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Specialized generalists: constraints on host range in some plusiine caterpillars

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Abstract Insects that feed on plants with secretory canals often cut trenches across leaves, thereby depressurizing the canals and eliminating exudation at their distal feeding site. We compared the trenching ability of three species of polyphagous plusiines (Lepidoptera: Noctuidae) and tested if trenching scores correlate with larval growth. The three plusiines (*Trichoplusia ni*, *Pseudoplusia includens*, and *Rachiplusia ou*) were each tested on prickly lettuce, *Lactuca serriola* (Asteraceae), which has latex canals, and on Italian parsley, *Petroselinum crispum* (Apiaceae) with oil ducts. To ascertain how secretory canals affect performance, larvae were tested on intact leaves and on excised leaves with depleted canals. *T. ni* larvae cut trenches in both plant species, whereas *P. includens* only trenched prickly lettuce and *R. ou* only trenched Italian parsley. Intact leaves of Italian parsley were acceptable to all three species. Trenching varied in *T. ni* and *R. ou*, but did not correlate significantly with larval growth. In contrast, trenching was required for feeding on intact prickly lettuce. Final-instar *T. ni* all cut trenches and developed rapidly. *P. includens* varied in trenching and performance; their trenching scores correlated with growth. *R. ou* larvae did not trench or feed even though most *R. ou* on intact Italian parsley cut at least partial trenches. All three plusiine species developed rapidly on excised leaves of both plant species, documenting the suitability of these plants when canals are inactivated. Our results document the efficacy of latex canals as a plant defense and suggest that trenching ability alone does not permit feeding. Larvae must also recognize the need to trench and must tolerate deterrent exudates during the trenching procedure.

Key words *Trichoplusia ni* · *Pseudoplusia includens* · *Rachiplusia ou* · Secretory canals · Trenching behavior

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Introduction

A polyphagous insect can potentially encounter any of a multitude of possible food plants, each with its own distinctive allelochemical composition (Bernays and Chapman 1994). The insect must decide whether to feed or to move on. The difficulty of this task has led to the suggestion that polyphagy is uncommon in insects because of neural constraints. The limited ability of insect herbivores to process information efficiently may favor specialization and the use of specific cues that indicate acceptable food (Bernays 1998; Bernays and Funk 1999).

Identifying suitable food may be especially difficult for cabbage loopers (*Trichoplusia ni*) and other polyphagous members of the subfamily Plusiinae (Lepidoptera: Noctuidae). These caterpillars must not only evaluate the nutritional and allelochemical composition of a leaf, they must also determine if a plant requires trenching. Larvae cut trenches to deactivate canal systems that emit defensive secretions such as latex or resin (Dussourd 1993; Dussourd and Denno 1994). The larvae nibble back and forth across the leaf, thereby rupturing canals and preventing secretion from flowing to their prospective feeding site. The trench also drains secretion from this distal section. A larva detecting deterrent substances should not necessarily abandon a leaf if the plant defense can be neutralized by trenching.

Cabbage loopers cut trenches in members of the Asteraceae with latex canals (tribe Lactuceae), Apiaceae with oil ducts, and Cucurbitaceae with phloem canals that emit sap (Dussourd and Denno 1994). These three families are classified in three different orders (Angiosperm Phylogeny Group 1998) and have canals that differ greatly in anatomy and chemical content. Cabbage loopers also attack many other plant species that do not release exudates; these plants are not trenched (Dussourd and Denno 1994). To feed on such disparate hosts and to recognize which require trenching, the larvae must respond appropriately to diverse chemistries. In addition, trenching loopers must tolerate persistent contact with exudates oozing from the leaf. For example, on prickly lettuce, cabbage loopers repeatedly contact latex during trenching and stop to groom ~20 times before completing a trench (Dussourd 1999).

Over 15 species of polyphagous plusiines that feed on plants in three or more families occur in North America (Eichlin and Cunningham 1978; Lafontaine and Poole 1991). Although extensive host records are available for some species, particularly for pests on agricultural crops (Eichlin and Cunningham 1978), little is known about what factors determine their host ranges. In this paper, we explore the proposition that host range in plusiines is determined not just by the suitability of a particular plant, but also by the ability of larvae to recognize which plant defenses can be disarmed by trenching and to tolerate exudates while cutting a trench.

