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Induced resistance against leafminer eggs by extrusion in young potato plants

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Abstract
Egg extrusion patterns were investigated as an inducible defensive mechanism in potato plants against the leafminer *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae). Increased multiplication rates in leaf cells surrounding an egg of *L. huidobrensis* leads to its exposure through the leaf cuticle, which might increase the risk of mortality. Extrusion rates were evaluated in laboratory tests, in relation to plant and leaf age in *Solanum tuberosum* L. var. Spunta. Stratified field sampling was also carried out in order to assess leafminer distribution on new and old leaves. Extrusion was higher in young plants, being restricted in older ones to new, still expanding leaves. Plant reaction was independent of egg density. In the field, damage was concentrated in older foliage, in line with the extrusion results. The relevance of egg extrusion for pest management is discussed.

Keywords: Liriomyza huidobrensis*, plant defences,* Solanum tuberosum*, damage distribution, egg mortality*

1. Introduction

The pea leafminer *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) is known as a pest on various crops throughout the New and Old Worlds (Dempewolf 2004). Serpentine mines resulting from larval feeding activity, as well as leaf stippling caused by adult females when feeding and inserting their eggs into the leaf parenchyma, reduce photosynthetic rates and mesophyll conductance (Parrella et al. 1985), thereby inducing considerable yield losses (Spencer 1973; Dempewolf 2004).

Plant resistance mechanisms against insect herbivores include, in addition to constitutive defences, the inducible production of various chemical compounds and structural traits following herbivore damage. Physical and chemical changes induced by feeding insects may affect the pest directly, e.g. by toxin production (Karban and Baldwin 1997), or indirectly by attracting natural enemies (Thaler 1999b; Kessler and Baldwin 2001). Plant defensive responses, ranging from chemical changes to plant tissue alterations, can also be elicited by insect egg deposition (reviewed by Hilker and Meiners 2006). Oviposition-induced resistance has been shown to reduce herbivore field populations either directly or via increased predation and parasitism (Thaler 1999b, Kessler and Baldwin 2001).

Some potato varieties have shown a particular mechanism of oviposition-induced resistance against *L. huidobrensis*, namly egg extrusion. Increased multiplication rates in leaf cells surrounding an egg of *L. huidobrensis* leads to its exposure through the leaf cuticle, thus increasing the risk of mortality from predation and desiccation (Gonzales Bustamante 1994; Cisneros and Mujica 1997). Egg extrusion has been suggested to vary with potato phenology (Gonzales Bustamante 1994), although no quantitative data have supported this observation. Since potato crops are especially susceptible to *L. huidobrensis* infestations, causing crop losses of up to 100% (Cisneros and Mujica 1997), egg extrusion could contribute to reduce leafminer damage.

Female leafminers are expected to select the most favourable hosts for their offspring, with their development being constrained by that choice (Valladares and Lawton 1991). Between-host differences in preference and performance have been shown for *Liriomyza huidobrensis* (Parrella and Bethke 1984; Martin et al. 2005; Videla et al. 2006). At the within-plant scale, leaves with high egg extrusion rates should be suboptimal in terms of progeny performance and therefore less preferred by ovipositing females. Varying patterns of host use in potato crops have been reported, with leafminer larvae being observed to be more abundant on the lower (Gonzales Bustamante 1994; Cisneros and Mujica 1997) or upper foliage (Weintraub 2001) or evenly distributed (Martin et al. 2005).

We tested experimentally the hypothesis that egg extrusion is linked to plant phenology, for *Liriomyza huidobrensis* on *Solanum tuberosum* L. var. Spunta.

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If egg extrusion affects leafminer preference and performance, patterns of plant use in the field should reflect any variation in extrusion capability. This possibility was evaluated by assessing the within-plant distribution of *L. huidobrensis* larvae in field crops, through stratified sampling.

2. Materials and methods

2.1. Laboratory bioassay

Egg extrusion patterns were evaluated on young (all leaves still expanding) and mature (at least four fully expanded leaves) plants of *S. tuberosum* var. Spunta. Twelve young plants, inside separate entomological cages (wood, glass and gauze, 30 cm on each side), were exposed for 4 h to two mated *L. huidobrensis* females. On each plant, one basal and one apical leaf containing eggs were labelled and examined daily for egg extrusion.

Oviposition into mature plants, fully expanded and still growing leaves was separately examined by exposing a leaf within a clip cage (7 cm high, 2.5 cm diameter) to two leafminer females for 4 h. Two apical and two basal leaves from each of 13 plants were considered.

Individual leaf area was measured from leaf tracings. Eggs (total and extruded) were quantified using a stereo microscope, due to their small size (0.3×0.1 mm).

