LEAF-MINER DEFENSES IN *BROMELIA PINGUIN* L. (BROMELIACEAE) IN VERACRUZ, MEXICO

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ABSTRACT

Leaf-miners are present on leaves of all adult sexually reproducing individuals of *Bromelia pinguin* (Bromeliaceae), but not on leaves of vegetatively reproducing or immature individuals; thus, we hypothesized that there should be differences in defenses between them. No differences were found when we compared metabolic contents, humidity, and nitrogen of mined and unmined leaves, but found significant differences in ash, fiber and lipid contents. Mined leaves had more fiber and lipids and less ash than unmined leaves, but differences may exist only during a short period of time and were not detected by our research. The leaf-miner *Melanagromiza* sp. (Diptera: Agromizidae) attacks leaves with the highest fiber contents. Cited research is on trees and their seedlings, but results could differ in large clonal plants where metabolites move between ramets. The response of leaf-miners could be to a combined series of factors other than food quality or the amount or type of defenses, such as a plant-herbivore-parasitoid complex.

INTRODUCTION

Plants cover most of the Earth's surface, and even though subject to varying degrees of herbivory by a diversity of organisms, they are not eliminated because, among other things, they ensure their own defense (Crawley, 1983; Howe and Westley, 1988; Thompson, 1982; Weis and Berenbaum, 1989). Plant defenses include mechanical protection on the surface of the plant, complex polymers or silica crystals that reduce plant digestibility, and plant toxins that kill or repell herbivores at very low concentrations (Coley and Aide, 1991; Howe and Westley, 1988; Rico-Gray, 1989). There are large differences among plant species in both the amount and type of anti-herbivore defense toxins in their leaves (Coley, 1988). Defenses against herbivory should be allocated in direct proportion to the tissue or plant part that confers the greatest fitness to the individual plant (Dirzo, 1984). Plant defenses change with time (e.g., leaves toughen as they mature, and sometimes potent toxins in young leaves are replaced by lignified or silicified tissues in older leaves and twigs), and virtually all plants and plant shoots become less palatable as they mature (Dirzo, 1984; Howe and West-

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ley, 1988). In general, young leaves are more vulnerable to herbivores than are mature leaves (Coley and Aide, 1991), and leaf-miners have been found to be more abundant on seedlings in comparison with mature plants of the same species (Godfray, 1985).

In a tropical dry forest on the coast of Veracruz, Mexico, the leaf-miner *Melanagromiza* sp. (Diptera: Agromizidae) was present on leaves of all adult, sexually reproducing individuals of *Bromelia pinguin* L. (Bromeliaceae), whereas, leaves of vegetatively reproducing or immature individuals did not have leaf-miner tunnels. *Bromelia pinguin* is monocarpic, dying slowly after fruiting, usually leaving a living offshoot (García-Franco and Rico-Gray, 1995). We hypothesized that there should be differences in defenses between dying, sexually reproducing individuals, and younger, non-sexually reproducing individuals. Plants of *B. pinguin* present many features considered to be protection against herbivores. The straplike leaves are highly fibrous, they have hard pointed tips, with sharp hooked thorns on their margins, and thick cuticles (García-Franco and Rico-Gray, 1995; Hallwachs, 1983). Leaves of *B. pinguin* also have flavonoids (penduletine, cirsimaritine, casticine), ferulic acid, diterpenoids derivated from filoctadone (3-oxofilocladan-16-ol, filocladan-16α-diol, 3-oxopimar-15ene-7β, 8β-diol), sterols (estigmasterol, β-sitosterol, β-D-glucositosterol), and β-D-glucopiranose (Chávez-Gallardo, 1993, and references therein). Despite this range of defenses, the plants are subject to attack by different organisms (Table 1); in particular a leaf-miner, the larva of a fly, *Melanagromiza* species.

Study Site

Field work was conducted in a lowland tropical deciduous forest at Centro de Investigaciones Costeras La Mancha (CICOLMA) on the coast of the state of Veracruz, Mexico (19° 36' N, 96° 22' W; altitude <50 m). Annual precipitation varies greatly (1100-1700 mm), but most falls between June and September, and mean temperature is 22°-26°C (minimum 10°C, maximum 38°C; García-Franco and Rico-Gray, 1995). *Bromelia pinguin* inhabits the sandy understory of the tropical dry and deciduous forests, which have a relatively simple structure and composition, with tree species such as *Bursera simaruba* (L.) Sarg. (Burseraceae), *Brosimum alicastrum* Swartz (Moraceae), *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae), *Cedrela odorata* L. (Meliaceae), *Ficus cotinifolia* Kunth (Moraceae), and shrub species such as *Nectandra coriacea* (Sw.) Griseb. (Lauraceae), and *Coccoloba barbadensis* Jacq. (Polygonaceae) (Blain, 1988; Blain and Kellman, 1991).

