
Plasticity of leaf traits and insect herbivory in *Solanum incanum* L. (Solanaceae) in Nguruman, SW Kenya

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Abstract

Plasticity of leaf traits of *Solanum incanum* was evaluated by comparing its expression in three sites differing in soil moisture (dry, intermediate, humid) in Nguruman, SW Kenya. Leaf size and shape, and leaf traits related to defence against herbivores, varied significantly among sites. The relationship between leaf traits showing among-site variation and insect herbivory was evaluated at a within-site scale. Leaf thickness was correlated with the level of foliar herbivory by a flea beetle (*Epitrix* sp.). This correlation was negative at the dry site and positive at the humid site. No relationship was found at the intermediate site. Interestingly, leaf thickness and toughness were positively and significantly correlated at the dry site, but not elsewhere. Finally, overall patterns of herbivory by the flea beetle and unidentified defoliators differed among sites. The importance of scale when evaluating plant plasticity is discussed.

Key words: beetles, herbivory, leaf, plasticity, *Solanum incanum*

Résumé

On a évalué la plasticité des caractères de la feuille de *Solanum incanum* en comparant son expression dans trois sites différant par l'humidité du sol (sec, intermédiaire, humide), à Nguruman, au s-o de Kenya. La taille et la forme des feuilles, ainsi que leurs caractères de défense contre les herbivores, variaient significative-

ment entre les sites. La relation entre la présence des caractères présentant une variation entre les sites et la présence d'insectes herbivores a été évaluée à l'échelle des sites. L'épaisseur des feuilles a été mise en corrélation avec le taux de consommation foliaire due à une puce-coléoptère (*Epitrix* sp.). Cette corrélation s'est révélée négative au site sec et positive au site humide. On n'a trouvé aucune corrélation au site intermédiaire. Il est intéressant de remarquer que l'épaisseur et la dureté des feuilles étaient liées positivement et significativement au site sec mais pas ailleurs. Enfin, le schéma général de consommation par la puce-coléoptère et d'autres consommateurs indéterminés différait selon les sites. On discute de l'importance de l'échelle dans l'évaluation de la plasticité des plantes.

Introduction

Plant species occurring in different environments often show plasticity in their physiology and/or morphology as a means of maximizing their growth and reproduction (Sultan, 1995). In their turn, herbivorous insects must face not only the environmental challenges on their own physiology, but also the environment-mediated changes in the traits of the plant species they are associated with (Weis, 1992). As a result, it is difficult to predict whether herbivorous insects will be positively or negatively affected by the combined effect of plastic plant traits and the environment (Miller & Weis, 1999). A study addressing the effect of stressed plants (i.e. plants growing in extreme environments) on herbivore performance has shown that the sign as well as the magnitude of the effect depends on the insect guild (Kori-

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cheva *et al.*, 1998). On the other hand, patterns of variation in abundance of herbivorous insects among different sites could be caused by biotic (Ernsting *et al.*, 1995) as well as abiotic (Fuentes-Contreras *et al.*, 1999) factors, and their interaction (Stiling & Rossi, 1996). Some of these factors are likely to outweigh the effect of environment-mediated changes in plant traits on herbivore performance (e.g. Rausher, 1981).

Solanum incanum L. (Solanaceae) (sodom apple; ntu-lele in Kimaasai) is a native African shrub (Jaeger & Hepper, 1986). It is regarded as the direct wild ancestor of the cultivated eggplant, *S. melongena* L. (Pearce & Lester, 1979). In Kenya, this species is very common in waste ground and secondary vegetation; it is considered a weed in grassland (Beentje, 1994). *S. incanum* foliage sustains herbivory from a wide variety of insects, chrysomelid beetles (Coleoptera) and noctuid caterpillars (Lepidoptera) being the major consumers (Olckers *et al.*, 1995).

The main goal of the present work was to explore the relationship between environment-mediated variation of leaf traits in *S. incanum* and herbivory by *Epitrix* sp. (Coleoptera: Chrysomelidae: Alticinae), a cosmopolitan flea beetle genus associated with Solanaceae (Hsiao, 1986). To do this, we compared plant traits and levels of herbivory at three sites located in Nguruman, SW Kenya, showing obvious differences in soil moisture. However, as indicated above, other ecological factors might be confounded if comparisons are made among sites. Therefore, we refined the precision of the analysis by evaluating, within-sites, the relationship between beetle herbivory and leaf traits. We focused on leaf traits showing among-site variation, i.e. plastic traits.

Materials and methods

This study was performed in the surroundings of the ICIPE (International Centre of Insect Physiology and Ecology) field station at Nguruman, SW Kenya (1°50'S, 36°05'E), within the Maasai Olkiramatian Group Ranch, which stretches from Lake Magadi to the Nguruman escarpment. *Solanum incanum* L. is a native shrub very common around the study area, occurring in dry as well as in moist habitats. Three sites with differing soil moisture were defined following consultation with A. Ochieng (University of Nairobi, Department of Botany). The sites will be referred to as

dry, intermediate and humid. Although no actual measurement of soil moisture was undertaken, obvious differences in vegetation type and cover indicated clearly that these sites differed in soil moisture. The dry site was an open *Acacia* wood/bushland, i.e. a typical savanna habitat. The intermediate site was a relatively closed bushland. The humid site was located within farmland, very close to a minor river course. Vegetation density was highest at the latter site. Distance between sites was 2.5, 6 and 8 km for the dry–intermediate, intermediate–humid and dry–humid, respectively.

