue.

Variables	MANOVA	Gall	Stem	Gall-Stem
Total nitrogen	$P < 0.001$ ($F_{4,100} = 8.04$)	$P < 0.001$ ($F_{2,50} = 15.29$)	$P < 0.001$ ($F_{2,50} = 12.64$)	$P = 0.844$ ($F_{2,50} = 0.17$)
Sodium	$P < 0.001$ ($F_{4,98} = 7.53$)	$P < 0.001$ ($F_{2,49} = 12.06$)	$P < 0.001$ ($F_{2,49} = 21.69$)	$P = 0.031$ ($F_{2,49} = 3.74$)
Potassium	$P < 0.001$ ($F_{4,100} = 7.77$)	$P = 0.033$ ($F_{2,50} = 3.66$)	$P < 0.001$ ($F_{2,50} = 15.78$)	$P = 0.530$ ($F_{2,50} = 0.64$)
Na^+/K^+	$P < 0.001$ ($F_{4,98} = 5.88$)	$P < 0.001$ ($F_{2,49} = 13.39$)	$P < 0.001$ ($F_{2,49} = 13.39$)	$P = 0.003$ ($F_{2,49} = 6.67$)

[a] NaCl (0, 8,000, 16,000 PPM).

The leaf tissue sampled on plants grown at higher salinity conditions significantly affected the feeding behaviour of the leaf-chewer (Table 3). Larvae of *T. borealis* spent less than half the time feeding on the leaves of goldenrods treated with salt compared with the same period observed on the leaves of control plants (Fig. 4). The total leaf area chewed was smaller for salted tissues but the differences were not significant because of large variation (Table 3 and Fig. 4). For this experiment all leaves contained the same amounts of total nitrogen (Table 3 and Fig. 4; n = 12, 10, and 6 for the 0, 8,000 and 16,000 PPM of NaCl, respectively). However, the ratio of sodium to potassium ions in goldenrod leaves

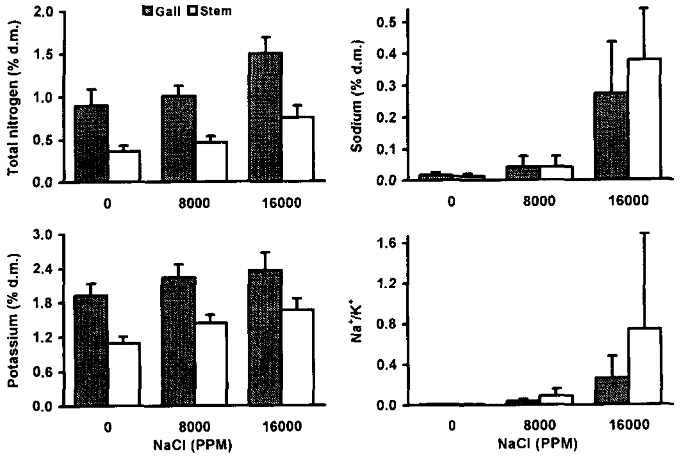

Fig. 3. Effect of soil salinity on the mineral content of gall and stem tissues of *S. altissima*. Means + 95% confidence limits.

was significantly affected by the amount of salt added to the soil (Table 3). As the gall and stem tissues, ratios increased exponentially with soil salinity (Fig. 4).

TABLE 3. Results for the statistical analyses performed on the variables considered for the experiments with the leaf-chewing (*T. borealis*) and leaf-mining (*M. vittata*) insects. 1-way ANOVA were used for all variables.

Variables	Salt treatment[a]
Leaf-chewer	
Feeding periods	P = 0.046 ($F_{2,36}$ = 3.37)
Leaf area consumed	P = 0.306 ($F_{2,36}$ = 1.22)
Leaf total nitrogen	P = 0.875 ($F_{2,25}$ = 0.13)
Leaf Na^+/K^+	P = 0.002 ($F_{2,36}$ = 7.55)
Leaf-miner	
Leaf area mined	P = 0.001 ($F_{2,18}$ = 9.94)
Adult biomass	P = 0.261 ($F_{2,18}$ = 1.45)

[a] NaCl (0, 8,000, 16,000 PPM).

Feeding by the leaf-miner was also affected by salt-stressed host plants. *M. vittata* larvae feeding on *S. altissima* treated with 8,000 and 16,000 PPM NaCl solutions mined significantly smaller areas than those feeding on the control plants (Table 3 and Fig. 5).

