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GLANDULAR HAIRS IN THE ARBUTUS XALAPENSIS COMPLEX IN RELATION TO HERBIVORY[1]

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ABSTRACT

The morphological boundaries between *Arbutus xalapensis* and *A. glandulosa* are diffuse. Many individuals share traits of both species. The character most commonly used to distinguish the species is the presence of glandular hairs in *A. glandulosa*. Comparisons in the field of the number of colonies and level of defoliation by *Eucheira socialis* (Lepidoptera, Pieridae), an *Arbutus*-specific herbivore, showed that the damage is greater for glabrous than pilose trees and greater for pilose than glandular trees. Additionally, the geographic distribution of glandular trees is strongly correlated with that of *E. socialis* while that of non-glandular trees is not. We suggest that the glandular and non-glandular forms could belong to one single polymorphic species in which the glandular characteristic is maintained by differential herbivory.

CLASSIFICATION OF THE Mexican species of *Arbutus* (Ericaceae) has proven to be a difficult task. Standley (1924) described seven species, though he acknowledged that all could be variants of *A. xalapensis* H.B.K.: "The Mexican plants of this genus are extremely variable and seem not to possess a single constant character. It appears probable that ultimately all of them will have to be considered mere forms of *A. xalapensis*. No confidence can be placed in the characters used in the following key. Of the species listed, the one most clearly distinct from *A. xalapensis* is *A. glandulosa,* but even the characters by which it can be recognized are far from constant."

More recently, McVaugh and Rosatti (1978) added "with some trepidation" a new species to Standley's list. Their caution was based on the fact that the taxonomy of the genus in Mexico is still largely a matter of debate and in need of a serious revision. Within the whole group, however, *A. xalapensis* and *A. glandulosa* Mart & Gal. are described by these authors as markedly distinct, often sympatric species. According to McVaugh and Rosatti, *A. glandulosa* was originally described as "having the branches, petioles and peduncles hirsute-tomentose with dark, glandular hairs, and the leaves spinulose-denticulate and cordate at the base." McVaugh and Rosatti go on to say that *A. glandulosa* is "readily distinguishable" from *A. xalapensis* "by the glandular-setose herbage, by its flowering season, which seems to be consistently 3–4 wk earlier than that of *A. xalapensis,* and by its rough, flaking but persistent bark, which often contrasts markedly with the smooth bark of *A. xalapensis* that results from the loosening of the outer layers."

However, we have found morphological boundaries between *A. xalapensis* and *A. glandulosa* to be diffuse. Individiuals that combine characteristics of both species are frequently encountered both in the herbaria and in the field. A high proportion of non-glandular trees possess denticulate leaves, while many glandular madrones (*Arbutus*) have leaves with entire margins. Bark smoothness seems also to be independent of the presence of glands.

In this paper we present data on herbivory and geographic distributions of different forms of madrones. We discuss the possibility that the two alleged species are really morphs of the same species, maintained by differential herbivory.

Differential herbivory—During a field expedition to the Western Sierra Madre in March 1984, glandular and non-glandular madrones were often observed growing together. More than half of the non-glandular individuals were glabrous, while the rest showed varying degrees of hairiness in leaves, petioles and peduncles. The glabrous individuals were often intensely defoliated by the larvae of *Eucheira socialis* (Lepidoptera, Pieridae), an *Arbutus*-specific herbivore with gregarious larvae that spend the day protected in colonies within a papery bag and that forage during the night on the leaves (Beutelspacher, 1980, 1983).

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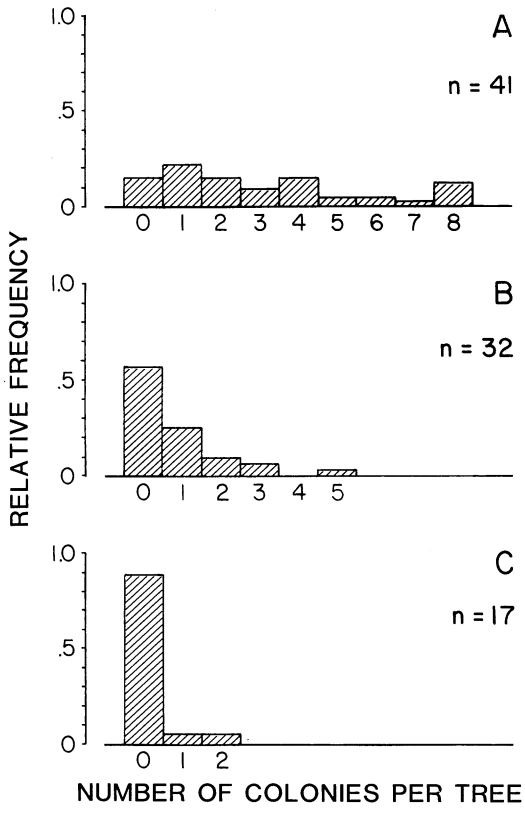

Fig. 1. Relative frequency distribution of the number of *Eucheira socialis* colonies per tree for (A) glabrous (B) pilose and (C) glandular individuals of *Arbutus*.