Sixteen 1.5–2 m tall fruiting individuals of *S. incanum* were sampled at each site to evaluate leaf traits. The evaluated traits were related to (i) size: area, perimeter, (ii) shape: area/perimeter ratio, and (iii) adaptations against water stress, i.e. xeromorphic features (Crawley, 1997): toughness, thickness, pubescence, spines. Some of the latter traits have also been related to plant defence against herbivory (e.g. Coley, 1983; Myers & Bazely, 1991). Four leaves were collected from each plant. Leaves were from the second to fourth pair starting from the top of the branch. The average values of measurements were used to represent plant individuals. Leaf length, width, thickness and relative toughness were measured in the field. Leaf thickness was determined with a calliper and leaf toughness was evaluated with a penetrometer (Mitutoyo®). Area and perimeter of collected leaves were assessed from drawings. Leaf area was calculated assuming the shape of the leaves to be a rhombus and using leaf length and width as the major and minor axis, respectively. Hairs in a 1 mm wide cross-section of the upper surface of the leaf were counted. The number of spines along the mid-vein of the leaf was recorded and expressed as spines cm length⁻¹. Finally, the area/perimeter ratio was calculated as a means of describing leaf shape. Leaf herbivory by the flea beetle *Epitrix* sp. and by unidentified defoliators was separately evaluated. The former was accomplished by recording the small, distinctive feeding punctures produced by the beetle. The total number of punctures per leaf was determined and expressed as punctures cm⁻². Evaluations of herbivory by defoliators was limited to prevalence of damage, i.e. only presence/absence was noted.

A one-way ANOVA was used to compare leaf traits among sites when such traits met normal distribution. Otherwise, a Kruskal–Wallis ANOVA or a χ^2 -test was applied. Data on leaf thickness and beetle herbivory

Table 1 Leaf traits (mean \pm SE), herbivory by the flea beetle *Epitrix* sp. (punctures cm^{-2} , mean \pm SE) and prevalence of unidentified defoliators (mean) on *Solanum incanum* at three sites differing in soil moisture ($n = 16$). See text for methodological details

	Humid site	Intermediate site	Dry site	P-value
Area (cm^2)	116.1 \pm 6.4 a	61.9 \pm 4.2 b	33.7 \pm 3.1 c	< 0.001
Area/perimeter	3.21 \pm 0.14 a	2.33 \pm 0.11 b	1.93 \pm 0.08 c	< 0.001
Thickness (mm)	0.15 \pm 0.01 a	0.22 \pm 0.01 a	0.45 \pm 0.05 b	< 0.001
Toughness index	26.95 \pm 0.74	28.52 \pm 0.83	27.89 \pm 1.09	NS
Hairs per mm	22.14 \pm 0.65	23.39 \pm 0.63	22.72 \pm 0.74	NS
Spines per cm	0.13 \pm 0.04	0.01 \pm 0.01	0.07 \pm 0.02	NS*
Beetle damage	0.75 \pm 0.08 a	2.74 \pm 0.55 b	0.10 \pm 0.02 c	< 0.001
Defoliation prevalence	0.94	0.38	0.69	< 0.005#

Means followed by a different letter are significantly different ($P < 0.01$, Tukey HSD test).

P-values after a one-way ANOVA, unless otherwise indicated.

Statistical significance was set to $\alpha = 0.00625$ after Bonferroni correction.

NS = non-significant.

*Kruskal–Wallis ANOVA.

χ^2 -test.

were square root-transformed before analysis in order to meet normality. In order to reduce the probability of type I error, the sequential Bonferroni correction was applied to the statistical evaluations listed in Table 1 (eight analyses). Thus, the level of statistical significance was set to $0.05/8 = 0.00625$, regardless of the test performed. ANCOVAs were performed in order to examine the influence of leaf traits on beetle damage, including the site as a main factor and beetle damage as a covariate. The dependent variables were those leaf traits showing plasticity among sites. In the case of significantly non-parallel slopes among sites after the ANCOVA, the within-site relationship between beetle herbivory and the leaf trait was assessed by regression analyses. Finally, prevalence of defoliator damage at each site was evaluated and compared using a χ^2 -test.

Results

Leaf traits related to size (area) and shape (area/perimeter) varied significantly among sites (Table 1). Of those traits to some extent related to defence against herbivores, leaf thickness was the only one showing variation (Table 1). Among-site levels of herbivory by flea beetles as well as prevalence of defoliation differed significantly (Table 1).