We compare the growth and survivorship of three species of generalist plusiines: *T. ni*, *Pseudoplusia includens*, and *Rachiplusia ou*. *T. ni*, the cabbage looper, is a cosmopolitan pest on crucifers, lettuce, and other crops; it reportedly attacks plants in over 30 families (Eichlin and Cunningham 1978; Sutherland and Greene 1984). *P. includens*, the soybean looper, attacks soybean and members of over 10 other plant families (Lafontaine and Poole 1991; Sullivan and Boethel 1994). The third species, *R. ou*, feeds on herbaceous plants in at least seven families (Eichlin and Cunningham 1978; Lafontaine and Poole 1991). *Trichoplusia* and *Pseudoplusia* are classified in the tribe Argyrogrammatini, whereas *R. ou* is placed in the tribe Plusiini (Kitching 1987; Lafontaine and Poole 1991).

The plusiines were tested on prickly lettuce (*Lactuca serriola*, Asteraceae) and Italian parsley (*Petroselinum crispum*, Apiaceae). Prickly lettuce and other members of the tribe Lactuceae have latex canals (laticifers) that form an intricate network in the plant (Olson et al. 1969; Fahn 1979). Latex is stored under pressure within living cells. Damage causes an immediate release of latex, which flows through the laticifers to the site of injury. The latex coagulates upon exposure to air. Early-instar caterpillars of *Spodoptera ornithogalli* on prickly lettuce sometimes become fatally trapped in congealing latex or have their mouthparts stuck together (Dussourd 1993). The drying latex also interferes with trenching by larger *T. ni* larvae, for example by temporarily gluing legs together (Dussourd 1999). Lactuceae latex also contains a variety of allelochemicals, such as sesquiterpene lactones, triterpenes, and sterols (Crosby 1963; Gonzalez 1977), some of which are known to deter feeding by insect herbivores (Rees and Harborne 1985). Prickly lettuce is a wild relative of cultivated lettuce, *L. sativa*; recent molecular evidence suggests that the two should be classified as a single species (Koopman et al. 1998).

Italian parsley and other umbellifers have canals that emit droplets of secretion containing essential oils and resins (Hegnauer 1971). The canals occur as intercellular spaces that form elongate ducts throughout the plant (Warning 1934; Esau 1940; Metcalfe and Chalk 1950). Parsley leaves emit substantially smaller volumes of exudate than leaves of prickly lettuce (Dussourd and Denno 1991). With such tiny amounts, it seems unlikely that exudate viscosity or adhesiveness could deter insect feeding, particularly with larger larvae. However, parsley leaves contain furanocoumarins, terpenes, and phenylpropanoids (Porter 1989; Knogge et al. 1987), compounds that are well known for their antifeedant and toxic effects on herbivores (Berenbaum 1990; Zangerl 1990; Gershenzon and Croteau 1991; Berdegue et al. 1997). These compounds presumably occur at least partly in the oil ducts as documented with other umbellifer species (Hegnauer 1971; Camm et al. 1976; Zangerl and Bazzaz 1992; Stahl-Biskup and Wichtmann 1991).

We compared the growth and survivorship of plusiine larvae on intact plants and on excised leaves with depressurized canals. Our goal was to determine if the three plusiine species differ in trenching, and if differences affect larval performance on plants with secretory canals.

Methods

Insects and plants

Moths were collected in June, July, and August 1998 at Forrest City and Conway, Arkansas. To minimize any possible host plant bias, only adults attracted to lights were used to obtain eggs. Furthermore, for each experiment, only a single offspring from each female was tested on a plant species. This design maximized genetic diversity and allowed us to compare individuals both within and between caterpillar species.

