Does low nutritional quality act as a plant defence? An experimental test of the slow-growth, high-mortality hypothesis

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Abstract. 1. The slow-growth, high-mortality hypothesis was experimentally tested in this study by investigating the effects of plant quality and natural enemies on leaf-miner growth, performance, and survivorship. Two leaf miners (*Acrocercops albinatella* and *Brachys tesselatus*) occurring on the turkey oak *Quercus laevis* were studied using a factorial design that manipulated predation/parasitism pressure and plant nutritional quality.

2. Forty trees were randomly divided into four treatments: (1) control plants (nutrients and natural enemies unaltered); (2) nutrients added, natural enemies unaltered; (3) nutrients unaltered, natural enemies reduced; and (4) nutrients added and natural enemies reduced. Water content, leaf toughness, tannin concentration, and foliar nitrogen were quantified monthly for each plant, and mine growth and survivorship were assessed by tracing mines on a 2–3-day interval and by following the fates of 50 mines per species per treatment combination.

3. Fertilised plants exhibited significantly higher amounts of nitrogen, but no significant differences among treatments were observed for water content, leaf toughness, and tannin concentration. These results only partially support the slow-growth, high-mortality hypothesis, as mines were significantly smaller and developed faster on fertilised plants, but neither fertilisation nor natural enemy exclusion significantly affected mine survivorship or mortality caused by natural enemies.

Key words. Fertilisation, leaf miners, natural enemies, plant quality, slow-growth–high-mortality hypothesis, tri-trophic interactions.

Introduction

Resources and natural enemies, as well as the interaction between them, have the potential to affect herbivore abundance, distribution, performance, and survivorship. The effects of both resources and natural enemies on herbivory rates experienced by plants have been widely discussed (e.g. Moran & Hamilton, 1980; Augner, 1995; Williams *et al.*, 2001) and low plant quality can affect insect performance directly, by reducing growth rate, fecundity, and survival (Slansky, 1993; Haggströn & Larsson, 1995) or indirectly

by affecting the risk of mortality caused by natural enemies (Feeny, 1976; Price *et al.*, 1980; Clancy & Price, 1987). The interaction between variation in host-plant quality and risk of attack by natural enemies was formalised into the slow-growth, high-mortality hypothesis (hereafter SGHMH; Clancy & Price, 1987). According to this hypothesis, herbivores feeding on plants of low nutritional quality (e.g. low nitrogen, high levels of secondary compounds, high toughness and/or lignin content) do not necessarily increase damage on their host by overcompensatory feeding if increased development time due to poor host quality increases the window of vulnerability of herbivores to natural enemy attack. Specifically, the SGHMH proposes that the nutritional quality, allelochemistry, and/or morphology of the host plant can act as a sub-lethal plant defence by prolonging development of herbivorous insects and

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subsequently increasing mortality inflicted by predators and parasitoids (Benrey & Denno, 1997). Clancy and Price (1987) wrote, 'many more individual case studies are needed to determine if the SGHMH should be generally rejected or accepted'. Since then, relatively few tests of the SGHMH have been performed, with mixed results. In a factorial manipulation of plant quality and predation pressure, Loader and Damman (1991) found that *Pieris rapae* larvae growing on low-nitrogen plants developed more slowly and were more likely to be killed by predators than conspecifics growing on high-nitrogen plants. Parasitism rates, however, were higher in herbivores feeding on high-nitrogen plants. For galling sawflies on arroyo willows, Clancy and Price (1987) also observed higher parasitism rates in fast-developing *Pontania* galls and slow-growing galls were less vulnerable to attack from parasitoids. Benrey and Denno (1997), on the other hand, observed that slow-developing larvae of *P. rapae* were more heavily parasitised by *Cotesia glomerata* than fast-developing larvae reared on artificial diets, but slow growth did not translate into increased parasitism when variation in larval growth was achieved with the use of natural variation of plant quality caused by interspecific differences. Williams (1999) reviewed the evidence for the SGHMH and found that, usually, slow-growing, surface-feeding herbivores were at less risk from parasitism but greater risk from predation, than faster-growing herbivores. For concealed herbivores, such as gall-formers and leaf miners, the SGHMH was rejected in approximately half of the cases reviewed, regardless of natural enemies being predators or parasitoids.

