LEAF MINER SUCCESS ON *PIPER* IN SUN AND SHADE HABITATS

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Abstract. We examined the effects of leaf phenotype on herbivore attack and success rates in sun and shade habitats. Leaf area and leaf specific mass were assessed on *Piper* spp. trees found in both habitats. The frequency of attacks by agromyzid larvae and the proportion of attacks that were successful were quantified on individual trees. Leaf specific mass was significantly higher in the shade than in the sun. Leaf area varied as a joint function of habitat and height stratum on tree, but the habitat effect alone was not significant. The frequency of agromyzid attacks was higher in the shade than in the sun, although success rates were similar in both habitats. Variation in leaf miner success was most related to leaf area or the leaf characteristics that covary with leaf area such as leaf chemistry or development time. However, it appeared that adult agromyzis oviposited at random with respect to leaf area and were not able to detect the most suitable leaves for larval development.

Key words: herbivore defense, leaf miner, leaf morphology, pheneotypic plasticity, Piperaceae

INTRODUCTION

Many studies of tropical plant-herbivore interactions have focused on genotypic variations in defense among plants adapted to different light conditions. There is less understanding of how individual plant species respond phenotypically to different light conditions and how these responses affect plant resistence to herbivory. We examined herbivory by leaf-mining larvae of the Agromyzidae on a single *Piper* species that is found in both sun and shade habitats. *Piper* species are distinguished by their candlestick inflorescences and shrub or small tree growth form. Agromyzid larvae mature by eating their way through leaf mesophyll and forming an easily recognizable tunnel that widens as they develop.

We hypothesized that phenotypic adjustment in *Piper* spp. to different light conditions would affect patterns of herbivory by leaf miners. Possible phenotypic adjustments include changes in leaf chemistry and morphology that may have positive or negative effects on leaf miner success. For example, as plants increase leaf nitrogen and specific mass to maximize photosynthesis under high light, they may become more attractive to leaf miners by providing better nutrition and increased protection. Alternatively, the production in high light of smaller leaves with higher concentrations of secondary metabolites may lower leaf miner success by making leaves less palatable. We predicted that differences in leaf miner attack and success rates would correspond to differences in leaf morphology and chemistry across sun and shade habitats .

METHODS

Research was conducted near the San Luis Biological Station, Guanacoste Costa Rica, on 20 and 21 January 1996. We selected 20 individual *Piper* plants of a common single species: 10 in a high-light habitat east of the dormitory on the main park road, and 10 in a low-light habitat along the trail behind the dormitory. Each plant was separated into upper and lower strata by approximately halving the distance between the first branch with leaves and the meristem. Within each stratum, we counted the total number of leaves, haphazardly picked 3 leaves for measurement of mass and area, and collected all leaves that contained agromyzid mines.

We measured length and width on each of the 120 haphazardly picked leaves. Ten of these leaves, representing a range of sizes and plants, were mapped on graph paper to determine leaf area. We calculated the area for the remaining 110 leaves using a linear regression developed from the subsample of 10 leaves (Area = 0.545 * LW + 273.48, $r^2 = 0.9748$, where LW = the product of length and width) We measured the mass of one leaf per stratum per plant to calculate leaf specific mass (= mass per unit area). Leaf area and specific mass were compared between habitats, trees, and tree strata.

Leaf miner success was assessed by examination of mined leaves. Mines with distinct exit holes or live late instar larvae were classed as successful; those in which the miner died before emerging were classed as unsuccessful; (34.9% of the mines were classed as unknown because the evidence was equivical, usually

because part of the leaf was missing).

We tested for patterns in leaf area and habitat specific mass with an ANOVA model that included habitat, tree within habitat, and height stratum. We compared the frequency of of leaf miner attacks between habitats with a Chi-square, and used correlation analysis to test for relations betwen leaf properties and larval success.

RESULTS

Leaf area varied as a joint function of habitat and height stratum (habitat x height interaction, Figure 1).

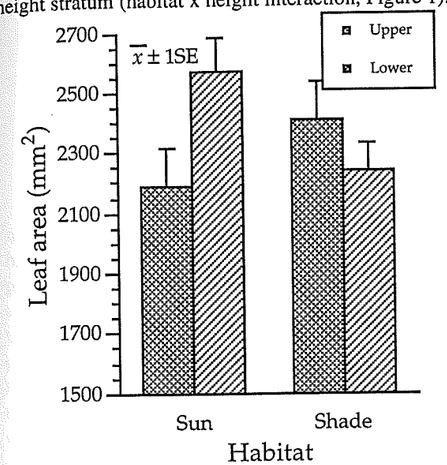

Fig. 1. Leaf area of *Piper* leaves in the upper and lower strata of trees in the sun and shade.