All prickly lettuce and Italian parsley used in the study were grown from seeds in a temperature-controlled greenhouse and were used only once. Plants tested with larvae were from 1 to 5 months old; they all lacked reproductive structures and had not yet bolted. Although *L. serriola* is native to the Mediterranean area (Ryder and Whitaker 1976), it has become abundant in North America and is attacked by several generalist plusiines that trench its leaves (*Anagrapha falcifera*, *Autographa precationis*, *Megalographa biloba*, *Trichoplusia ni*; Dussourd and Denno 1991, 1994). *P. crispum* (syn. *P. sativum*) is also indigenous to the Mediterranean region, but has been widely cultivated in the United States (Schery 1972; Craker and Simon 1986). The Italian variety (*neapolitanum* Danert) was selected for our study because the leaves are broader and thus trenches are easier to detect and score. Several generalist plusiines, such as *A. falcifera*, *A. precationis*, and *T. ni* feed on umbellifers and readily accept Italian parsley (Dussourd and Denno 1994).

Growth experiment

We compared the growth of final-instar larvae of *T. ni*, *P. includens*, and *R. ou* over a 24-h test period. Newly emerged larvae from field-collected females were randomly assigned to either prickly lettuce or Italian parsley. The larvae were reared to the early final instar on excised leaves that were cut in sections to depressurize secretory canals. Trenching is not required for larval development on excised leaves (Dussourd 1993; Dussourd and Denno 1994). Upon reaching the final instar, the larvae were randomly assigned to be tested on either excised or intact leaves of the same plant species used for rearing. Larvae were weighed, then were enclosed either in a plastic cassette with excised leaves or in a mesh sleeve with intact leaves on a potted plant (one larva per plant). All larvae were offered two newly mature leaves and were tested at 25°C. At the end of the 24-h period, the larvae were reweighed. A total of nine larvae of each caterpillar species were tested on excised leaves and on intact leaves of each plant species. The 18 larvae tested with each plant species all came from different females.

During the 24-h period, larvae were checked at least three times to score trenches and to replace leaves that were mostly eaten. The following four-point scale was used:

(1) No trench produced during the 24-h period.
(2) Larva left bite marks in a band across the leaf, but the individual bites were not joined to form a complete trench.
(3) Larva cut a trench that extended across the entire leaf, but the trench was thicker than 1 mm (measured from leaf base towards tip). A thick trench often indicates that a larva is having difficulty with exudates and must extend the trench to avoid placing its mouth into latex exuding from the trench (Dussourd 1999).
(4) Larva cut a narrow trench (<1 mm) that extended completely across the leaf.

For larvae that cut multiple trenches, only the first trench was scored.

Survival experiment

Our second experiment tested if the three plusiine species can develop on prickly lettuce and Italian parsley. We replicated the previous experimental design using first-instar larvae and measured their survival until pupation. Newly emerged larvae were isolated individually in plastic cassettes with excised leaves or were enclosed within clip cages on intact leaves. Only a single larva was tested on each plant. When the larvae outgrew the clip cages, they were isolated with mesh sleeves that enclosed entire leaves. To minimize disruption of secretory canals, the clip cages and sleeves were padded where they attached to the leaves. Early-instar larvae were transferred to new leaves every 2–3 days, whereas late-instar larvae were transferred daily. As previously, 18 larvae of each plusiine species were tested on each plant species; half of the larvae were enclosed with excised leaves, whereas the other half received intact leaves. All 18 larvae tested with each plant species were the offspring of different females.

Performance was measured as percent survival, time from hatching until pupation, and pupal weight, which was recorded 2 days after pupation. Trenches of late-instar larvae were evaluated periodically using the four-point scale described previously. Larvae were tested indoors at 25°C.

Statistical analysis

In the 24-h experiment, we assessed the effects of caterpillar species and leaf treatment (excised versus intact leaves) on larval mass change using two-way ANOVAs. One-way ANOVAs were then used to analyze effects of caterpillar species on mass change separately for excised and intact leaves. Data not conforming to statistical assumptions of homogeneity of variance were log transformed. Post hoc comparisons between species were made using Tukey HSD multiple comparisons. ANOVAs were also used to compare the mass change of each species on excised versus intact leaves.

Differences among the three plusiine species in trenching scores were assessed with nonparametric Kruskal-Wallis tests. For plusiine species that varied in trenching, we tested for correlations between trenching score and mass change using Spearman rank correlations.