Most of the data used to test the SGHMH has been observational in nature, and only a few studies have experimentally manipulated aspects of plant quality that potentially affect herbivore growth and development and might consequentially affect natural enemy attack (see Loader & Damman, 1991; Benrey & Denno, 1997; Lill & Marquis, 2001). Furthermore, among the 41 studies reviewed by Williams (1999), only five studies were conducted with leaf miners, and none of these studies were specifically designed to test the SGHMH, as most of them assessed leaf-miner survivorship under natural variations in host-plant quality (i.e. differences in host-plant species, within-host variation in quality, effects of plant hybrids) and none of these studies manipulated natural enemies to assess their effects on leaf-miner survivorship and performance.

The current study aimed to test the SGHMH for two very distinct species of leaf miners, *Acrocercops albinatella* (Lepidoptera: Gracillaridae) and *Brachys tesselatus* (Coleoptera: Buprestidae), feeding upon the turkey oak *Quercus laevis* (Fagaceae), with a factorial manipulation of both plant quality and natural enemy pressure. Manipulation of the third trophic level was achieved by reducing invertebrate predators and parasitoids, and manipulation of plant nutritional quality was achieved by plant fertilisation. Specifically, the following predictions were tested: (1) Low tissue quality cause herbivores to feed for longer periods of time and lengthens larval development time. Therefore, leaf miners feeding on fertilised plants should exhibit smaller mines and shorter development times than leaf miners on control plants. (2) Lengthened development time or increased feeding results in increased mortality caused by natural enemies. Therefore, leaf miners feeding on fertilised plants should exhibit higher survivorship/lower mortality caused by predators and parasitoids than leaf miners on control plants. (3) If natural enemies are a significant source of mortality for leaf miners on turkey oaks, mines feeding on plants in which natural enemies were reduced should exhibit higher survivorship than mines on control plants. Because both plant quality and natural enemies were manipulated in the factorial design, here it was also predicted that (4) leaf miners feeding on fertilised plants in which natural enemies were excluded should exhibit the highest survivorship amongst all treatments.

Study system

The turkey oak, *Quercus laevis*, is one of the characteristic trees associated with the sand hill community throughout Florida. *Quercus laevis* is a moderately fast to fast-growing tree and presents deciduous glabrous leaves, alternately arranged with usually five lobes, although this number may vary from three to seven (Nixon, 1997). Although a common tree in Florida native vegetation, there are relatively few studies concerning herbivory in this plant species. *Acrocercops albinatella* (Lepidoptera: Gracillaridae) is a microlepidopteran species whose larval stages feed on young leaves, creating distinct linear-blotch mines on the lower surface of *Q. laevis* leaves. Larvae typically appear in early spring (late February or early March) and feed on the palisade parenchyma cells, completing their development in approximately 10 days. Larvae emerge from the blotch mine and usually pupate on the same leaf from which they emerge (T. Cornelissen, pers. obs.). *Brachys tesselatus* (Coleoptera: Buprestidae) is a beetle species that also forms distinct blotch mines in *Q. laevis* leaves. The adults emerge from mid-March to mid-April, coinciding with budburst of turkey oak. Adults initially feed on the early leaves until mating and oviposition. Eggs are deposited singly on the upper surface of the leaves and after hatching the larvae mine into the mesophyll creating distinct, characteristic damage. Contrary to what happens in South Carolina (Waddell *et al.*, 2001) *Brachys* in the study sites here go through two generations, instead of just one. The first mines appear in early April and remain active until late June, when larvae complete their development and pupate inside the mines. New adults emerge in early July and oviposit to form new *Brachys* mines that remain active until September–October. Pupation and overwintering of this second generation occurs within the leaves after they have senesced and abscised from the tree. New adults emerge from the leaf litter in the following spring (Waddell *et al.*, 2001). Turkey

oak leaves are also attacked by many other herbivores, such as the leaf roller weevil *Homoeolabus analis* (Coleoptera: Atellabidae), the eastern buck moth *Hemileuca maia*, the white-marked tussock moth *Orgyia leucostigma* (Lepidoptera: Lymantriidae) and, less commonly, other leaf miners such as *Stigmella* spp. (Lepidoptera: Nepticuliidae) and *Cameraria* spp. (Lepidoptera: Gracillariidae).

Generalist predatory ants (Hymenoptera: Formicidae) and the green lynx spider *Peucetia viridans* (Araneae: Oxyopidae) are among the most common arthropod predators in these study sites. The leaf miners studied are also attacked by several microhymenopteran parasitoid species, including *Zagrammosoma multilineatum* (Hymenoptera: Eulophidae) and *Chrysonotomyia* sp. (Hymenoptera: Eulophidae).

Materials and methods

Data collection

This study was conducted between February and November of 2003 on natural stands of scrub oak vegetation in Tampa, Florida. Forty *Q. laevis* trees ranging between 1.5 and 2.5 m in height were marked at an unburned patch at the University of South Florida ECOAREA (for a description of the study site see Mushinsky *et al.*, 2003).