Sun leaves were larger than shade leaves in the upper height stratum, but smaller than shade leaves in the lower height stratum. Leaves in the sun had significantly higher specific mass than leaves in the shade. In both habitats, bottom leaves tended to have lower specific mass, although the difference was not significant (Figure 2).

The frequency of leaf miner attacks on leaves was higher in the shade (11.1% of leaves) than in the sun (8.4% of leaves; $X^2 = 9.46$, df = 1, $P < 0.005$). The percent of attacks that were successful ranged from 69% in the sun to 73% in the shade, and there was no significant difference between the two habitats ($X^2 = 0.45$, df = 1, $P < 0.5$).

In both habitats, there was a strong positive correlation between leaf area and leaf miner success ($r = 0.76$, df = 14, $P < 0.01$; Figure 3). Success was highest on trees with larger leaves. There was no correlation between leaf area and percent attack, nor betweenspecific mass and percent success or percent attack (Figure 3).

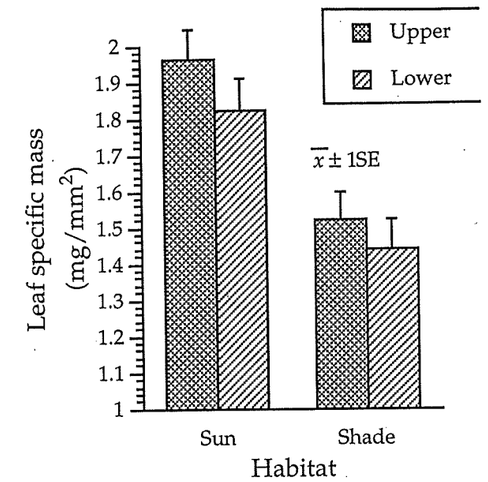

Fig. 2. Specific mass of *Piper* leaves from the top and bottom of trees in sun and shade.

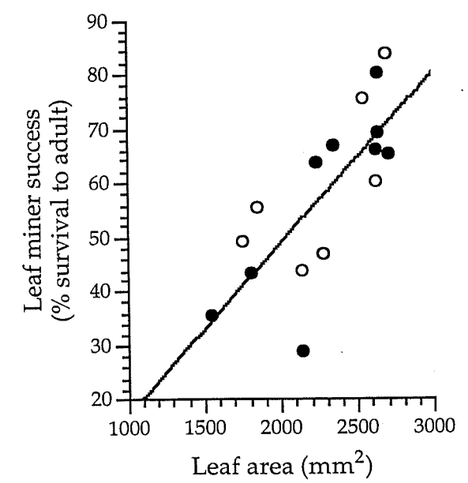

Fig. 3. Correlation of leaf area and leaf minor success in the sun (open circles) and shade (closed circles).

DISCUSSION

Results supported the hypothesis that *Piper* plants adjust to environmental variation between sun and shade habitats with phenotypic adjustments of leaf

morphology. *Piper* in high-light habitats appeared to produce leaves with thicker mesophyll presumably because thicker mesophyll increases per unit area light absorption and allows the plant to absorb a larger portion of high intensity light. It was surprising that leaf area did not change with habitat as did leaf specific mass. The habitat effect may indicate that there is more change in light levels between upper and lower strata in shade plants than in sun plants, and therefore less benefit to increasing leaf area in the bottom strata.

Frequency of leaf miner attacks was somewhat higher in the shade than in the sun (11.1% vs 8.4%) This is surprising because the higher leaf specific mass that we observed in the sun would actually seem to support more herbivory in the sun, not less, by providing leaf miners greater protection and nutrition. The slightly higher leaf miner attack rate in the shade may have resulted from higher agromyzid abundance in the shade. The difference in attack rate between habitats may not be biologically relevant because herbivory was low on plants in both habitats.

Leaf miner success was strongly related to leaf area and/or to leaf characteristics that covary with leaf area. The success of miners on larger leaves did not appear to be related to larger available leaf area because miner tracks covered only small portions of leaves in both size classes. Rather, leaf miner success may relate to leaf phenology if larger leaves have a longer development period. If immature leaves have lower concentrations of chemical defenses, then leaf miners that spend a larger portion of their development in immature leaves may have greater success. Testing for covariations in nitrogen and carbon-based secondary metabolites, leaf toughness, and water content may further explain differences in leaf miner success across habitats.

If leaf miner success is correlated to leaf development time, then selection should favor adult agromyzis that can detect immature leaves destined to have relatively long development periods. However, the lack of correlation between leaf miner attack rate and leaf area suggest that ovipositing adults lack this ability, perhaps because there are no suitable chemical or physical cues. In any case, it appears that agromyzis oviposit randomly with respect to the probability of larval success. Future studies could look for correlations between attack rates and leaf maturation and compare leaf miner development in mature and immature leaves.