In the survival experiment, we tested for differences between species and between leaf treatments (excised versus intact leaves) in the number of larvae surviving to pupation with Fisher exact tests (Daniel 1978). We did not use two-way ANOVAs to compare caterpillar species in pupal mass or time to pupation because the three plusiine species differed in size; we would therefore expect differences in development and pupal mass irrespective of treatment. Instead, we used a multivariate analysis of variance (MANOVA) for each species to examine the effect of leaf treatment on pupal mass and time to pupation. Pillai's trace was used for hypothesis testing. Where significant, MANOVAs were followed by separate ANOVAs for pupal mass and for time to pupation. Data analyses were performed with Systat 7.0.1 statistical package (SPSS Inc., Chicago, Ill.).

Results

Prickly lettuce

In the 24-h experiment, plusiine growth was affected by an interaction between caterpillar species and leaf treatment (Fig. 1, Table 1). Larval mass change on excised leaves did not differ significantly between species (one-way ANOVA, $F_{2,24}$=0.545, P>0.5). The larvae increased their weight on average by 103%, a substantial gain for a 24-h period. In contrast, growth on intact leaves varied substantially between species ($F_{2,24}$=51.043, P<0.0001; Fig. 1). *T. ni* larvae gained significantly more mass than larvae of *R. ou* or *P. includens*, both of which lost weight. For all three species, mass change was significantly higher on excised leaves than on intact leaves (Fig. 1). Two *R. ou* larvae that each lost 15% of their initial weight on intact prickly lettuce were allowed an additional 24 h on the same leaves, which were now removed from the plant. The larvae, on average, increased

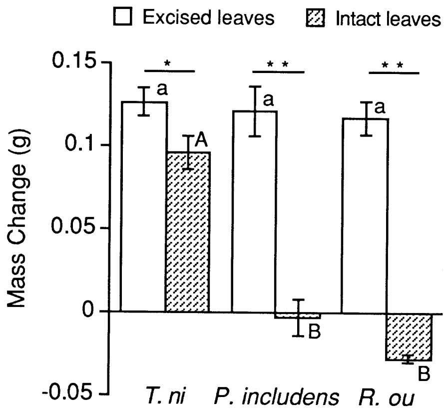

Fig. 1 Change in mass (mean±SE) of final-instar plusiine larvae over 24 h. The larvae were offered either excised or intact leaves of prickly lettuce, *Lactuca serriola* (n=9 larvae/treatment). Species that differ significantly (P<0.05 Tukey) in mass change have different letters above the bars (lowercase letters for excised leaves, uppercase letters for intact leaves). Significant differences within a species in mass change on excised versus intact leaves are indicated above the line connecting the contrasted pair (*P<0.05; **P<0.001; ANOVA)

Table 1 Analysis of variance for the effects of caterpillar species and leaf treatment (excised vs intact leaves) on mass change of plusiine larvae enclosed with prickly lettuce leaves for 24 h

Source	*df*	MS	*F*	*P*
Caterpillar species	2	0.003	18.247	<0.001
Leaf treatment	1	0.026	151.522	<0.001
Species×treatment	2	0.004	22.157	<0.001
Error	48	0.000		

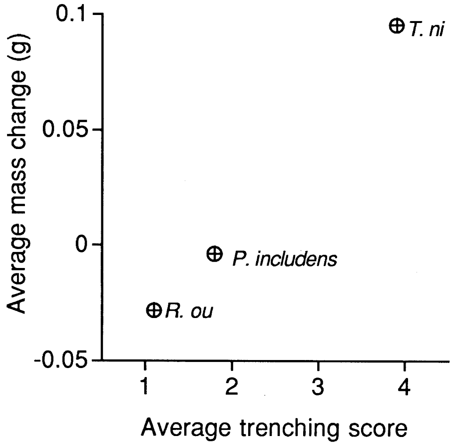

Fig. 2 Correspondence between mass change over 24 h and trenching score for three plusiine species that were tested on intact leaves of prickly lettuce, *Lactuca serriola*. Nine larvae were tested for each species. Trenching scores: *1* no trench, *2* partial trench, *3* complete trench that was usually thick, *4* complete narrow trench