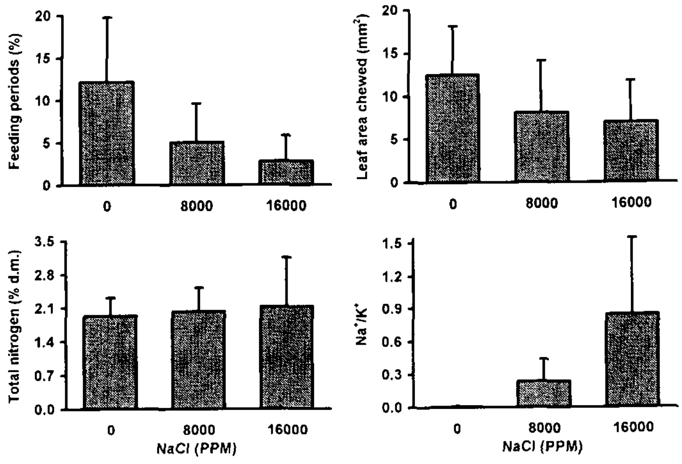

Fig. 4. Effect of salinity conditions on the feeding behaviour of third-instar larvae of *T. borealis* and the mineral content of *S. altissima* leaves. Means + 95% confidence limits.

Several larvae did not survive but the mortality rate was not significantly affected by the treatments (Fisher's exact test; P > 0.1, n = 14, 10, and 10 for the 0, 8,000 and 16,000 PPM of NaCl, respectively). In addition, the biomass of emerging adults did not differ significantly between the treatments (Table 3 and Fig. 5).

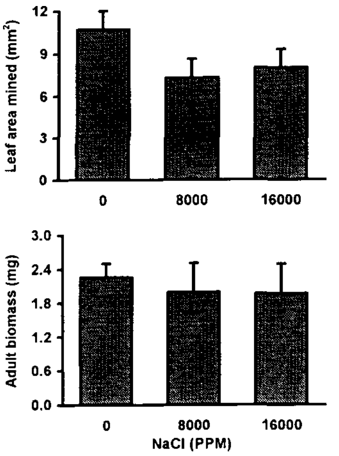

Fig. 5. Performance of *M. vittata* when fed on *S. altissima* grown at 3 salinity conditions. Means + 95% confidence limits.

DISCUSSION

The performance of non-halophilic plants is optimal in the presence of trace amounts of salt in the soil and salt stress generally reduces their growth rate very rapidly. This can be the result of impaired nutrient and water uptake caused by Na^+-dominated soils and the subsequent accumulation of Cl^- and Na^+ in tissues (Greenway & Munns, 1980; Grattan & Grieve, 1992). Therefore, it is not surprising to find in this study that high soil salinity reduces the growth of *S. altissima*, affecting especially its root development. In a field experiment, root growth of potted *S. altissima* exposed to de-icing salts near a highway was only slightly reduced (Martel 1995b), probably because the salt concentrations used in the greenhouse experiment were higher than those found in roadsides. Indeed, damage to the root system caused by toxic levels of salt in the soil was probably pivotal in the responses observed in this study since root growth and function can be altered by high ratios of sodium ions to other cations (Grattan & Grieve, 1992). All these salt-induced changes in the plant may have important consequences for insect herbivores, which have been investigated in this study.

Gall-inducing larvae were smaller when the highest concentration of salt was applied to the plants. There are two possible explanations for this. First, reduced growth could be caused by lower resource availability since galls were also smaller. It means that the larva living inside cannot chew the same area of tissue. In effect, *E. scudderiana* is more like a sessile stem-borer that promotes continuous growth of the inner tissue and indeed there are several congeneric species with the strictly boring habit (Miller, 1976). This contrasts with other insects that induce galls with well-differentiated tissues like *E. solidaginis* (Uhler, 1951). Larvae of *E. scudderiana* live in a relatively small and rudimentary gall that is probably less demanding in terms of nutrients compared with more complex galls. In spite of this, poor plant performance influenced gall growth but the effects of salinity on the gall tissue were proportionally lower, as indicated by the larger proportion of biomass and resources allocated to galls in salt-treated plants. Furthermore, increasing soil salinity did not cause larval mortality in *E. scudderiana* nor retarded instar development. The gall-inducer was always stimulating tissue growth inside the gall, which imposed an enduring allocation cost to the host plant. This high tolerance to stress-induced changes in the host plant could explain why soil salinity above background levels in roadside environments, which is lower than the extreme conditions used in the greenhouse experiment, did not affect significantly the growth or survival of *E. scudderiana* larvae or the gall tissue induced by them, in spite of a reduced shoot growth in *S. altissima* (Martel, 1995a). Second, direct effects of sodium on the nutritional balance of the gall-inducer might have produced the lower larval biomass. Increases in Na^+ levels of plant tissues were more substantial in the 16,000 PPM treatment than the other concentration used in the experiment and it was also the highest NaCl concentration applied to the plants that resulted in lower biomass of the gall and the gall-inducer.