Table 1. Herbivores observed on *Bromelia pinguin* and the plant structure affected at La Mancha, Veracruz, Mexico during the period of April 1989-March 1991.

Leaf:	(larva) *Melanagromiza* sp. (Diptera:Agromyzidae)
	(larva) *Mandura quinquemaculata* (Lepidoptera:Sphingidae)
	(adult) *Gecarcinus lateralis* (Decapoda:Brachyura)
Spike:	(ant-tended) Membracidae (Homoptera)
Fruit:	(larva) Drosophilidae, Sarcophagidae (Diptera)
	(larva) Lepidoptera
Seed:	(adult) *Gecarcinus lateralis*
Seedling:	(adult) *Gecarcinus lateralis*

Materials and Methods

Bromelia pinguin is a terrestrial plant in dry habitats from Mexico to Venezuela and on the Caribbean Islands, from sea level to 780 m elevation (Hallwachs, 1983; Smith and Downs, 1979). Serial monocarpy or sympodial dichotomy (Benzing, 1980), sexual reproduction, and clonal growth are present in its life cycle. In CICOLMA it forms dense patches or subpopulations (demes) on sandy soils in deciduous forest. Flowers are present for a few days during the dry season (March-April). Butterflies and hummingbirds (*Amazilia beryllina, Cyranthus latirostris*: Trochilidae) are the main flower visitors (García-Franco and Rico-Gray, 1995). Although a high fruit set with abundant seeds is produced every year, seed and seedling predation by red land crabs (*Gecarcinus lateralis* Frem.) is so high that few genets are recruited (García-Franco et al., 1991).

Plant material was collected between August and September of 1989, air dried and sent to the laboratories (5 kg dry weight each of mined and unmined leaves to each laboratory). Collections were made just after peak rainfall, to avoid possible differences due to environmental stress. In general, herbivores use plants because either they are rich in nutrients (e.g., nitrogen, humidity content) or poor in defenses (physical or chemical); thus two types of analyses were needed. Ash, humidity, fiber, lipids, and nitrogen analyses were conducted at the Departamento de Química y Biología, Universidad de las Américas. Determinations were made in duplicate according to the methods in Horwitz (1980) with an error margin of 0.1-2.0%. Metabolic contents (MeOH extract), to test for allelochemicals, were analyzed with chromatography (HPLC) and visible UV light spectrum at the Departamento de Farmacía, Facultad de Química, U.N.A.M. (Chávez-Gallardo, 1993). Insects were collected throughout the study period (April 1989-March 1991).

Results

No differences in metabolic contents were found when mined and unmined leaves were compared (Figure 1). We did not find significant differences when humidity (ANOVA, $F_{(1,2)}=1.22$, $p>0.384$) and nitrogen (ANOVA, $F_{(1,2)}=9.9$, $p>0.088$) contents were compared between mined and unmined leaves (Figure 2). On the other hand, we found significant differences in the percent of ash (ANOVA, $F_{(1,2)}=54.366$, $p<0.018$), fiber (ANOVA, $F_{(1,2)}=16.341$, $p<0.05$), and lipid (ANOVA, $F_{(1,2)}=133.031$, $p<0.007$) contents, between mined and unmined leaves. Mined leaves had more fiber and lipids, and less ash than did unmined leaves (Figure 2).

Discussion

Leaf-miners attack leaves on old and decaying *Bromelia pinguin* plants: the toughest leaves, the ones with the highest fiber content. We found no differences in nitrogen or water content, or in secondary compounds, between leaves in young and old plants, unless the higher lipid contents of older leaves is attractive to miners.