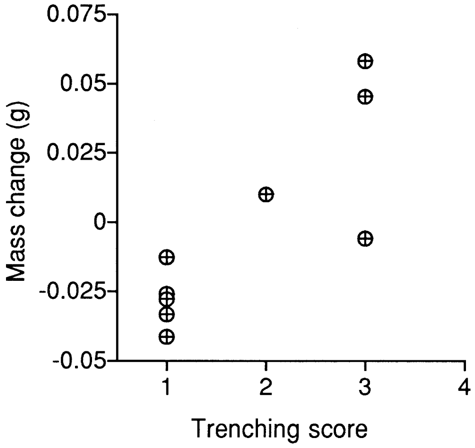

Fig. 3 Correspondence between mass change and trenching score for individual soybean loopers, *Pseudoplusia includens*, on intact leaves of prickly lettuce, *L. serriola*

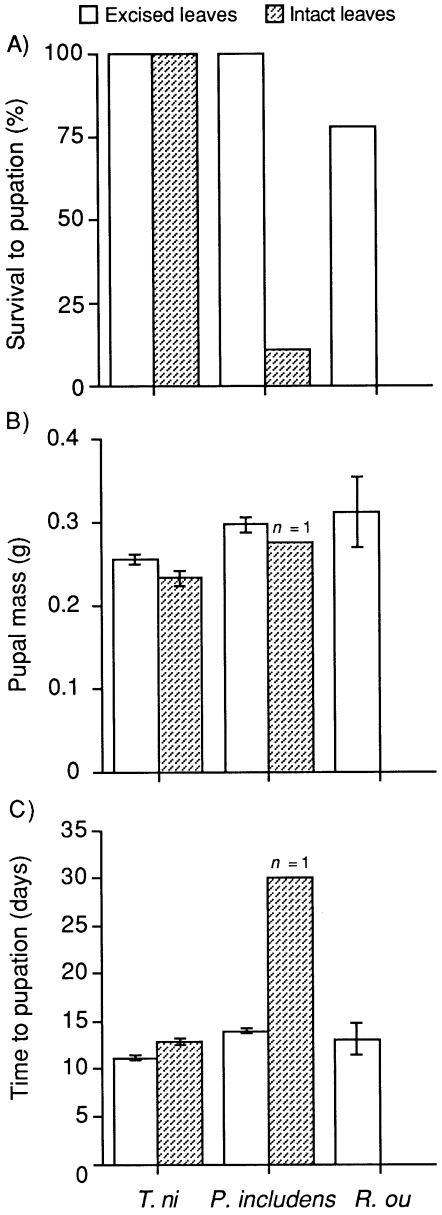

Fig. 4A–C Performance of plusiine larvae reared from egg hatch to pupation on prickly lettuce, *L. serriola* (*n*=9 larvae/treatment). **A** Percentage of larvae that pupated. **B** Pupal mass (mean±SE). **C** Time until pupation (mean±SE) for larvae that survived to pupate. None of the *R. ou* and only one of the *P. includens* larvae on intact leaves pupated

in weight by an astounding 179%, thus compensating for the earlier period of starvation and documenting how profoundly excision affects leaf acceptability.

Trenching scores differed significantly between the three plusiine species (H=20.5, P<0.0001; Fig. 2). *T. ni* larvae all cut excellent trenches (one 3 and eight 4s on the 4-point scale) and gained mass. *P. includens* larvae varied in trenching scores. Three of the four larvae with a trenching score of 2 or 3 gained mass, whereas all larvae that scored 1 lost mass (Fig. 3). Larval mass change in *P. includens* correlated significantly with trenching score (r=0.86, P<0.01). None of the *R. ou* larvae cut trenches (trenching score=1); all lost weight (Fig. 2).