The effects of plant quality and pressure exerted by natural enemies on the abundance, performance, and survivorship of two different leaf miners (*A. albinatella* and *B. tesselatus*) on *Q. laevis* were investigated using a 2×2 factorial design. The 40 trees were randomly divided into four treatments, allowing 10 replicates of each treatment, as follows: (1) −F, +P: control plants with nutrients and natural enemies unaltered; (2) +F, +P: nutrients added, natural enemies present (unaltered); (3) −F,−P: nutrients unaltered, natural enemies reduced; and (4) +F,−P: nutrients added and natural enemies reduced. Plant quality was manipulated by the addition of 150 g of 46:0:0 NPK fertiliser to assigned *Q. laevis* trees bi-weekly from April to June. Unfertilised plants had soil around the tree slightly disrupted, but no granular fertiliser was added. Plants did not significantly differ in height, number of leaves on 10 shoots and leaf area (five leaves per tree) before treatments were assigned (one-way ANOVAs, all $P > 0.05$). A previous study with the same system indicated that predation by spiders was a negligible mortality factor for the leaf miners (Cornelissen & Stiling, 2005a), hence only mortality caused by predatory ants and parasitism caused by microhymenopterans were manipulated. A preliminary count of green spiders on all marked plants in March 2003 showed that spider abundance was very low (average 0.8 ± 0.2) and did not differ among plants assigned to the four treatments. Ants were excluded by placing masking tape covered with Tanglefoot® around the base and twigs of assigned oak trees at the beginning of the experiments and by handpicking ants already present on the trees. Efficiency of ant

trapping was checked monthly by counting ants during 5 min per tree on all treatment combinations. Tanglefoot® was reapplied on assigned turkey oak trees in May 2003. Parasitoid reduction was achieved by adding between 12 and 15 yellow 13×8 cm Sticky Strip traps (Gempler's, Belleville, Wisconsin) per assigned tree. Previous studies with gall-formers and leaf miners have shown that yellow traps are efficient at capturing parasitoids in other systems such as salt marshes and oak hammock communities (e.g. Moon & Stiling, 2002, 2004). Traps were placed throughout the tree canopy using binder clips and were replaced bi-weekly. Old traps were collected and individually wrapped in plastic and frozen for further analyses. To assess sticky trap efficiency, the number of microhymenopterans and other invertebrates caught on the traps were counted on three 4×4 cm quadrats on two traps per plant at the beginning and at the end of the season.

To assess variation in host-plant quality among treatments, water content, foliar nitrogen concentration, tannin concentration, and leaf toughness were evaluated monthly for each plant, between April and September of 2003. On each sampling date, eight undamaged leaves were collected from each tree and placed immediately on ice. Leaf toughness was evaluated using an Effegi FT-011 penetrometer (International Ripening Co., Alfonsin, Italy) and water content was quantified by the difference between leaf wet and dry weights. Leaves were further oven-dried and milled to a fine powder. Tannins were extracted from 50 mg of dry tissue, and tannin concentration was quantified using the radial diffusion assay with tannic acid as a standard (for details see Hagerman, 1987). Nitrogen content was determined using a CE Instruments NC2100 CN Analyzer (CE Elantech, Incorporated, Lakewood, New Jersey).

To test for differences in mine growth and survivorship among treatments, five mines of each leaf-miner species ($n = 50$ mines per species per treatment combination) were permanently marked on each plant using a permanent black ink marker as soon as the eggs hatched and larvae initiated mine formation. *Acrocercops* mines were measured at 2-day intervals by tracing the numbered mines using acetate sheets. *Brachys* mines were traced at 3-day intervals. At the end of the experiment, mine drawings were digitised and mine size was measured using the software UTHSCSA Image Tool (University of Texas, San Antonio), with digital pictures calibrated to the nearest 0.01 mm. We compared final mine size (cm²), developmental time (days to pupation) and mine growth rate among treatments for each leaf-miner species. Mine growth rate on each leaf was calculated as Growth rate = (Final mine size – Initial mine size)/number of days mine was growing. After mine termination, all leaves were inspected under a stereomicroscope to assess leaf-miner survivorship and identification of mortality factors. Leaf miners offer a good opportunity to assess population survivorship and mortality factors as a record of the miner success is clearly observed on the leaves: parasitised mines have tiny circular exit holes on the mine's surface and/or pupae within the mine, and predated mines are usually found ripped open and the larva is

absent. Successfully emerged larvae of *Acrocercops* cut open the mines and pupate usually on the same leaf where the mine developed. *Brachys* larvae pupate inside mines and/or cut circular holes on the underside of the leaf.

