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Rapid-Terpene-Bath and “Squirt-Gun” Defense in *Bursera schlechtendalii* and the Counterploy of Chrysomelid Beetles

Bursera spp., the source of copal or incense of prehispanic and present-day Mexico, produce an array of monoterpenes such as alpha and beta pinene, camphene, phellandrene, cineole, limonene, etc. (Mooney & Emboden 1968; Rzedowski & Ortiz 1982, 1988) that are distributed in a reticulating network of resin canals in the cortex of the stems and throughout the leaves (Guillaumin 1909). While the toxicity and repellent nature of these substances have not previously been investigated in *Bursera*, a number of these compounds has been shown to be toxic or repellent in conifers for a variety of beetle pests (summarized in Mabry & Gill 1979).

Many species of *Bursera* appear to actively deploy these terpenes in a facultative response to herbivory which we have investigated in *Bursera schlechtendalii* Engl. in the Zapotitlán basin of the Tehuacán valley in central Mexico (28°20'N, 97°28'W). The antiherbivore response apparently takes two forms. When an entire leaf of *Bursera schlechtendalii* is plucked, a fine syringe-like spray of terpenes (the “squirt-gun” response) is triggered that may persist up to three or four seconds and travel 5–15 cm (Fig. 1a). If, however, a small leaf disk is removed, there is a rapid release of terpenes in a highly fluid front that, within a few seconds, covers up to half or more of both leaf surfaces (the “rapid-bath” response; Fig. 1b). The squirt-gun response saturates locally after one leaf is plucked, though leaves on other branches tens of centimeters away still respond. The rapid-bath response apparently requires less turgor pressure and multiple neighboring leaves are capable of responding to damage.

We suggest that the squirt-gun response may have defensive relevance against the actions of macroherbivores which eat entire leaves. Our hands and camera lens became covered with the sticky exudates when plucking leaves to take the photos for Figure 1a. We found no evidence of macroherbivore damage to burseras growing in areas otherwise heavily grazed by cattle and goats.

The rapid-bath response is likely to have greater relevance against smaller herbivores and we were able to investigate it on *B. schlechtendalii* with herbivorous larvae of an unidentified chrysomelid beetle (subfamily Chrysomelinae). These larvae can be important defoliators. We observed ca 50 larvae on one small plant and an entire leaf may be consumed in less than 15 minutes. The only other damage we observed was due to leaf miners which, by leaving the reticulate network of veins intact, are apparently able to evade the rapid-bath response.

When a leaf is artificially damaged, inducing the rapid-bath response, a larva will rapidly withdraw and abandon the leaf after attempting to clean itself. This indicates that the rapid-terpene-bath response in *Bursera* is an effective feeding deterrent against this beetle. However, these larvae have developed the ability to block the rapid-terpene-bath response. When climbing on a new leaf, a larva positions itself along the midrib with head facing the petiole (Fig. 2a) and begins a slow process of biting the midrib at the blade base. We observed many larvae blocking the resin canals in this fashion but never observed the rapid-bath response occurring naturally during this process. On one occasion while we bent the leaf blade back to observe the blocking process we unintentionally supplied enough tension to the petiole to open the midrib where the larva was biting it. The rapid-bath response was triggered and the larva quickly withdrew and subsequently abandoned the leaf. We inspected 48 intact leaves, none of which had the characteristic incision scar at the leaf base (Fig. 2b), and another 41 damaged leaves, all of which had the incision scar. We checked the efficacy of the larval surgery at eliminating the rapid-bath response by artificially removing small discs of leaf with our fingernails (as in Fig. 1b) on 25 intact leaves, 23 of which exhibited the rapid-bath response. None of 20 leaves with the incision scars gave the rapid-bath response. Another 23 leaves were artificially defused by incising the base of the midrib with a sewing needle. Only three of these gave any subsequent rapid-bath response.

While similar behavioral adaptations that bypass facultative chemical defenses of plants have been documented (especially with regard to latex production; see review in Dussourd & Eisner 1987), the high



FIGURE 1. Facultative chemical defenses of *Bursera schlechtendalii*. (a) When a leaf is removed, a fine syringe-like spray of simple terpenes is released. This spray may last up to three or four seconds and travel 5 to 15 cm. (b) The leaf surface is rapidly soaked with liquid terpenes when a small leaf disk is pinched off with a thumb nail. Within another half-second, approximately half of both surfaces of the leaf blade are covered with the liquid exudate.

turgor pressure maintained in the resin canals of *Bursera* and the fluid nature of the terpenes seem to create special problems for chrysomelid larvae. The rapid-bath response is so quick that larvae do not have time to retreat and wait for the turgor pressure to defuse, as in the typical scenario for latex bearing plants. Rather than severing the midrib, the larvae are obliged to block it in an operation that takes 30 min to one and a half hours to complete. This means that the larvae actually spend more time "in surgery" than in consuming a leaf (only 10–20 min). Thus, while the larvae have apparently developed the behavioral adaptations necessary to overcome the rapid-bath response of *Bursera*, they have only done so at a serious cost in terms of handling time. The larvae are subject to predation while feeding and severing resin canals and the significant delays involved may delay growth and the onset of pupation as well. We have observed predation by adult pentatomid bugs (*Oplomus dichrous* Herrich-Schaeffer), and nymphs of the same were spotted walking around on the stems. Thus while the rapid-terpene-bath response of *Bursera* does not represent a completely effective antiherbivore response against these chrysomelid beetle larvae, it does impose a handling cost which exposes the larvae to an increased risk of predation.