In the survival experiment, all three species developed rapidly on excised leaves. Pairwise comparisons between species revealed no significant differences in survival to pupation (P>0.05, Fisher exact tests; Fig. 4A). Two first-instar larvae of *R. ou* died trapped by their head or legs in latex exudate, but all other larvae survived to pupate. In contrast, on intact leaves, survival differed dramatically. Significantly more *T. ni* pupated than either *P. includens* or *R. ou* (P<0.005 for both comparisons). *P. includens* and *R. ou* larvae both had lower survivorship on intact leaves than on excised leaves (P<0.005). Most of the *P. includens* and all of the *R. ou* on intact leaves died in the first instar. Two of the *R. ou* larvae were stuck by their legs in exudate. Only a single *P. includens* larva pupated; this individual was also the only soybean looper in the experiment that cut trenches (trenching scores 3, 3, 3, and 4).

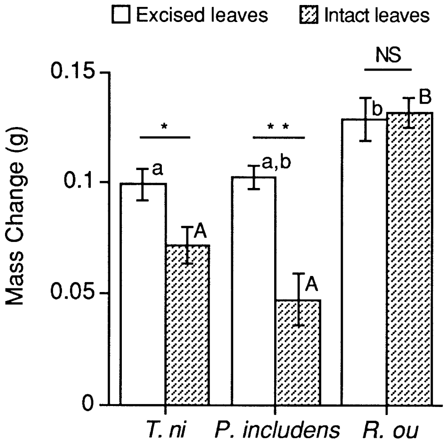

Fig. 5 Change in mass (mean±SE) of final-instar plusiine larvae over 24 h. The larvae were offered either excised or intact leaves of Italian parsley, *Petroselinum crispum* (n=9 larvae/treatment). Species that differ significantly (P<0.05 Tukey) in mass change have *different letters* above the bars (*lowercase letters* for excised leaves, *uppercase letters* for intact leaves). Significant differences within a species in mass change on excised versus intact leaves are indicated above the line connecting the contrasted pair (NS not significant; *P<0.05, **P<0.001, ANOVA)

Table 2 Analysis of variance for the effects of caterpillar species and leaf treatment (excised vs intact leaves) on mass change of plusiine larvae enclosed with Italian parsley leaves for 24 h

	df	MS	*F*	*P*
Caterpillar species	2	0.016	21.800	<0.001
Leaf treatment	1	0.010	13.588	0.001
Species×treatment	2	0.004	5.329	0.008
Error	48	0.001		

Although all *T. ni* survived, leaf treatment affected larval performance as measured by pupal mass and time to pupation (MANOVA, $F_{2,15}$=7.516, P=0.005). Pupal masses were smaller on intact leaves than on excised leaves, although this difference was not statistically significant (ANOVA, $F_{1,16}$=4.054, P=0.06; Fig. 4B). Time to pupation was significantly longer on intact leaves (ANOVA, $F_{1,16}$=13.846, P<0.005; Fig. 4C).

Italian parsley

Plusiine growth in the 24-h experiment was affected by an interaction between caterpillar species and leaf treatment (Fig. 5, Table 2). All larvae on Italian parsley gained weight, but there were significant differences between species in mass change on both excised ($F_{2,24}$=4.130, P<0.05) and intact leaves ($F_{2,24}$=19.924, P<0.0001). *R. ou* larvae had similar mass changes on intact and excised leaves, unlike *P. includens* and *T. ni* larvae which gained more mass on excised leaves (Fig. 5).

Trenching scores varied substantially between species (H=10.9, P<0.005). All *P. includens* scored 1, whereas *T. ni* and *R. ou* were variable (*T. ni*: four 1, one 3, four 4; *R. ou*: one 1, six 2, two 4). Trenching scores did not correlate significantly with mass change for either *T. ni* (r=0.37, P>0.05) or *R. ou* (r=0.00, P>0.05).