Data analysis

All the variables analysed were first submitted to Lilliefor's test for data normality and transformations (log transformation and arcsine square rooted) were employed to stabilise variances and normalise the data. However, for the sake of clarity, figure axes and means (+ 1 SEM) show untransformed data. Seasonal variation in turkey oak quality was described elsewhere (Cornelissen & Stiling, 2005b) and on this study only variation in plant quality among treatments is emphasised. To test for differences in plant nutritional quality among treatments, we first averaged tannin concentration, nitrogen content, water, and toughness using all eight leaves sampled for each plant on each collection date and two-way ANOVAS were used to assess effects of treatment on host-plant quality. A paired *t*-test was used to assess differences in leaf area of *Q. laevis* before and after fertilisation and Pearson correlations were used to examine the relationship between tannin and nitrogen concentration and between water and toughness on each individual plant. To test for differences in leaf-miner growth and survivorship among treatments, differences in mine size, days to pupation, and growth rate of mines that survived to pupation were analysed using a two-way ANOVA with fertilisation and natural enemies as main factors. Differential survivorship among treatments as well as the proportion of mines killed by natural enemies (parasitoids and predators) and proportion killed by unknown factors (e.g. plant resistance, larvae dead inside mine) on each treatment were also analysed using a two-way ANOVA. All statistical analyses were performed using SYSTAT 9.0 for Windows (Wilkinson, 1999).

Results

Treatment effectiveness

Application of Tanglefoot® on assigned turkey oak tress proved effective in keeping ants away from treated trees compared with control trees (control trees: 14.6 ± 1.1 ants, treated trees: 0.92 ± 0.22 ants, $F_{1,28} = 137.6$, $P < 0.001$). Sticky traps also proved efficient in capturing microhymenopterans and other small invertebrates. Microhymenopterans were much more abundant on the traps than other insects such as ants, ladybugs, and flies (microhymenopterans 32.3 ± 1.56, other invertebrates 11.24 ± 0.19). No significant differences were observed in the abundance of parasitoids caught on traps from plants treated with traps only (29.66 ± 0.75 parasitoids per trap) vs. plants that were fertilised and had sticky traps added (29.47 ± 1.05, $F_{1,38} = 0.22$, $P = 0.74$).

Treatment effects on host-plant quality

Fertilisation significantly increased the amount of foliar nitrogen on *Q. laevis* trees ($F_{1,36} = 8.993$, $P = 0.005$) and fertilised trees showed a tendency for decreased tannin concentration (Fig. 1), although differences in tannins among treatments were not statistically significant (Fertiliser effect: $F_{1,36} = 2.82$, $P = 0.092$). No significant differences among treatments were observed for leaf toughness and leaf water content (all $P > 0.05$). Linear regressions revealed that, for *Q. laevis*, no significant relationship was observed between tannin and nitrogen concentration per individual plant ($P = 0.361$), or between water and leaf toughness ($P = 0.688$). Paired *t*-tests revealed no significant difference in leaf area before and after fertilisation ($t = -0.778$, $P = 0.441$).

As expected, natural enemy removal did not affect host-plant quality (natural enemies effect, all $P > 0.05$) and no significant interactions between treatments were observed.

Treatment effects on leaf-miner performance

Fertilisation significantly decreased mine size of *Acrocercops* ($F_{1,126} = 12.71$, $P = 0.001$; Fig. 2a) and of both generations of *Brachys* (first generation $F_{1,96} = 21.74$, $P < 0.0001$; second generation: $F_{1,66} = 4.85$, $P = 0.031$; Fig. 2d). Analysis conducted only for mines that survived showed that *Acrocercops* mines on fertilised plants were approximately 56% smaller than mines growing on control plants, whereas *Brachys* mines on fertilised plants were approximately 16% smaller than mines on control plants. Removal of natural enemies did not significantly affect the size of *Acrocercops* mines ($F_{1,126} = 2.97$, $P = 0.09$) or the size of *Brachys* mines (first generation: $F_{1,96} = 2.23$, $P = 0.138$; second generation: $F_{1,96} = 31.30$, $P = 0.583$).