Females of *L. huidobrensis* were obtained from a laboratory colony maintained on *Cucurbita maxima* var. *zapallito* (Carr.) Millan (Cucurbitaceae, 'courgette') and used in the experiments when they were 4–7 days old.

2.2. Field sampling

Three potato fields on the outskirts of Córdoba city, in central Argentina (31°20′S; 64°10′W), were surveyed at approximately 15-day intervals from October to December in 2002. On each sampling date, 75 leaves from the upper (first four apical leaves), middle (leaves fifth to tenth from top) and lower (11th and below) plant canopy were randomly collected and the percentage of mined leaves of each stratum was recorded.

2.3. Statistical analysis

Extrusion frequency in basal and apical leaves was compared by *G*-test. In order to detect possible influences of egg density on egg extrusion rates, the former was compared between leaf categories by *t*-test (or Mann–Whitney *U*-test when data were found to be not normally distributed). Relationships between extrusion rate and egg density were then analysed through Spearman rank order correlations. Analyses were carried out separately for young and mature plants, on account of differences in the methodology used. Extrusion frequency in leaves presenting similar egg densities from both plant types was also compared by *G*-test. Percentages of mined leaves recorded from field sampling were arc-sine square root transformed and compared among strata by ANOVA followed by Scheffe's test.

3. Results

Up to 80% of 122 leafminer eggs were extruded in young potato plants (Figure 1), with no significant differences being found between basal and apical leaves ($G = 0.91$, $P = 0.33$). Egg extrusion rates varied depending on leaf age in mature potato plants ($G = 66.83$, $P < 0.0001$): 17% of 291 eggs were extruded in apical, still expanding leaves, whereas there was no evidence of extrusion for the 260 eggs inserted in basal, fully expanded leaves (Figure 1). No significant differences were found in egg density between basal and apical leaves, neither in mature plants (2.06 ± 0.26 and 2.05 ± 0.46 eggs/cm^2, respectively; $U = 191.00$, $P = 0.35$) nor in young plants (basal 0.43 ± 0.07, apical 0.49 ± 0.1 eggs/cm^2; $t = -0.46$, $P = 0.65$).

The number of eggs per unit of leaf area was higher in mature than in young plants, which might have affected plant response. However, extrusion in mature plants was still remarkably lower ($G = 45.99$, $P < 0.0001$) when only leaves of both plant types with equivalent values of egg density were compared (range: 0.1–0.97 eggs/cm^2). Moreover, there was no correlation between egg density and extrusion rate, neither in mature ($r = 0.17$, $P = 0.44$, apical leaves only) nor in young plants ($r = -0.17$, $P = 0.56$).

Field data showed a significant decrease ($F = 10.69$, df $= 2$, $P = 0.010$) in the percentage of mined leaves, from lower to upper foliage (Figure 2).

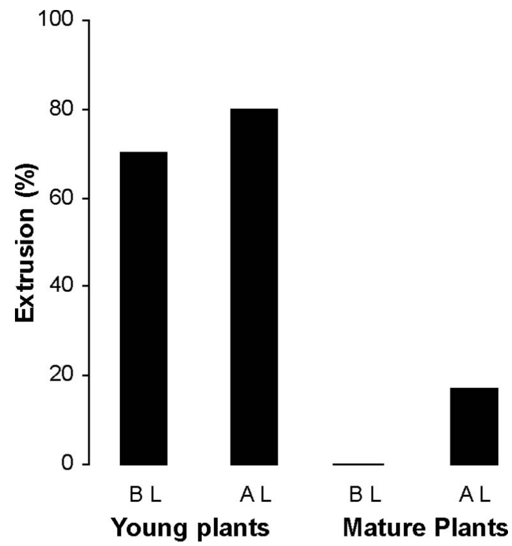

Figure 1. Extrusion rates (%) on basal (BL) and apical (AL) leaves of young and mature plants of *Solanum tuberosum* var. Spunta plants, in laboratory trials with *Liriomyza huidobrensis*. Different letters within plant categories indicate significant differences (*G*-test, $P < 0.05$).

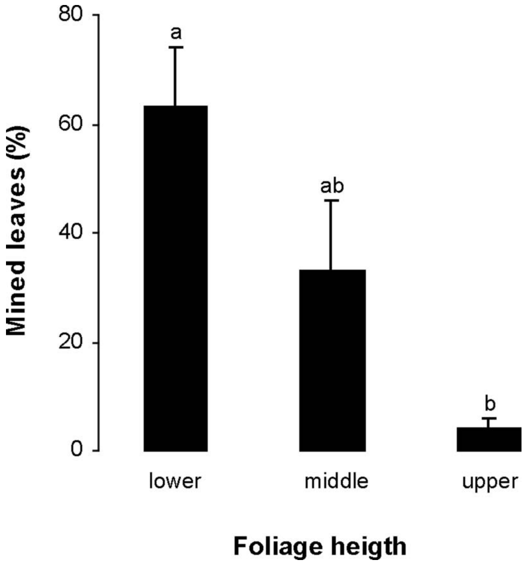

Figure 2. Within-plant larval distribution of *Liriomyza huidobrensis* on potato crops in central Argentina. Different letters indicate significant differences (Scheffe's test, $P < 0.05$).