Coley (1987) found that in *Cecropia*, herbivores show significant preference for leaves from larger plants, suggesting that leaf defenses decrease with plant size or age. Cooke et al. (1984) demonstrated that young leaves of several tree species have more toxins and less nutritive value than do mature leaves. How-

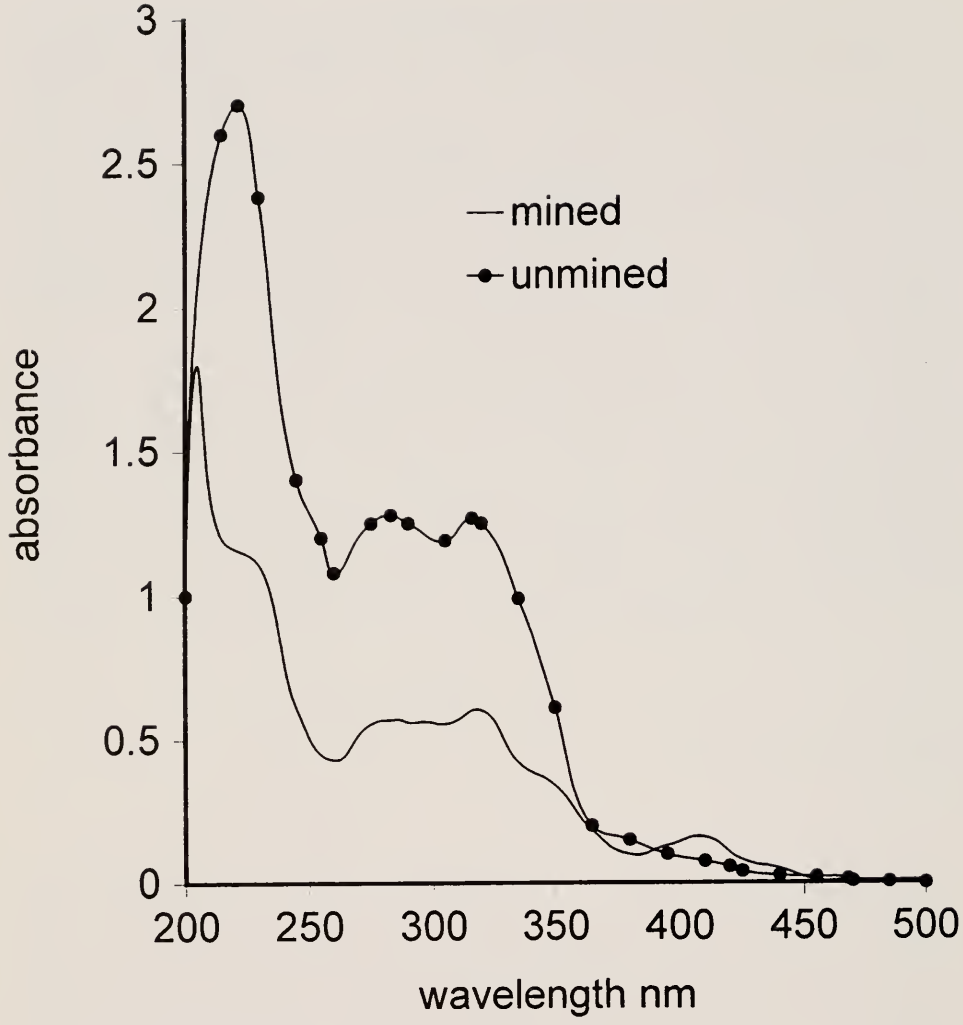

Figure 1. Ultraviolet spectra of the methanolic extract of *Bromelia pinguin* for mined and unmined leaves.

ever, the response of leaf-miners could also be to a combination of factors other than food quality or the amount or type of defenses.

Flowering and fruiting by *B. pinguin* may act as a mating cue for adults of the *Melanagromyza* fly. Female flies oviposit on the leaves of decaying plants, whereas their offspring develop during the warm-humid portion of the year. The mating time and ovipositing behavior of adult *Melanagromyza* flies could be a response to an absence of predators or parasitoids. Instead of a direct response to plant phenology, *Melanagromyza* flies might be influenced by a plant-herbivore-parasitoid complex (Price et al., 1980, 1986), or fly behavior may be influenced by wasp activity patterns (Thompson, 1994).