Fertilisation also significantly affected the development of leaf miners. *Acrocercops* mines growing on fertilised plants pupated earlier ($F_{1,126} = 9.69$, $P = 0.002$) and developed faster ($F_{1,126} = 16.74$, $P < 0.001$) than mines growing on control plants (Fig. 2b,c). For the first generation of *Brachys* mines, significant effects of fertiliser on performance was also observed, as mines required fewer days to pupate ($F_{1,96} = 4.19$, $P = 0.043$, Fig. 2e) and developed faster ($F_{1,96} = 5.83$, $P = 0.018$, Fig. 2f) than mines developing on control plants. For the second generation of *Brachys* mines, fertilisation significantly decreased the number of days required to pupation ($F_{1,66} = 20.15$, $P = 0.001$), but no significant effects were observed on mine growth rate ($F_{1,66} = 2.35$, $P = 0.07$). No significant interactions between fertilisation and removal of natural enemies were observed for either leaf miner (all $P > 0.05$).

In general, high survivorship was observed for all the leaf miners studied (Fig. 3) and for both *Acrocercops* and *Brachys*, survivorship was not affected by experimental manipulation (fertiliser and natural enemy effects: all $P > 0.05$). For *Acrocercops*, however, miners experienced
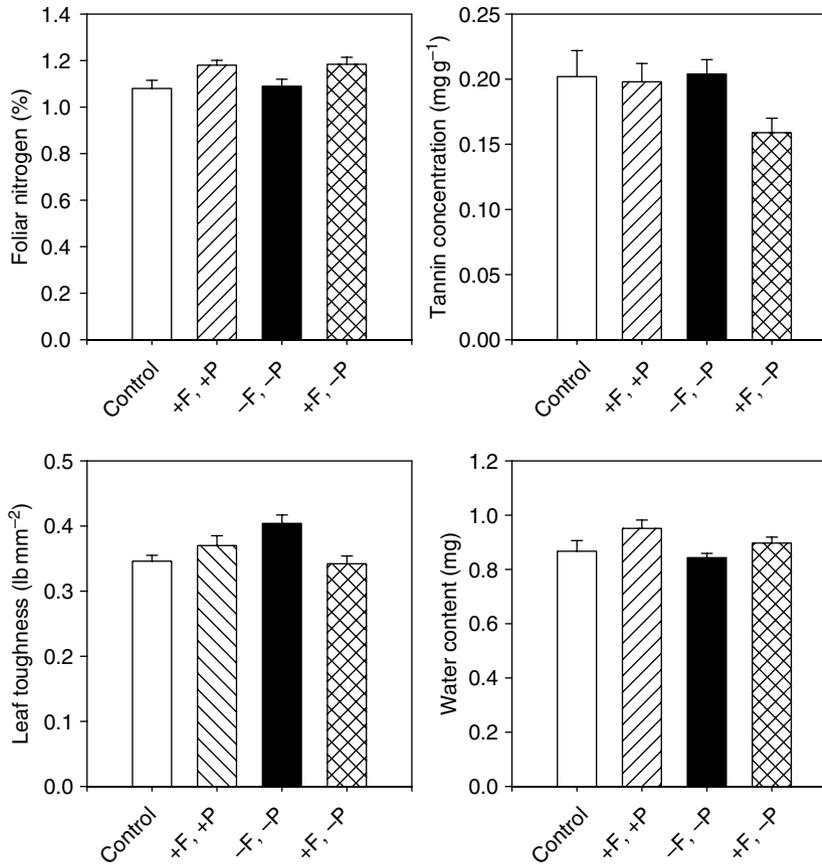
Fig. 1. Treatment effects on the concentration of foliar nitrogen, tannin concentration, leaf water, and foliar toughness of *Quercus laevis*. Bars shown mean (+ 1 SE) of averaged monthly samplings (control: plants with nutrients and natural enemies unaltered; +F, +P: nutrients added, natural enemies present (unaltered); –F, –P: nutrients unaltered, natural enemies reduced; +F, –P: nutrients added and natural enemies reduced.).

lower mortality inflicted by predators when developing on fertilised plants compared with control and/or trapped plants ($F_{1,36} = 12.72$, $P < 0.001$), but no significant effects of fertiliser were observed when natural enemies were parasitoids ($F_{1,36} = 2.34$, $P = 0.159$). For both generations of *Brachys*, no significant effects of fertiliser addition or natural enemy removal were observed on the proportion of mines killed by predators or parasitoids (all $P > 0.05$).