Tests of parallelism following ANCOVAs showed that there were no significant differences in the relationship between beetle herbivory and either leaf area ($F =$

1.768, $P > 0.18$) or area/perimeter ratio ($F = 2.539$, $P > 0.09$) among sites. In contrast, significantly non-parallel slopes of the relationship between beetle damage and leaf thickness were found among sites ($F = 5.941$, $P < 0.005$). Furthermore, within-site regression analyses indicated that whereas a marginally non-significant positive relationship between beetle damage and leaf thickness was found at the humid site ($r = 0.46$, $P = 0.073$), no significant relationship was found at the intermediate site ($r = -0.38$, $P > 0.14$). Results from the dry site showed a marginally non-significant negative relationship between beetle damage and leaf thickness ($r = -0.48$, $P = 0.058$). Interestingly, leaf thickness and toughness were positively and significantly correlated at this site ($r = 0.65$, $P = 0.006$), whereas no correlation was observed at either the intermediate ($P > 0.41$) or the humid sites ($P > 0.82$).

Discussion

Leaves of *S. incanum* are described in the botanical literature as 'ovate or elliptic, entire or slightly lobed, base cuneate to rounded' (Beentje, 1994). In accordance with this description, *S. incanum* exhibited a remarkable plasticity in the leaf traits evaluated. The direction of the variation of some of these leaf traits (namely leaf thickness, area and shape) agreed with predictions based on morphological responses to increasingly xeric environments (Crawley, 1997). In contrast, the expres-

sion of other traits traditionally associated with xeric environments, such as leaf toughness, hairiness and spines (Crawley, 1997), was not significantly higher at the dry site. The limited expression of such xeromorphic features could be due to an insufficient gradient of soil moisture encompassed by this study. Alternatively, unmeasured biotic factors, e.g. goat herbivory (Stuth & Kamau, 1990), able to affect those features (Myers, 1987) could have played a role in the lack of such a pattern by partially counteracting the effect of environmental conditions.

Leaf thickness was the only putative defensive trait showing among-site variation. Interestingly, the within-site relationship between leaf thickness and beetle herbivory was different at each site, ranging from positive (humid site) to null (intermediate site) to negative (dry site). The latter result may be explained by considering the strong correlation between leaf thickness and toughness that was found at the dry site (and only there). Leaf toughness has been reported to reduce feeding, growth rate and survival of chrysomelid beetles (Tanton, 1962; Raupp, 1985; Matsuki & McLean, 1994). Thus, feeding by flea beetles may have been hampered on thicker (and hence tougher) leaves, leading to a preference for thinner leaves. It is noteworthy that leaf toughness did not show any variation among sites. On the other hand, it did vary at the dry site, this variation being related to that of leaf thickness. This stresses the importance of scale when evaluating plasticity in plants. On the other hand, an increase in herbivory with leaf thickness was detected at the humid site, as has been described elsewhere (Louda & Rodman, 1996). This may be interpreted in terms of the quantity of resource the beetle obtains before leaving the leaf-patch. The thicker the leaf the more plant tissue is available, hence rendering thicker leaves a preferred feeding site. This holds as long as leaf thickness is not correlated with a trait that hinders beetle feeding. As indicated above, leaf toughness was not correlated with leaf thickness at this site. From a similar viewpoint, leaf size would have been expected to correlate with beetle herbivory at the humid site. Moreover, it has been reported that flea beetles show enhanced orientation towards larger objects (Bach, 1993a). However, beetle herbivory was not related to leaf area at any site.

The overall level of beetle herbivory, an indirect indication of local population density, was highest at the intermediate site, lowest at the dry site, and intermedi-

ate at the humid site. Interestingly, a somewhat matching pattern has been described by an experimental study, which showed that the survival of flea beetle pupae was highest at the intermediate level of moisture, and greater in the most humid than in the dry treatment (Rickelmann & Bach, 1991). On the other hand, a different pattern was found for defoliators, whose prevalence was highest at the humid site and lowest at the intermediate site. Among-site comparisons of patterns of herbivory by flea beetles and defoliators could suggest that, although they feed on the same plant species, different insect species (or guilds) react differently to environment-mediated changes in the plant. This has been reported previously (Hysell *et al.*, 1996). Alternatively, it is likely that other ecological factors, differentially acting along environments, could dominate over those changes in plants. Density of neighbouring plants, which markedly differ among sites, could play a role in such an effect. There is opposing evidence about the effect of stand density on the movement behaviour of flea beetles, which in turn might lead to differences in population density (García & Altieri, 1992; Bach, 1993b). Another factor, previous injury to leaves, has been shown to increase preference by flea beetles (Vaughn & Hoy, 1993). However, had this factor been operating in our study an association between defoliation prevalence and beetle damage would have been expected. As described above, this was not observed.

The present field study illustrates that the outcome of evaluations of plasticity in plant traits, and of its relationship with patterns of herbivory, may be scale-dependent. Whereas among-site comparisons allow the detection of clear differences in both trait expression and herbivory levels, it is difficult to ascertain causality between them because of the unmeasured variation in other ecological factors from site to site. In contrast, within-site comparisons of plastic traits have a reduced number of confounding factors, but sometimes the degree of variation is too narrow to allow the detection of significant relationships.

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