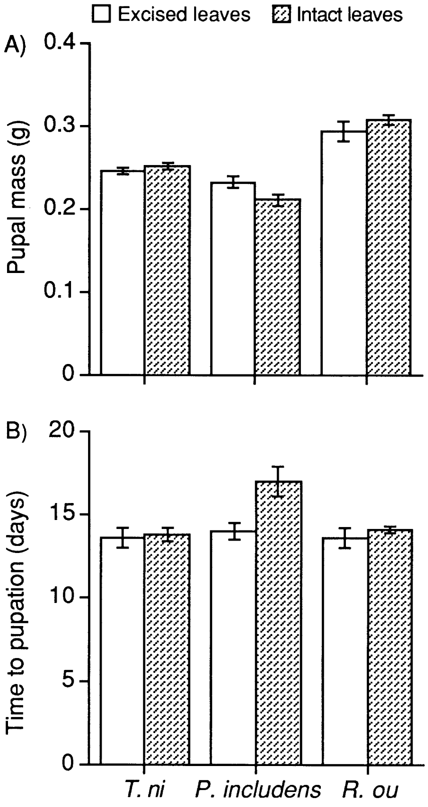

Fig. 6 Pupal mass (mean±SE) (**A**) and time until pupation (mean±SE) (**B**) for plusiine larvae reared from egg hatch on Italian parsley, *Petroselinum crispum* (n=9 larvae/treatment)

In the survival experiment, all larvae of all three species survived to pupate. However, leaf treatment significantly affected performance of *P. includens* (MANOVA, $F_{2,15}$=9.143, P=0.003). Larvae on intact leaves had smaller pupal masses (ANOVA, $F_{1,16}$=5.040, P<0.04) and longer pupation times (ANOVA, $F_{1,16}$=7.096, P<0.02) than larvae on excised leaves (Fig. 6A,B). For *T. ni* and *R. ou*, pupal mass and development time were not significantly affected by leaf treatment (MANOVA, P>0.4 for each species).

Discussion

Unlike many groups of herbivorous insects, plusiines vary enormously in diet and in diet breadth. The larvae feed on a diverse assortment of herbs, plus grasses, conifers, poplars and other woody plants (Kitching 1987; Lafontaine and Poole 1991). Some plusiines specialize on a single plant genus, whereas others feed on multiple genera in a single family or even on an assortment of families. The factors that allow plusiines to utilize so many different hosts and that cause divergence in diet breadth are poorly understood.

Previous work has implicated trenching as an important adaptation allowing polyphagous plusiines to feed on hosts with defensive canal systems (Dussourd 1993; Dussourd and Denno 1994). The present study documents variation among polyphagous species. *T. ni* larvae cut trenches in both prickly lettuce and Italian parsley, *P. includens* only trenched prickly lettuce, whereas *R. ou* only trenched parsley. The behavior of the plusiines differed markedly even though all three species are general feeders on herbaceous plants.

On prickly lettuce, trenching was mandatory for successful feeding. All *T. ni* trenched and gained weight, *P. includens* larvae varied in trenching and performance, whereas all *R. ou* failed to trench and starved. Excised leaves were universally acceptable, documenting that prickly lettuce provides adequate nutrition for all three species. The lack of trenching by *R. ou* was noteworthy because eight of nine larvae on Italian parsley cut at least partial trenches. Prickly lettuce may not have elicited trenching because it is an introduced species in North America (Ryder and Whitaker 1976); perhaps insufficient time has elapsed for *R. ou* to evolve adaptations for exploiting this plant. However, *R. ou* larvae sleeved on a native congener, *Lactuca canadensis*, likewise did not trench (D.E. Dussourd, unpublished data). On both *Lactuca* species, the larvae left bite marks scattered around the leaves, many with orange drops of dried exudate. An earlier study (Dussourd and Denno 1994) found that growth of the nontrenching generalist *S. ornithogalli* on prickly lettuce was comparable on excised leaves and on leaf tips beyond trenches cut by *T. ni*. As with *R. ou*, *S. ornithogalli* starved on intact prickly lettuce. Evidently, if *R. ou* and *S. ornithogalli* could trench prickly lettuce, they could feed and develop. *R. ou* larvae fail to utilize this potential host apparently because leaf chemicals trigger a deterrence response instead of trenching.