Discussion

Herbivorous insects often suffer reduced growth rates when feeding upon sub-optimal hosts and, although poor diets are not lethal in themselves, it is assumed that they nevertheless increase the mortality rate by prolonging the vulnerable stages of herbivores (Rostas & Hilker, 2003), which might lead to higher levels of enemy attack (Moran & Hamilton, 1980; Clancy & Price, 1987). Plant nitrogen concentration influences important interactions between herbivorous insects and plants (Kyto *et al.*, 1996) and low nitrogen supplies might result in increased total plant consumption through increased consumption rates and/or prolonged periods of feeding, digestion, and development (Mattson, 1980). Kyto *et al.* (1996) reviewed the evidence for the effects of soil fertilisation on

phytophagous insects and concluded that enhanced nitrogen availability benefited herbivores by improving host-plant quality, but also affected population-regulating processes such as predation, parasitism, and competition. Our results have demonstrated the beneficial effects of plant fertilisation in terms of increased availability of foliar nitrogen and a tendency for decreased concentration of tannins. Previous studies in the same oak system indicated that several herbivore guilds respond to improved plant quality caused by fertilisation with an increase in density (Cornelissen & Stiling, 2005b). In this study, it has been shown that leaf miners also respond to improved plant quality by altering development and reducing the length of the larval stage. Mines were significantly smaller on fertilised plants, developed faster and pupated earlier than mines growing on control plants. Similar responses to improved plant quality have been reported for other leaf miners (e.g. DeBruyn *et al.*, 2002), gall-formers (e.g. Clancy & Price, 1987; Stiling & Moon, 2005), and free-feeding herbivores (e.g. Myers, 1985; Loader & Damman, 1991).