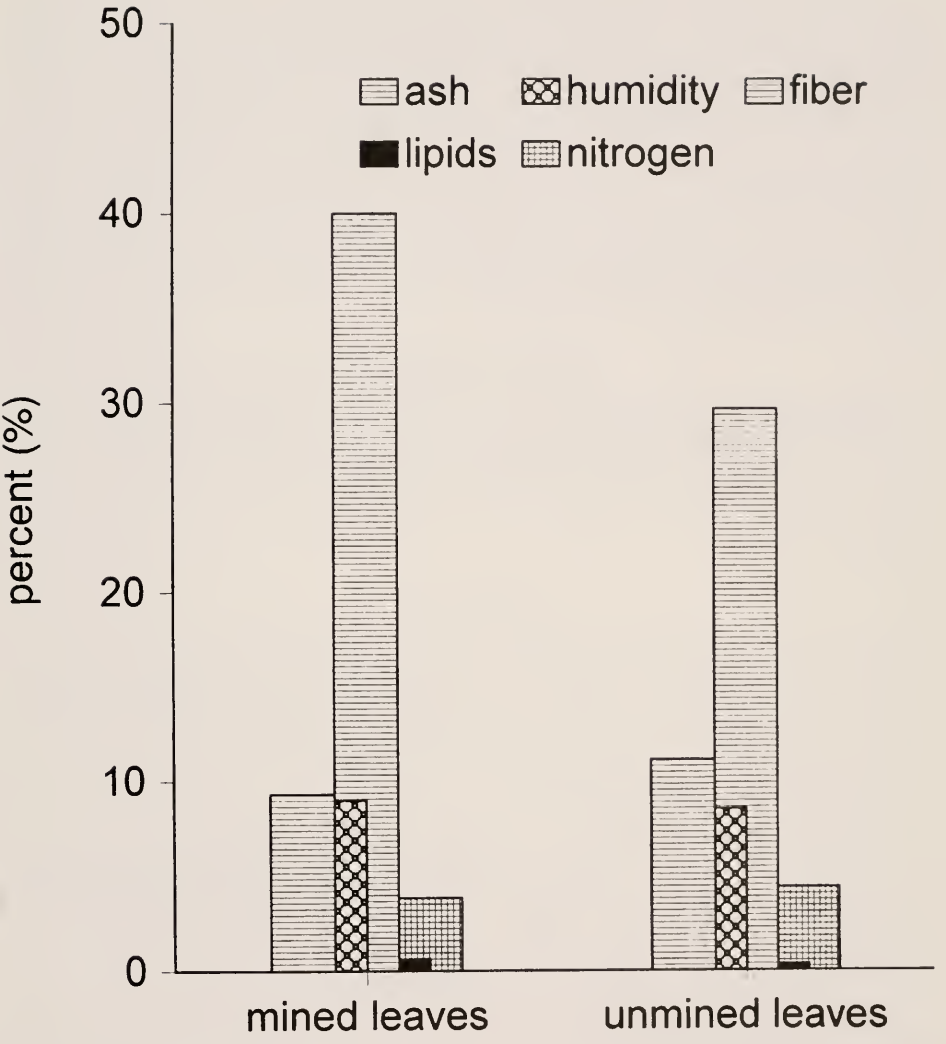

Figure 2. Percent contents of ash, water, fiber, lipids, and nitrogen for mined and unmined leaves of *Bromelia pinguin*.

In certain situations, a heavy attack by leaf-miners could be considered beneficial because it increases the chance of leaf abscision and elimination of miners (Simberloff and Stiling, 1987). The effect of leaf-miners on *B. pinguin* should be negligible because the attack is on dying leaves whose main compounds already should have been relocated to offshoots, fruits, and seeds (Jackson et al., 1985). Leaf-miners were only found in decaying individuals, but mined and unmined leaves did not differ in secondary metabolites.

The question remains: Why are only the decaying individuals attacked? The response of a plant to attack from herbivores or pathogens depends in part on its condition, and in part on its inherited ability to relocate resources. If serious stress diverts energy from chemical defense, plants or even parts of plants weak-

ened by shade, disease, poor soil, or recurrent defoliation may be vulnerable to herbivory (Howe and Westley, 1988). In our example, old plants ("mother plants") could be weakened as a result of relocation of metabolic products to offshoots ("daughters") and fruits (Cook, 1985; Pitelka and Ashmun, 1985). Finally, much work has been done on the effect of certain metabolic products (e.g., tannins) and nitrogen levels on insect growth and food preferences, with conflicting results (Cooke et al., 1984). Although our results do not show major differences between mined and unmined plants, differences may exist during a short period of time, but were not detected by our research. Also, cited research is on trees and their seedlings, and results could differ in large clonal plants, where metabolites move between ramets.

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