P. includens was the only species that varied in trenching on prickly lettuce. Individuals that did not trench all lost weight in the 24-h experiment, whereas three of four larvae with trenching scores 2 or better gained weight. We do not yet know if only some larvae are capable of trenching or if all larvae trench, but only some are stimulated to trench prickly lettuce. *P. includens* now feeds extensively on soybean, which did not become an important field crop in the US until the 1940s; in 1999, 72 million acres were planted (Abelson and Hines 1999). Soybean lacks secretory canals that emit exuclate (Dussourd and Denno 1994). It is possible that selection for trenching in *P. includens* has diminished and that larvae lacking this adaptation can now survive with little or no cost. We have never found a soybean looper on prickly lettuce in nature, although *P. includens* in the field do trench and feed on cucumber (*Cucumis sativus*), which has exuding phloem sap, and on mulberry (*Morus* sp.), which emits latex (Dussourd and Denno 1994; D.E. Dussourd, unpublished data).

On Italian parsley, trenching scores varied both within and between caterpillar species, but did not correlate with performance. Evidently, trenching is not required for plusiine feeding on this species. Nevertheless, both *T. ni* and *P. includens* gained less weight on intact leaves than on excised leaves in the 24-h experiment. *P. includens* larvae, which were never observed to trench Italian parsley, also had lower pupal weights and longer development times on intact leaves. Whether the poorer performance of these larvae on intact leaves was due to secretory canals or to inducible responses, which have been reported in parsley and another umbellifer (Kombrink and Hahlbrock 1986; Zangerl 1990), is not known. Certainly, the oil ducts of Italian parsley were less effective than the latex canals of prickly lettuce at deterring feeding by *P. includens* and *R. ou*. Either the greater volume of exudate in prickly lettuce, its chemical composition or adhesiveness produced a more potent defense.

Early- and late-instar larvae performed similarly in our experiments. For example, first-instar larvae of *R. ou* on intact prickly lettuce all died in the survival experiment, whereas the final-instar larvae all lost weight in the 24-h experiment. Performance was similar even though early-instar larvae do not have to trench in order to feed. First-instar *T. ni* on intact prickly lettuce, for example, feed between leaf veins, thereby avoiding laticifers concentrated in the veins. The larvae do not begin trenching until the second instar (Dussourd 1993). Nevertheless, first-instar larvae of *R. ou* (also most *P. includens*) were unable to develop on intact prickly lettuce. Evidently, both early and late instar larvae contact sufficient latex to deter feeding.

Feeding on intact prickly lettuce incurred costs even for larvae that cut trenches. For example, *T. ni* in the 24-h experiment had a significantly lower mass change on intact leaves than on excised leaves. Likewise, larvae in the survival experiment took longer to develop a smaller pupa on the intact leaves. Poorer performance on intact leaves can be attributed in part to costs associated with trenching. Completing a single trench on prickly lettuce requires approximately 2 h (Dussourd 1999), time that is not available for feeding. In addition, trenching uses energy, exposes larvae to defensive compounds when exudates ooze onto the trench surface, and undoubtedly also increases larval visibility to predators.

The discovery of trenching in *R. ou* extends the previously known distribution of trenching behavior within the Plusiinae. Specifically, *R. ou* is the first species known to trench within the subtribe Autoplusiina of the tribe Plusiini, which has two other subtribes: Plusiina and Euchalciina (Lafontaine and Poole 1991). Three genera of Plusiina also have trenching species: *Anagrapha*, *Autographa*, and *Megalographa* (Dussourd and Denno 1991, 1994). Another plusiine tribe, Argyrogrammatini, contains the trenching genera *Anadevidia* (Takeuchi and Tamura 1993), *Chrysodeixis* (Compton 1989), *Pseudoplusia* and *Trichoplusia* (Dussourd and Denno 1991, 1994). This broad distribution of trenching suggests that the trait either appeared early in the evolution of the plusiines or has evolved repeatedly. Only one other noctuid species is known to trench: *Amphipyra tragopoginis* in the Amphipyrinae cuts trenches in dandelion and prickly lettuce (Dussourd and Denno 1991). Since the Amphipyrinae is distantly related to the Plusiinae (Mitchell et al. 2000), trenching presumably evolved separately in this group.

In summary, plusiine performance differed within and between caterpillar species, on different plant species, and on leaves with intact or severed canals. Trenching ability proved to be prerequisite, but not sufficient for plusiine feeding on intact prickly lettuce. The larvae also must be stimulated to trench and they must persist in trenching despite latex exudation.

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