4. Discussion

High extrusion rates were observed in all leaves of young potato plants, with similar values to those reported from the cultivar Canchán (Cisneros and Mujica 1997). Since 27.91% ($\pm$12.06) of eggs survived to larval stage, extrusion (ranging from 70 to 80%) seems to explain virtually all the egg mortality observed here, emphasising the defensive role of this mechanism. For other cultivars (Tomasa Condemayta, Perricholi, Ticahuasi and Revolución), egg extrusion has been reported without indication of its magnitude (Gonzales Bustamante 1994). The presence of this response among potato cultivars and its relative efficiency remain unknown.

The response of mature potato plants to leafminer eggs was less pronounced than that of young plants and was affected by leaf age. Plant defensive mechanisms can vary with plant development as changes occur in the resources and structures that can be allocated to defences (Karban and Baldwin 1997; Karban and Thaler 1999). Our results coincide with other mechanisms of induced resistance showing a stronger response in young leaves (Karban and Baldwin 1997).

Induced responses of plants can also vary according to damage level (Underwood 2000), hence the weaker reaction of leaves in mature plants could be attributed to their heavier egg load. However, the differences in plant reaction recorded here are unlikely to arise solely from density-dependent effects, since new leaves in mature plants were more responsive than basal leaves despite egg density values being similar. Moreover, this idea is supported by the lack of correlation between egg density and extrusion rate, in both plant types, as well as the higher extrusion rates found in young plants when compared to old ones at similar egg densities.

As expected from these observations, the field data revealed a pattern of decreasing presence of mined leaves, from lower to upper foliage. Such a distribution pattern could also result from a female preference for laying eggs on older leaves (Facknath 2005), which would be consistent with a preference–performance linkage if egg survival were higher on those leaves. Although preferences were not actually tested, it should be noticed that in our laboratory trials similar numbers of eggs were recorded on basal and apical leaves. The concentration of damage on mature foliage has been observed in other potato cultivars also showing extrusion (Gonzales Bustamante 1994; Cisneros and Mujica 1997). However, the opposite trend with mines being more abundant in the apical portion of the plant, has also been recorded (Weintraub 2001). This observation reinforces the idea that extrusion could have contributed to the low rate of mined leaves in the upper foliage observed throughout the season in our system, while suggesting that extrusion in growing leaves is not a ubiquitous resistance mechanism among potato cultivars.

Knowledge about the mechanisms and ecological effects of plant responses induced by oviposition is still very limited (Hilker and Meiner 2006). Although neoplasm formation may be induced in completely developed organs (Hilker and Meiner 2006), egg extrusion in potato seems to require actively growing tissue. The elicitors involved in this reaction remain unknown, with possibilities ranging from physical injury (which is greater for oviposition than feeding punctures) (Parrella 1987) to chemicals related either to the egg or to the female reproductive tract. In the laboratory, egg extrusion acted as a direct resistance mechanism, with extremely high mortality rates in absence of natural enemies. However, indirect effects (Thaler 1999b; Kessler and Baldwin 2001) cannot be ruled out.

Our results have several implications for the management of this leafminer pest. One such implication is related to pest monitoring, which for Agromyzidae is frequently based on adult trapping (Scheirs et al. 1997). High extrusion levels in young potato plants mean that leafminer adult populations might not be a good indicator of the larval population levels subsequently found in leaves, so that unnecessary pesticide applications could be made on the basis of adult monitoring (Weintraub and Horowitz 1996). This is not a minor point as the misuse of chemical control has already shown extremely adverse results in the case of *L. huidobrensis* and other leafminer pests (Cisneros and Mujica 1997).

Furthermore, as modern agriculture is increasingly moving away from reliance on exogenously applied pesticides, towards more 'environmentally friendly' methods, exploitation of inducible plant defences could represent an important endogenous component of integrated pest management (Thaler 1999a,b; Gatehouse 2002). Selecting potato varieties with high extrusion rates, or enhancing this defensive mechanism through conventional breeding strategies or genetic engineering, could contribute to lower levels of pesticide application by reducing leafminer populations either directly (egg desiccation) or indirectly (increased predation or parasitism).

In conclusion, we have shown that egg extrusion can represent a mortality factor for the leafminer *L. huidobrensis* on potato crops. This plant resistance mechanism deserves further study in the context of management programmes. Its application to closely related pest species such as *L. trifolii*, which is also more abundant on older potato leaves (Facknath 2005), merits further research.

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