The mineral content of plant and gall tissues was also altered by high soil salinity. Several physiological roles have been attributed to galls. The gall may act as a metabolic sink or a redirector, i.e. through a passive and partial blocking of the normal flow of resources or an active translocation of nutrients from other parts of the plant (e.g. Jankiewicz et al., 1970; McCrea et al., 1985). Salt-stressed plants typically contain more organic solutes (osmoprotectants), including nitrogenous compounds (Greenway & Munns, 1980). This may explain the increase in the total nitrogen concentrations found in gall and stem tissues for the plants grown in a soil watered with a 16,000 PPM NaCl solution. Gall nitrogen concentrations were always much higher compared with stems, suggesting that the gall may act as a sink for this nutrient, despite the drastic changes in salinity conditions. Higher nitrogen levels in gall tissues compared with their related normal tissues have also been reported for other species of stem-gall-inducers on goldenrod (Abrahamson & McCrea, 1986). Conversely, analyses of the mineral content of galls and their connected normal tissues under stress are not well documented in the literature and there seems to be no general trend in decreased or increased levels of most chemicals for a number of gall-host-plant systems. For example, Brewer et al. (1987) and Skuhravý et al. (1980) have shown that there is substantial variation in the concentrations of sodium in gall vs. leaf (normal) tissues. In this study, background levels of sodium were extremely low and did not differ between gall and stem tissues. Salt treatments resulted in higher levels of both sodium and potassium, which can be detrimental for insect herbivores (Stamp, 1994; Stamp & Harmon, 1991; Wulfson & Stamp, 1991). One of the most important finding of this study is that sodium concentrations and Na^+/K^+ ratios increased less rapidly in the gall tissue than in the stem tissue, implying that the gall tissue might retain only a fraction of the excess sodium contained in the ungalled tissue (stem). The gall might therefore protect its inhabitant from drastic changes in the mineral nutrient balance of the host plant. This "buffering capacity" of galls against environmental variation is supported by the distribution and abundance of gall-inducing insects in harsh habitats (Fernandes & Price, 1991) and at least one other experimental study (Fay et al., 1996b). A comparison of gall induction with other feeding guilds may give more support for this hypothesis.

The two leaf-feeding insects appeared to respond differently to salt stress-induced changes in their food plant. Leaf-chewing larvae of *T. borealis* spent less time feeding on salted tissues and consumed smaller amounts of food. These results suggest that salted tissue had a deterring effect on the leaf-chewer. Furthermore, insects feeding on salt-rich tissues may need to assimilate more sodium to fulfil their requirements in other nutrients. Stamp & Harmon (1991) reported negative effects of high salt concentrations on fecundity and survivorship of a leaf-chewing beetle, and feeding deterrence by NaCl on a caterpillar was detected in another experiment using sprayed leaves (Leuck et al., 1974). On the other hand, the experiment conducted with *M. vittata* tend to show that leaf-mining insects might benefit from salt-stressed changes in their host plant. Leaf-mining larvae needed a smaller quantity of tissue to complete their development and the biomass of emerging adults was not significantly affected when the larvae were feeding on salt-stressed plants. These results suggest that food quality was improved in the high salinity conditions. As opposed to insects that can eat the whole leaf, the mining habit may allow insect herbivores to select tissues within leaves that are more nutritious (Connor & Taverner, 1997; Kimmerer & Potter, 1987; Trier & Mattson, 1997). Perhaps those tissues on which the leaf-mining larvae were feeding became more abundant and/or nutritious in salt-stressed plants compared with control plants.

In conclusion, the working hypotheses of this study are not entirely supported by the results. Gall-inducing insects were negatively affected when feeding on salt-stressed plants whereas leaf-feeders were either negatively or positively affected. The results suggest that a higher degree of "intimacy" in plant-insect interactions may allow a better control of herbivores on the quality of their food despite the effects of fluctuating environmental conditions on the host plant. As opposed to leaf-chewers, feeding by leaf-miners was not affected by higher salt concentrations. Also, growth reduction and salinity-induced changes in the chemical composition of the gall tissue were lower compared with the normal tissue, which suggests that gall-inducing insects might have been partially protected against alterations in the quality of their food. Sedentary gall-inducers may be able to manipulate resource availability within their host for their own benefit in spite of fluctuating environmental conditions. This buffering function of the gall tissue is supported in this study by the proportionally and gradually decreasing effect of salinity on the growth of the stem, the gall and the insect, respectively, and awaits further research.

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