Although the experiments here have demonstrated that enhanced nutritional quality caused by plant fertilisation allowed mines to develop faster and pupate earlier, no significant effects of improving plant quality and/or removing natural enemies were observed on mine survivorship and mortality imposed by the third trophic level.
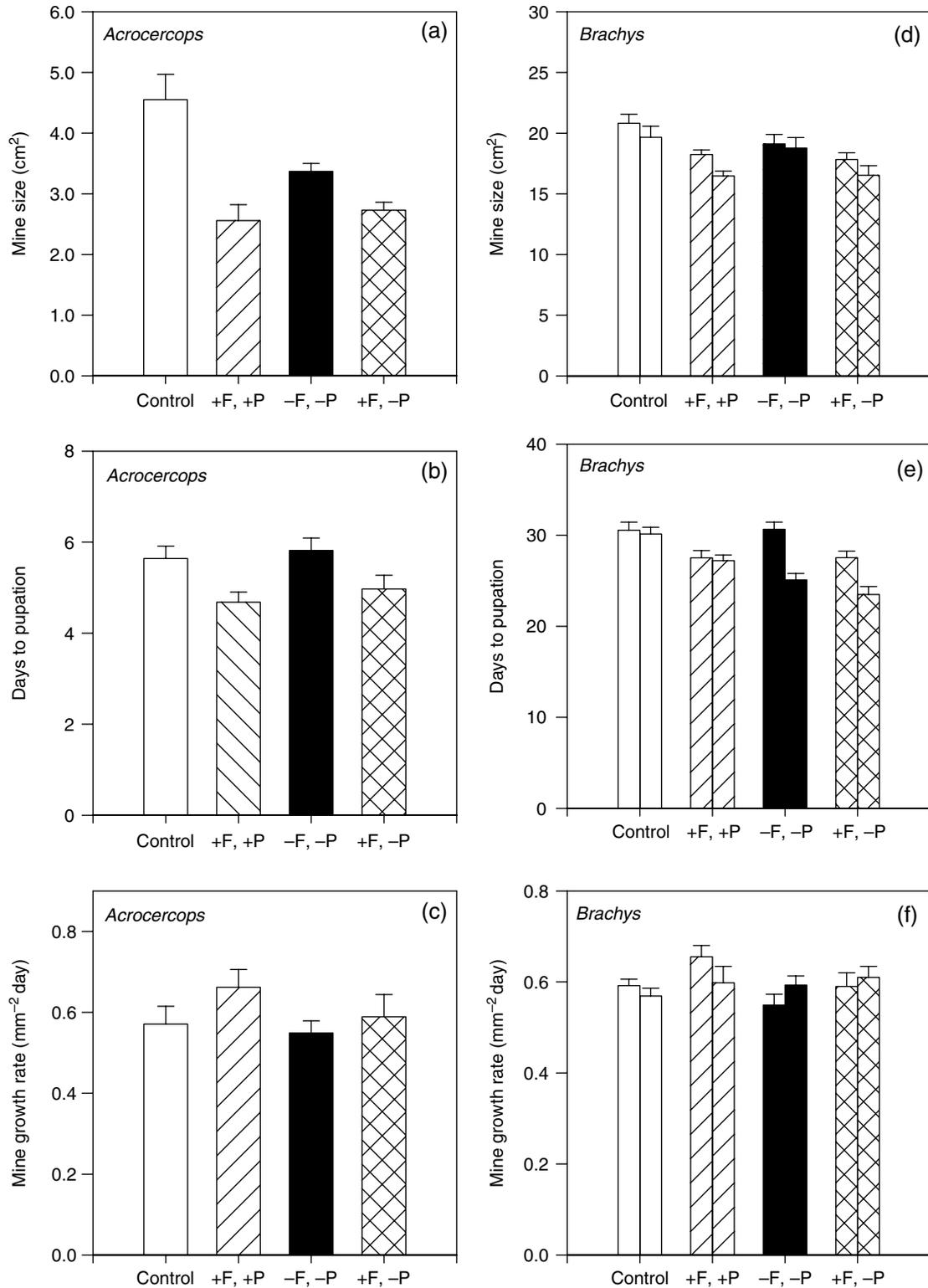
Fig. 2. Treatment effects on the size and development of the leaf miners *Acrocercops albinatella* and *Brachys tesselatus*. For *Brachys*, bars to the left indicate data for the first generation and bars to the right indicate data for the second generation. Bars show means (+ 1 SE) and treatment legends are as on Fig. 1.
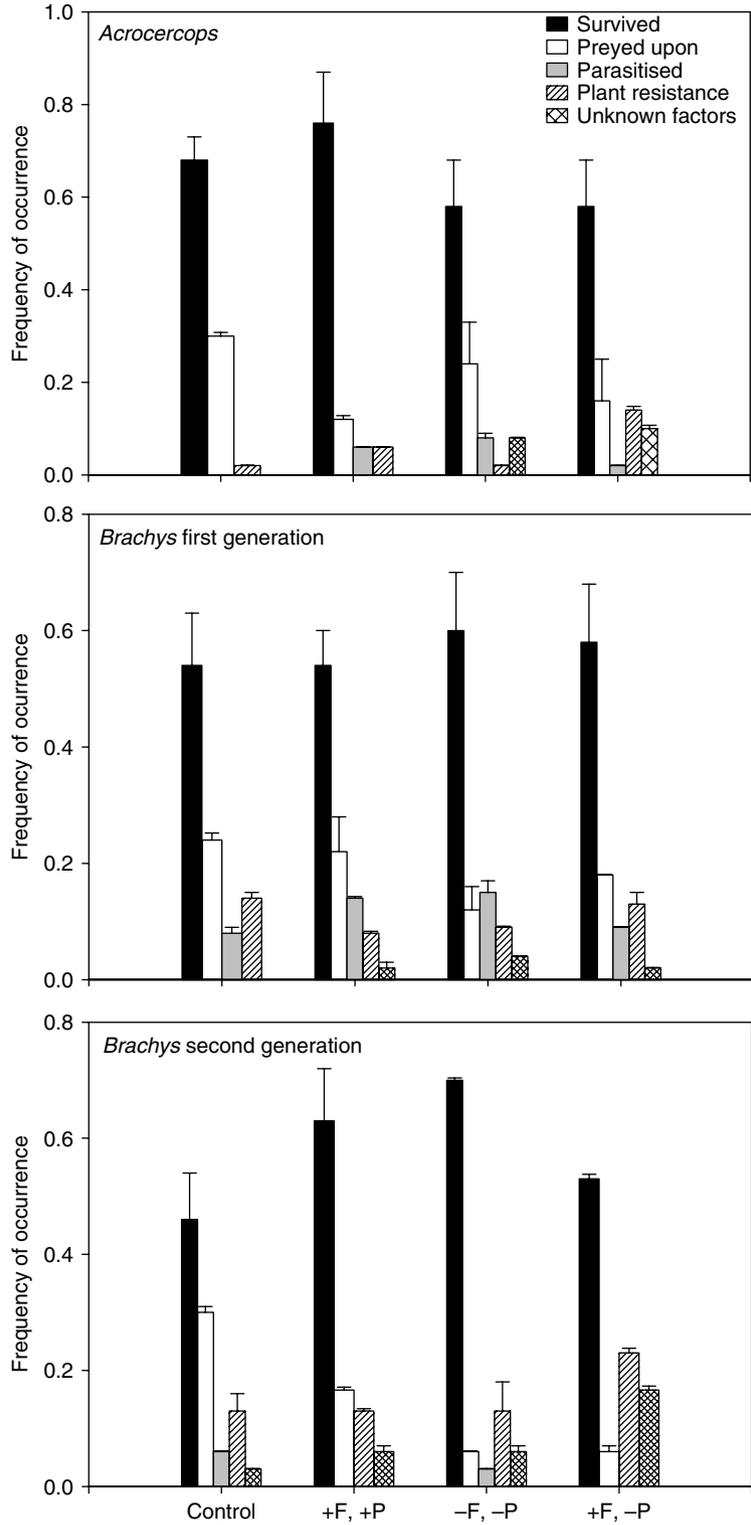
Fig. 3. Frequency of occurrence of mortality factors for leaf miners growing under four different treatments. Bars show means (+ 1 SE) and treatment legends are as in Fig. 1.