A sampling area was selected on the Mesa del Burro, within La Michilía Biosphere Reserve, in Durango, Mexico (23°25′ lat N, 104° 17′ long W), and the number of *Eucheira* colonies (larval bags) was counted on the first 90 trees found along a predefined transect. The trees were divided into three morphological categories. Plants without hairs or glands were designated as glabrous; plants with non-glandular hairs were considered pilose, and plants with any glandular hairs were called glandular. The relative frequencies estimated in the field for the three categories were 45% for glabrous, 36% for pilose, and 19% for glandular trees. The frequency distribution of *Eucheira* colonies differs significantly among the three forms (Fig. 1; $\chi^2 = 41.65$, df = 8, $P < 0.001$). The number of colonies on glabrous trees (averaging 3.0 col./tree) was higher than the number on pilose individuals (averaging 0.8 col./tree), while most (88%) of the glandular individuals had no colonies.

In addition to differences in number of colonies, differences were found in degree of defoliation and appearance of the larval colonies. A total of 12% of the glabrous madrones showed complete defoliation. In contrast, the two glandular trees that had *Eucheira* larvae showed such low levels of defoliation that it was difficult to detect any leaves with herbivore damage. The three larval bags that were found on these glandular madrones had thin, translucent walls, while the bags on the other forms had thicker, whiter walls which were much more resistant to tearing by hand.

Geographic distributions—The collection sites of all *Arbutus* specimens from the herbaria of the National University of Mexico and the School of Biological Sciences, National Polytechnic Institute, Mexico, are mapped in Fig. 2. Specimens were classified as glabrous, pilose, or glandular using the previously noted criteria. Glabrous and pilose forms occur in the Eastern and Western Sierra Madres, on the Central Volcanic Axis, and along the southern sierras in Oaxaca and in Chiapas. In contrast, glandular individuals are rare in the eastern sierras and frequent on the western sierras where they coexist sympatrically with the other forms.

The geographic range of *Eucheira socialis* (taken from Beutelspacher, 1983) coincides closely with the distribution of glandular madrones (Fig. 2c). This butterfly apparently cannot thrive in the humid conditions of the eastern ranges (Beutelspacher, pers. comm.). The overlap between the distribution of the different forms and the geographic area of *Eucheira* (calculated for each form as the percentage of all collection sites that fall within the area) was 71% for glandular, 55% for pilose and 41% for glabrous specimens. The glandular morph showed significantly greater overlap with *E. socialis* than the other two morphs which did not differ significantly in overlap. (χ^2 for the complete data set = 20.5, $P < 0.001$; χ^2 for pilose vs. glabrous = 2.3, N.S.; χ^2 for glandular vs. pilose + glabrous = 18.2, $P < 0.001$).

DISCUSSION—We have documented differences in abundance of and degree of defoliation by *E. socialis* on the three forms of *Arbutus* in a natural population. Furthermore, we have found that the distribution of the glandular form generally corresponds to the distribution of *E. socialis*. The apparent inability of *E. socialis* to inhabit and defoliate the glandular form taken together with the biogeographic evidence strongly suggests that the glands function to protect *Arbutus* against leaf damage by *E. socialis*.

There are however some glandular form *Arbutus* sites that fall outside the geographic range of *E. socialis*. The sites in Jalisco have been