The interaction documented here presents us with an interesting example of ploy and counterploy in the ongoing evolution of consumer–victim interactions. We have observed the squirt-gun response in other species of *Bursera*, all of which produce large quantities of terpenes in reticulating networks of resin canals. In a different genus of Burseraceae (in *Commiphora rostrata* in Kenya) McDowell *et al.* (1988) have found alkanes being released as a fine spray and free-flowing liquid from broken branches or twigs. Thus it seems these modes of defense may be widespread in the family. Curiously, anatomists have pointed out that the vasculature of the petioles is extremely diverse among species of *Bursera* (Guillaumin 1909). This suggests the possibility of a complex interspecific array of challenges to larval surgery. Further study of the Burseraceae and its herbivores is likely to document other interesting feeding adaptations.

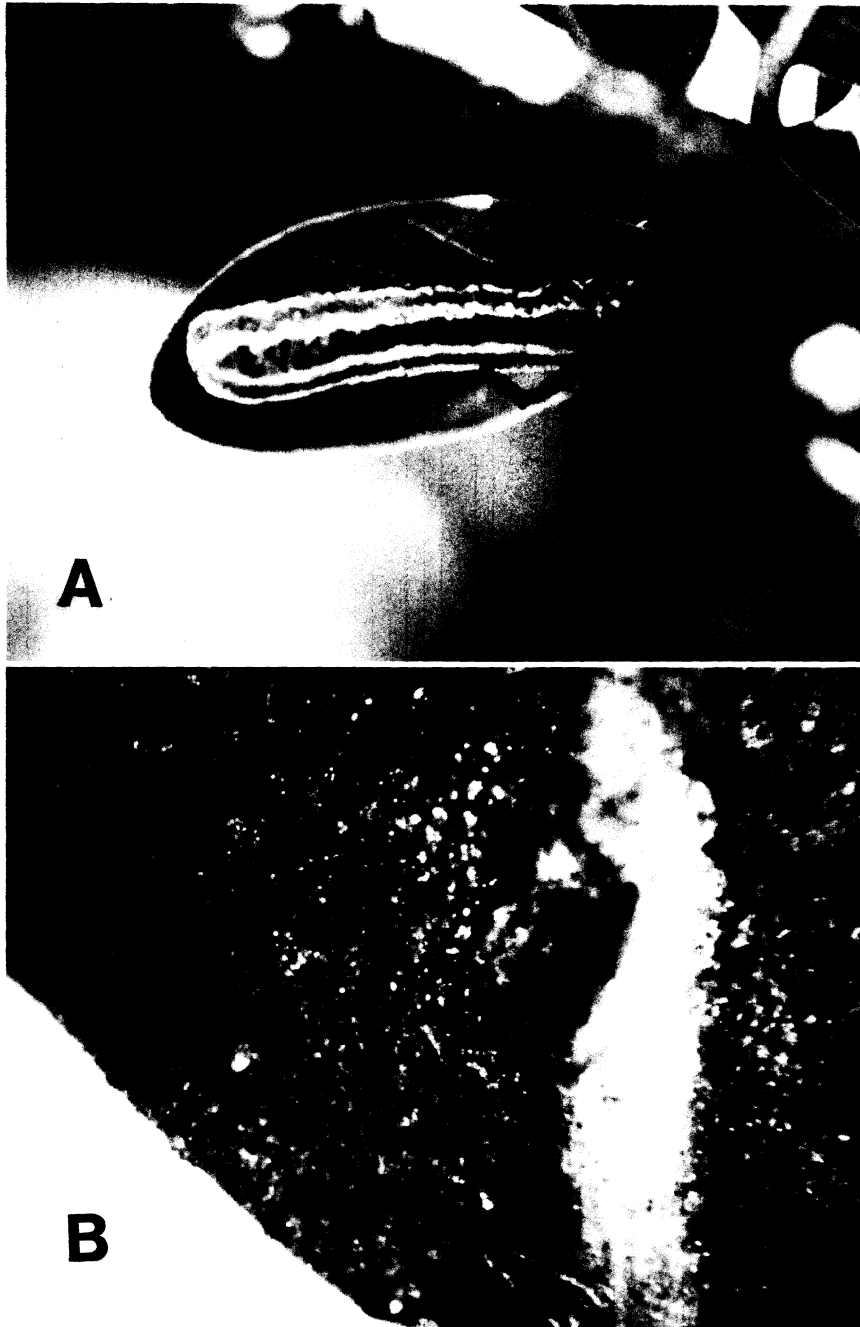


FIGURE 2. The counterploy of chrysomelid larvae. (a) A larva, positioned on the abaxial surface of a leaf of *Bursera schlehtendalii*, is in the process of surgically blocking the resin canals of the midrib at the base of the leaf blade. (b) Scar on the midrib at the base of the leaf blade from the activities of chrysomelid beetle larvae which block the resin canals.

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