Therefore, the shorter window of larval vulnerability did not translate into higher survivorship or escape from natural enemy pressure. Interestingly, these results demonstrated high survivorship rates for both leaf miners studied, regardless of experimental treatments. Other studies with leaf miners occurring in oaks (e.g. Faeth, 1980; Auerbach & Simberloff, 1988; Stiling & Simberloff, 1989; Connor & Beck, 1993) have reported much lower survivorship and emergence rates (range: ≈ 0.6–42%) and higher mortality inflicted by natural enemies (range: ≈ 21–38%). Adding sticky traps and treating experimental plants with Tanglefoot® proved efficient at removing natural enemies on experimental trees, although effects of the third trophic level on mine performance and survivorship do not seem to be relevant in our studied systems. Alternatively, the results reported here might also show that, although application of Tanglefoot® and use of sticky traps have been efficient in reducing natural enemy impact in other plant–herbivore–parasitoid systems (e.g. Moon & Stiling, 2004), it might have had limited efficiency in our oak trees, compared with other systems such as salt marshes (e.g. Moon & Stiling, 2002). Although Hawkins (1994) reported high parasitism rates for leaf miners compared with other feeding guilds in biological control studies, the results reported here suggest that, under natural conditions, the concealment provided by the leaf-mining habit might actually offer an advantage to larval stages of *Acrocercops* and *Brachys*. The hypothesis that the leaf mine might be adaptive is part of the broader concept that concealed feeding strategies serve as defences against natural enemies (for a review see Connor & Taverner, 1997) and seem to hold true at least for the leaf miners studied here.

Variation in host-plant nutrition and chemistry is often a primary cause of differences in feeding efficiency, growth rate, and pupal mass of herbivores feeding on different host plants and different parts within plants. These results generally demonstrated that leaf miners feeding on sub-optimal hosts tended to consume more tissue and develop for longer periods of time, although attack rates by natural enemies and survivorship did not differ among optimal and suboptimal hosts. Lower predation rates of *Acrocercops* mines on optimal hosts suggest that faster development did promote escape from natural enemies such as predatory ants. For *Brachys* mines, however, these results reinforce the idea that sub-lethal plant defences remain a paradox (Clancy & Price, 1987; Leather & Walsh, 1993). *Brachys* mines develop much slower than *Acrocercops* mines, may exhibit mines that damage more than 70% of the leaf in which they develop (T. Cornelissen, pers. obs.), and are therefore 'apparent' to natural enemies for longer periods of time. Moran and Hamilton (1980) suggested two other scenarios in which poor nutritive quality of foliage could evolve as an adaptation to insect herbivory: (1) if herbivores are able to detect differences in the nutritive quality of individual plants and if they preferentially feed upon more nutritious host individuals, then low nutritive quality of leaves is advantageous, and (2) if successive herbivore generations tend to feed upon the same host individual, then low nutritive quality will prevent future build up of herbivore numbers, thereby increasing plant fitness. Previous studies with leaf miners have shown high degrees of discrimination among hosts with varying degrees of nutritional quality (e.g. Faeth *et al.*, 1981; Auerbach & Alberts, 1992; Fox *et al.*, 1997) and high fidelity to individual natal hosts (e.g. Mopper *et al.*, 1995; Mopper *et al.*, 2000), corroborating both scenarios proposed as explanations for the adaptive significance of low nutritional quality of hosts. Alternatively, low densities of both *Acrocercops* and *Brachys* mines in our study site (mean ± 1 SE per 200 leaves: *Acrocercops*: 25.9 ± 2.26; *Brachys* first generation: 11.1 ± 1.02; *Brachys* second generation: 7.71 ± 0.97) might indicate that the detrimental effects of leaf miners on plant fitness are realised only during outbreak years.

Previous studies have demonstrated that the support for the SGHMH is mixed, varying among taxa and natural enemy guilds (Williams, 1999; Fordyce & Shapiro, 2003). In this study, low nutritional quality does not act as a plant defence and our results reinforce the idea that sub-lethal plant defences remain a paradox, although alternative explanations such as those provided by Moran and Hamilton (1980) might be sustained in the studied system.

Acknowledgements

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