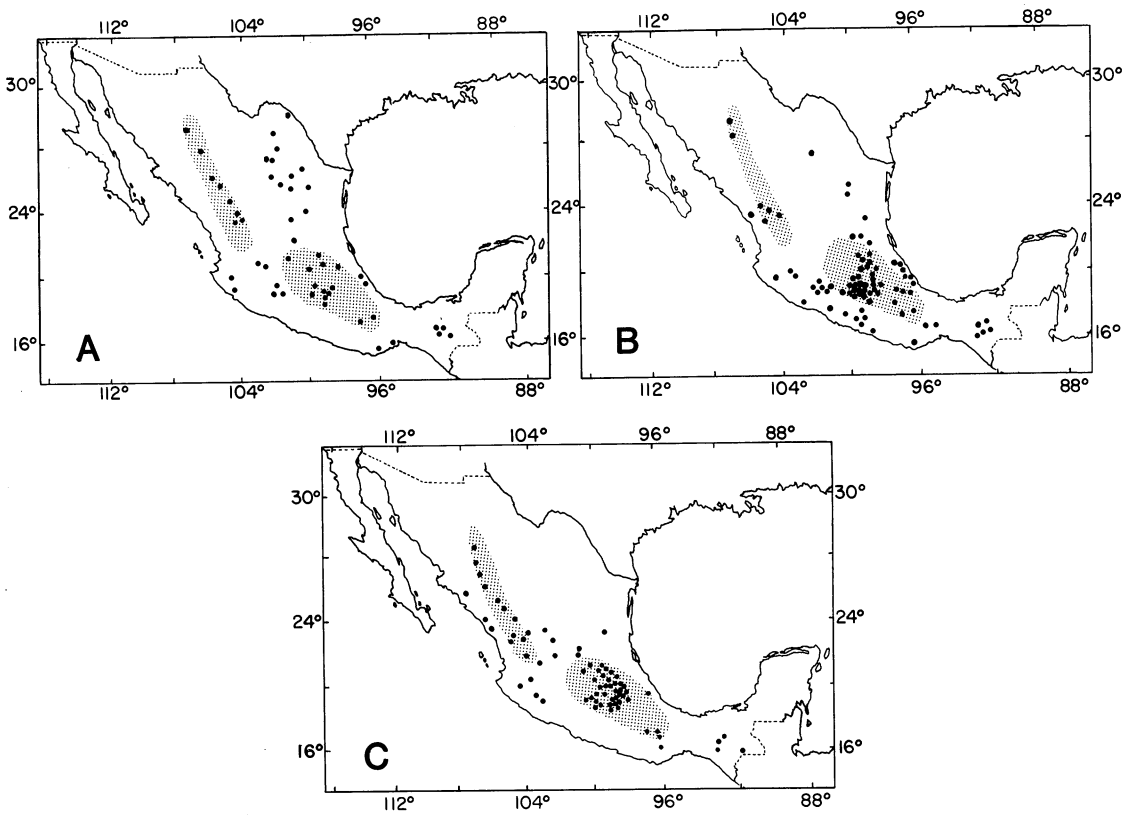

Fig. 2. Geographic distribution of (A) glabrous, (B) pilose, and (C) glandular individuals of *Arbutus*. The shaded areas indicate the distribtuion area of *Eucheira socialis* according to Beutelspacher (1983).

poorly collected for butterflies, but appropriate habitat for the *E. socialis* exists and the species is probably there (Beutelspacher, pers. comm.). In contrast, the butterfly fauna of Chiapas is better known and *E. socialis* has not been collected from this region. On the basis of our interpretation of the glandular trait, we hypothesize that a different herbivore playing a similar ecological role will be found in Chiapas. An investigation of the *Arbutus* herbivore fauna in Chiapas would thus constitute a test of our ideas.

In the light of the ecological and biogeographic information presented here we suggest that the glandular form may not be a separate species but could represent adaptative variation within *A. xalapensis*. Information on gene flow among the different forms of *Arbutus* is still lacking. However, the absence of other characters consistently associated with the presence of glandular hairs, and the continuous nature of variation within the group, support the contention that the different forms are part of one variable species.

It is possible that the observed phenotypic variation is the result of genetic differences between individuals and populations of *A. xalapensis,* or even the result of non-genetic developmental variation. Genetic polymorphisms maintained by parasitism (e.g., Jones, 1967) and by herbivory (e.g., Cates, 1975; Dirzo and Harper, 1982) are well documented. Of the mechanisms that can maintain genetic polymorphisms, the two more plausible ones for *Arbutus* are (a) spatial or temporal variation in natural selection, and (b) frequency-dependent selection. On the other hand, it has been reported that chemical and morphological defenses in plants can be induced by grazing (Abramson, 1975; Crawley, 1983).

Perhaps even more interesting than the absence of glands in the Sierra Madre Oriental is the coexistence of the three morphs throughout large geographic areas. More information on insect outbreaks, local scale spatial variation in herbivore pressure, and possible frequency dependent effects are necessary to begin to answer the question of how this variation is maintained.

Hopefully, the data presented in this paper will help to clarify the taxonomic questions in the genus and at the same time delineate in-

teresting ecological and evolutionary issues that remain to be solved.

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